A vibrant green hummingbird with a long, dark beak is perched on a thin branch. The bird's feathers are a bright, iridescent green, and its wings are dark. The background is a lush, out-of-focus green, suggesting a tropical or subtropical forest environment. The lighting is bright, highlighting the bird's colors.

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Juan Carlos Verhelst-Montenegro

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*To Lucas Rafaelis who
departed without having
even arrived, and to my wife
Laima and my family.*

FOREWORD

The aims of the Colombian Academy of Sciences are the development of Exact, Physical and Natural Sciences. To achieve its goals the Academy recognizes scientists who have made notable contributions to these branches of science, encourages and supports scientific research, contributes to the dissemination and appropriation of science as an element of culture and economic and social development. Within this context, the Academy has among its priorities support to its members and in general to the scientific community to publish books as product of their research activities and contributions to the development of natural sciences in the country.

It is a great pleasure the delivery in this edition of the book: Avifaunal Distribution in Colombia: Current Diversity and Potential Refugia Under Climate Change, which is a valuable contribution to the knowledge of the birds of Colombia from the point of view of its current diversity and possible effects to the facing climate change.

We want to get this book into the world of electronic publishing, in order to give a wider dissemination of the contributions of members of the Academy and in general of the Colombian scientific community.

Enrique Forero
President

Gabriel Roldán
Director of Publications

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ABSTRACT

Colombia is a megadiverse country facing major conservation challenges. Project BioMap (2002–2005) aimed to increase biodiversity knowledge in Colombia through the repatriation of data from bird specimens held in museums worldwide. The project compiled the Darwin–Hernandez Database, which holds nearly 220,000 georeferenced accessions. Here we use this database to model bird diversity in Colombia at high-spatial resolution under current and future climates. The database was revised and estimates of georeferencing uncertainty used to filter out highly uncertain accessions. DIVA–GIS and MAXENT were used to generate bird diversity maps at the national scale at different taxonomic levels and spatial resolutions; assessing correlations between estimated richness and sampling and effort bias. MAXENT also was used to project bird diversity in Colombia under future climate scenarios projected by the HadCM3 climate model. Diversity maps were validated using data obtained from the ProAves database and the Western Hemisphere Digital Bird Distribution Database. Projections of bird diversity under future climates were used to project potential refugia of bird diversity for different subsets of the Colombian avifauna, and to evaluate how the national reserve network captures these projected refugia.

Results showed that under future climates, richness is projected on average to decrease, while rarity is expected to increase. However, along the elevational gradient, richness is expected to decrease at low and mid elevations and to increase at high elevations, whilst rarity is predicted to decrease at low elevations and to increase at mid and high elevations. Potential refugia conserving high levels of family and genus richness may occur mainly along the mountains at $\approx 1,000$ – $3,000$ m and in adjacent lowland areas. Addressing rarity, potential refugia for families may occur principally in zones above $\approx 2,500$ m, whilst for genera may occur along the mountains at $\approx 1,000$ – $2,000$ m and in adjacent lowlands. Finally, results from this thesis suggest conservation efforts must focus predominantly in establishing a connected network of reserves – a “Trans–Andean Reserves Staircase” – connecting major types of forest ecosystems from the lowlands to the high mountains.

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CHAPTER 1
INTRODUCTION

Summary – Colombia is located in the northwestern corner of South America, between the Caribbean Sea and the Pacific Ocean. Its unique position and the Andean Cordillera make it a country with a wide variety of climatic and topographic conditions, matched by numerous ecosystems and lifeforms. Nevertheless, biodiversity in the country is highly threatened by human activities such as deforestation, agriculture, pasture and air, soil and water pollution, among others. Six species extinctions have been documented for Colombia so far. Moreover, vast areas remain poorly known in the country and still in need of inventory as part of Colombia’s commitment to the Convention on Biological Diversity (CBD). Limited economic resources for research in the country make it necessary to prioritise inventory and conservation decisions. In this context, the use of secondary sources of information such as biological collections have become of primary importance to study the potential spatial distribution of biodiversity in the country. Project BioMap was conducted during 2002–2005 with the aim of increasing biodiversity knowledge in the country through the repatriation of data from bird specimens in museums worldwide. As its main output, Project BioMap compiled an outstanding database with nearly 220,000 georeferenced bird accessions for Colombia, which presents a unique opportunity to develop analyses and models for bird diversity spatial distribution at national scale and study the potential impacts of climate change on this distribution. Furthermore, although conservation has received some attention in Colombia since the 1960’s, when the first national natural park was created, most of the reserves have been created *ad hoc* and not by careful spatial planning to optimise conservation in particular groups such as birds. A notable exception are the private ProAves reserves, each of which is designed specifically to protect a particular threatened bird species (and names accordingly). Analyses and predictions of current and future bird diversity distribution in the country might constitute an important input to “systematic conservation planning” representing a valuable “stepping stone” to advance biodiversity and conservation science in the country.

1.1. Location and geographical regions

Colombia is located in the northwest corner of South America, from 4°13’30” S to 12°26’46” N and from 79°02’33” W to 66°50’54” W (Arango & Lagos, 1998). Its

territory embraces 1,141,748 km² of continental area and 928,660 km² of maritime area, which includes 54 km² of insular area (IGAC, 1989, 1992). The continental boundaries of the country have a total length of 9,242 km, limited to the north by the Caribbean Sea, to the east with Venezuela, to the southeast and south with Brazil and Peru, to the southwest with Ecuador, to the west with the Pacific Ocean, and to the northwest with Panama. Furthermore, the country has maritime boundaries with Panama, Costa Rica, Nicaragua, Honduras, Jamaica, Haiti and Dominican Republic in the Caribbean Sea, and with Ecuador and Panama in the Pacific Ocean (IGAC, 2002).

Traditionally the country has been divided into six broad geographical (natural-cultural) regions (IGAC, 1989; CINEP, 1998a, b, c, d). This division is based on the most prominent characteristics exhibited in terms of relief and climate in each region, which then relate to other abiotic and biotic features such as soils, vegetation and land use (IGAC, 1989). Furthermore, these regions correspond remarkably well with different cultural elements and heritages present in the country. Thus, these six regions are (Figure 1.1.1): the Caribbean, the Eastern Plains or Orinoco, the Amazon,

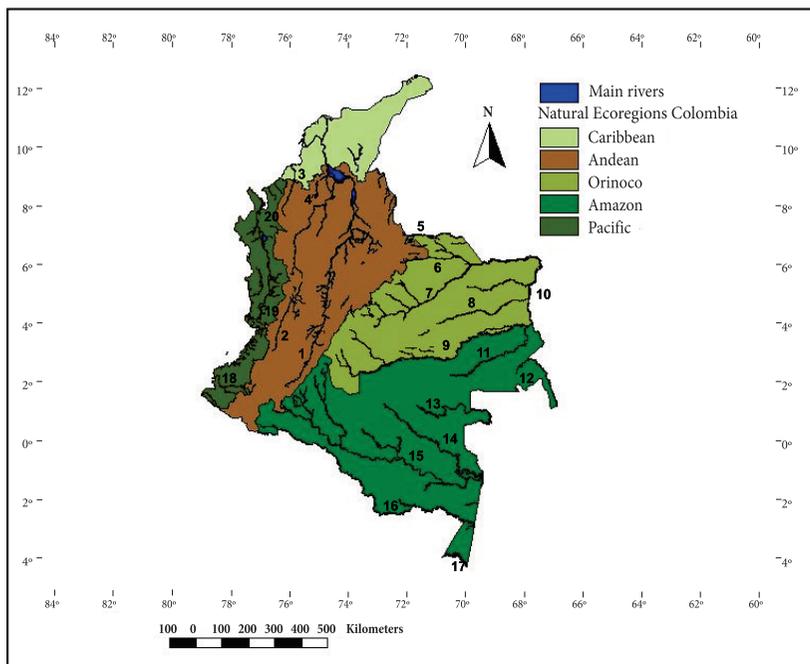


Figure 1.1.1. Natural Ecoregions Colombia. Main rivers: Magdalena R. (1), Cauca R. (2), Sinu R. (3), San Jorge R. (4), Arauca R. (5), Casanare R. (6), Meta R. (7), Vichada R. (8), Guaviare R. (9), Orinoco R. (10), Inirida R. (11), Guania R. (12), Vaupes R. (13), Apaporis R. (14), Caqueta R. (15), Putumayo R. (16), Amazon R. (17), Atrato R. (18), San Juan R. (19) and Patia R. (20). Just are presented continental Ecoregions.

the Pacific, the Andean and the Insular Territories. The Caribbean Region is located in the north of the country, its climate is warm and dry, and the topography is relatively flat, although it is broken by low hills and some major mountain systems such as the isolated Sierra Nevada de Santa Marta. The Orinoco Region is situated to the east, its climate is warm and is usually characterised by a very well marked dry season as in the Caribbean. The relief of the region is flat, although low hills and peaks break the terrain throughout the whole region. The third region, the Amazon, is located in the south and southeast, its climate is mainly warm and humid and the terrain is generally flat, although it is broken by low hills and some peaks. In this region, there are two main mountain systems of importance: the Serrania de La Macarena and Serrania de Chiribiquete. The Pacific Region, located to the west, has a warm climate and it is exceptionally humid, probably one of the wettest regions in the world. The topography is, in general terms, flat, although some low hills and the Serrania del Baudo break the plain landscape. Finally, the Andean Region is located in the centre of the country. Its climate is very variable ranging from warm to very cold and extremely humid to fairly dry depending on the position of the specific area in the altitudinal–latitudinal gradient and the relief of the areas around. The terrain of the region is very complex because of the Andean Cordillera, which divides in Colombia into three main ranges separated by two deep valleys formed by the main rivers in the area, the Magdalena River and the Cauca River.

For more details, a thorough account on the topography, climate and vegetation present in the country can be found in Appendix 1.

1.2. Biodiversity

Colombia is considered a megadiverse country (Mittermeier *et al.*, 1997). Its geographical position and the uplifting of the Andean Cordillera has favoured the existence of a wide variety of different ecosystems in which a vast diversity of lifeforms have evolved. In this sense, 13 of the 200 global ecoregions are represented in the country. Ecoregions have been defined as large units containing characteristic assemblages of natural communities (Olson *et al.*, 2001). The global ecoregions present in the country are: 1) the Amazon river and flooded forests, 2) the Choco–Darién moist forests, 3) the Guyanan highlands forests, 4) the Llanos savannas, 5) the Napo moist forests, 6) the northern Andean montane forests, 7) the northern Andean paramo, 8) the Orinoco river and flooded forests, 9) the Panama bight, 10) the Panama bight mangroves, 11) the Rio Negro–Jurua moist forests, 12) the Tumbesian–Andean valleys dry forests, and 13) the upper Amazon rivers and streams (WWF, 2007). Moreover, at country level these have been divided in 25 national ecoregions (Castro–Schmitz *et al.*, 1998). Moreover, two of the global biodiversity hotspots (*i.e.* areas

extremely rich in biodiversity and endemisms and highly threatened) are represented in the country (Myers, 1988, 1990; Myers *et al.*, 2000). These hotspots are the Tumbes–Choco–Magdalena and the Tropical Andes (Mittermeier *et al.*, 2004).

In Colombia nearly 10% of the world biodiversity is thought to exist (Chaves & Arango, 1998). Thus, within its boundaries about 51,220 vascular plants and 3,578 vertebrate species have been recorded; including 733 amphibians, 520 reptiles, 1,869 birds and 456 mammals (Chaves & Arango, 1998; Salaman *et al.*, 2001; Renjifo *et al.*, 2002; WRI, 2003; Rueda–Almonacid *et al.*, 2004; Salaman *et al.*, 2007b) making Colombia top–ranking globally in all of these groups, despite its small area compared with, for example, Brazil. Additionally, among insect groups 3,019 diurnal lepidopteran and 4,800 hymenopteran species have been registered (Chaves & Arango, 1998). For marine environments about 120 sponges, 144 corals, 2,500 molluscs, 970 crustaceans and 2,000 fish species have been registered (Chaves & Arango, 1998; Diaz & Acero, 2003). It is clearly a priority country for biodiversity research and conservation.

1.3. Rationale for this research

1.3.1. Biodiversity loss

From several decades ago, the scientific community have recognised a global biodiversity crisis, attributed to the consequences of anthropogenic activities. This crisis has been caused primarily by the destruction of ecosystems and the overexploitation of species and natural resources, driven by human population growth, the expansion of agriculture and pastures, and the pollution of the environment (Eldredge, 2001). Furthermore, it has been estimated that extinction rates have been increased about 100 to 1,000 times above natural rates (Lawton & May, 1995; May, 2002). According to some authors this crisis is so severe that it is heading towards a sixth massive extinction comparable to the geological mass extinctions (Wilson, 1992). At country level in Colombia the Alexander von Humboldt Biological Resources Research Institute (IAvH) in its first evaluation on the state of the Colombian biodiversity in 1997 identified the existence of several direct and indirect causes of biodiversity loss (Chaves & Arango, 1998). The direct causes of biodiversity loss in the country are listed as: 1) transformation and fragmentation of natural habitats and ecosystems, 2) exotic species introduction, 3) overexploitation of natural resources, 4) pollution, and 5) global climate change. The indirect causes are: 1) poor knowledge of potential uses of biodiversity, 2) the land tenure situation of the country, 3) low scientific and technological institutional capacity for monitoring and evaluation, 4) low governmental capacity to control activities which cause environmental degradation, and 5) lack of economic valuation systems for biodiversity and the inadequate redistribution of the profits from biodiversity uses.

Significant transformation and fragmentation of natural habitats and ecosystems in Colombia has resulted from accelerated deforestation during the last 50–60 years. Inadequate land use policies have resulted in an uncontrolled colonisation of pristine territories and in the expansion of the agricultural and pastoral frontier (Chaves & Arango, 1998). Thus, Etter *et al.* (2006) estimated that by 1998 about 35% of forested areas in the country were already cleared; equivalent to 180,600 km² of Andean forests (69% of the original cover) and 203,400 km² of lowland forests (30% of the original cover).

Furthermore, although there is no complete agreement on annual deforestation rates and their current trends in Colombia, it has been estimated that rates range between 0.6–2.8% a year (Viña & Cavelier, 1999). In the 1980's the American University (Tighe, 1995) estimated that annually about 3,998.3 km² were deforested by new settlements that converted forests to fields and pastures, 647.5 km² were deforested for the timber industry or agriculture (*e.g.* oil palms), and that more than 404.7 km² were cleared for illicit crops such as Marijuana (*Cannabis sativa*) and Coca (*Erythroxylum* sp.). Similarly, the Colombian Ministry of Environment (MofE) and the IAvH (MMA & IAvH, 1995), highlight as main causes of deforestation in the country: 1) colonisation and expansion of the agricultural and pastoral frontier (73.3%), 2) industrial timber extraction (11.7%), 3) firewood extraction for local use (11.0%), 4) wildfires (2.0%), and 5) illicit crops (2.0%). Moreover, the same authors list the development of motorways and settlements, and mining among other causes that have led to transformation of natural habitats.

The introduction of exotic species have detrimental effects on biodiversity due to competition and exclusion of less aggressive native species (MMA & IAvH, 1995). In Colombia, such invasions have occurred through policies such as the introduction of the Rainbow Trout (*Oncorhynchus mykiss*) and the Brown Trout (*Salmo trutta*) in the Andean lakes (IAvH, 2007) and the many reforestation projects involving species of the genera *Eucalyptus* and *Pinus*.

Overexploitation of non-renewable natural resources for industry and/or local use also have severe effects on biodiversity (MMA & IAvH, 1995). Overexploitation in Colombia is mainly for timber extraction though illegal poaching of species considered of value in wildlife traffic markets in Europe and the United States (MMA & IAvH, 1995) is also important. The Colombian Ministry of Environment (MofE) estimated that this traffic generate revenues up to £ 25 million a year. For the period between 1995–2004 the MofE reported 251,776 individual specimens from a wide variety of invertebrate and vertebrate taxa confiscated before export (Casa-Editorial-El-Tiempo, 1998; Revista-Dinero, 2006). Furthermore, for the period 1992–1998 a total of 135,778 eggs, 8,838 kg of different types of wildlife meat, 99 glass containers with turtle meat and 800 kg of dead coral was confiscated from poachers (Gomez-

Cely, 2000; MMA, 2002). Due to the illegal trafficking of wildlife in Colombia several species have already disappeared and there are many others threatened with extinction including 15 reptile, 58 bird and 30 mammal species (MMA & IAvH, 1995).

In addition, overexploitation is becoming a problem for the fresh-water fishing industry. According to the MofE production in the Magdalena river has been reduced by nearly 80%, from 78,847 t in 1974 to 16,998 t in 1994 (MMA & IAvH, 1995). Similarly, in the rivers Sinu and San Jorge production has decreased by nearly 70%, while in the Orinoco and Amazon watersheds it has increased about 54% and 192% respectively, but is expected to decrease substantially in the near future if present rates of extraction are maintained (MMA & IAvH, 1995).

Another important threat to biodiversity is environmental pollution. Although in Colombia its effects on biodiversity and the environment have not been clearly assessed, its negative consequences may be inferred from figures related to domestic and industrial waste management in the country (MMA & IAvH, 1995). According to the MofE, in Colombia only about 65% of urban and 27% of rural areas have appropriate sewage systems. Furthermore, from the 15,903 t of solid waste produced a day in the country just about 32% is deposited in adequate landfill disposals, meanwhile 3% is buried, 50% remains in open air dumps and 15% reaches water courses (MMA & IAvH, 1995). In relation to industrial solid waste, figures are extremely worrying since there is no treatment of any residuals and it is known that in the country just six companies have residual waste incinerators, while five have landfill disposals (MMA & IAvH, 1995). Another important source of pollution in the country is related to the intensive use of pesticides, herbicides and fertilisers in agriculture (MMA & IAvH, 1995). Although there are no published studies, it is well known that they are intensively used in coffee, banana and palm plantations in the country. The intensive use of these chemicals leads to their incorporation into the watercourses by runoff and percolation leading to the contamination and eutrophication of waterbodies (MMA & IAvH, 1995). Moreover, it is suspected that toxic compounds and heavy metals are being incorporated at different levels of trophic webs, although this is still in need of research in the country.

Finally, it is relatively well accepted that global climate change is a clear threat to ecosystems and thus to our own well-being as a species (MEA, 2005). Thus, if present trends of greenhouse gas emissions are maintained, projected rates of climate change may reach their highest values during the last 10,000 years. Furthermore, under those conditions it is expected that both species and ecosystems would be unable to adapt to the changes, leading to massive extinctions globally. Species ranges will certainly be affected (Thuiller *et al.*, 2008) and this may be particularly pronounced in mountain regions where climatic gradients are steep.

Measures to slow down the on-going erosion of biodiversity and to explicitly address the subject in conservation planning from a process perspective are urgently needed (Pressey *et al.*, 2007). Although, in Colombia the national biodiversity policy from the MofE acknowledges global climate change as an important and direct cause of biodiversity loss in the near future, studies assessing potential impacts are scarce and policies to mitigate its possible effects are developing very slowly.

1.3.2. Threatened species in the country

According to the International Union for the Conservation of Nature (IUCN), Colombia is among the top three countries for number of threatened species and threatened endemic species (Baillie *et al.*, 2004). In the country 604 species are considered as threatened – CR (critically endangered), EN (endangered) and VU (vulnerable) – (IUCN, 2001)¹, while 133 more are considered near threatened (NT) and for 192 species it is considered that data is deficient (DD) for an adequate assessment (IUCN, 2007). Among the threatened species are 222 plants: 3 liverworts (Marchantiopsida), 9 cycads (Cycadopsida), 11 monocots (Liliopsida) and 199 dicots (Magnoliopsida). As well as 382 animals: 2 insects (Insecta), 12 cartilaginous fishes (Chondrichthyes), 19 ray-finned fishes (Actinopterygii), 209 amphibians (Amphibia), 15 reptiles (Reptilia), 87 birds (Aves) and 38 mammals (Mammalia). Furthermore, it is important to highlight that already six extinctions have been reported in the country (Table 1.3.2.1), and that endemics constitute an important proportion of the threatened species of the country, being about 23–76% of all species for the best assessed taxonomic groups (Figure 1.3.2.1).

Specifically for Colombian birds, 149 species have been listed as threatened or near threatened in a global study by BirdLife International (2009). From the threatened species 12 are considered critically endangered (CR), 28 endangered (EN), 50 vulnerable (VU) and 59 near threatened (NT). On the other hand, the national assessment conducted by Renjifo *et al.* (2002) showed that at the national level 153

¹ IUCN categories (IUCN, 2001): CR – Critically endangered, EN – Endangered, VU – Vulnerable, NT – Near Threatened. Species are evaluated and classified in those categories by the Species Survival Commission based on the best available evidence supporting five main criteria: a) reduction in population size, b) small, fragmented and/or fluctuant geographic range, c) small population (< 10,000 individuals) in decline, d) very small (< 1,000 individuals) and restricted population distribution, and e) Population Viability Analysis. The different categories do not represent the probability of extinction in the wild for the assessed species but are an indication of the relative degree of risk of extinction if populations are not protected and/or the threats over them are not stopped. CR species face a very high risk of extinction in the wild at present time, EN species face a high risk of extinction in the near future if not protected, VU species may become endangered if threats are not stopped and NT are species that may become in the mid term threatened.

Table 1.3.2.1. Taxa reported as extinct* in Colombia.

Class (family)	Latin name
Mammalia (Phocidae)	<i>Monachus tropicalis</i> Gray 1850
Aves (Podicipedidae)	<i>Podiceps andinus</i> Meyer de Schauensee 1959
Actinopterygii (Trichomycteridae)	<i>Rhizosomichthys totae</i> Miles 1942
Magnoliopsida (Chrysobalanaceae)	<i>Licania caldasiana</i> Cuatrecasas
Magnoliopsida (Flacourtiaceae)	<i>Casearia quinduensis</i> Tulasne
Magnoliopsida (Sapotaceae)	<i>Pradosia mutisii</i> Cronquist

* Source IUCN (2007)

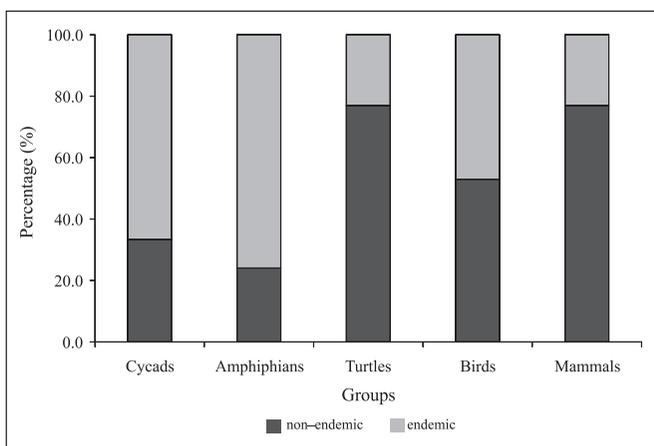


Figure 1.3.2.1. Percentage of endemic and non-endemic threatened species for different groups in Colombia. Data plotted from Baillie *et al.* (2004).

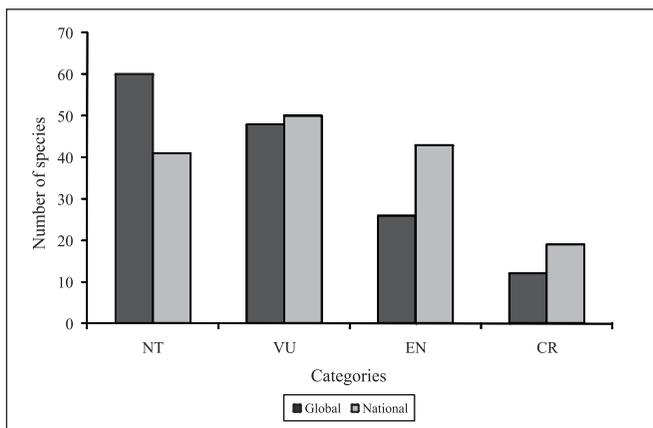


Figure 1.3.2.2. Threatened bird species globally and at the national scale for species occurring in Colombia. Data plotted from Renjifo *et al.* (2002) and BirdLife International (2009).

species are threatened or near threatened (Figure 1.3.2.2). Differences, between both treatments (global vs. national) result mainly as a consequence of species that are at national level considered as threatened because of their particular situation in the country, while globally they may have large and healthy populations in other countries or areas of the world.

The only bird species confirmed extinct in Colombia is the Andean Grebe (*Podiceps andinus*). This species of grebe, endemic to the high-plateau wetlands of the Eastern Cordillera and once relatively common, became extinct as a consequence of the combined effects of hunting, pollution and the introduction of exotic species of fish for recreational-fishing (Renjifo *et al.*, 2002).

According to Renjifo *et al.* (2002) the main threats to bird diversity in Colombia are, in order of importance: habitat destruction, hunting, and pollution. Habitat destruction affects 110 species and has as underlying causes of deforestation for agriculture and cattle, timber extraction and cultivation of illicit crops. Another key factor is the destruction of wetlands. Selective hunting for either subsistence or illegal trafficking of sought after species affects 34 species. Hunting affects principally waterfowl (Anseriformes), especially ducks (Anatidae) as well as big raptors (Falconiformes) and frugivores such as tinamous (Tinamidae), guans, chachalacas and curassows (Cracidae), toucans (Ramphastidae) and cotingas (Cotingidae). On the other hand, illegal trafficking affects mainly parrots (Psittacidae), while pollution may affect at least 17 species in the country. Mostly, species associated to wetlands such as for example the Bogota Rail (*Rallus semiplumbeus*) and the Apolinar's Marsh Wren (*Cistothorus apolinari*), and some species known to visit crops fumigated for pest control or inhabiting nearby fumigated illicit crops areas such as the Saffron-headed Parrot (*Pionopsitta pyrilia*).

1.3.3. Conservation planning

Management and conservation of the land is a practice deeply rooted in human societies. In this sense, since ancient times different civilisations have kept portions of land for diverse management purposes, such as for example patches of forests reserved for the gods such as “sacred grooves” by Romans, Greeks and Indians and the royal forests reserved for hunting in England (Chandrashekara & Sankar, 1998; Margules & Pressey, 2000). Nowadays the definition of areas for conservation has as a main objective to sustain global biodiversity (Pressey *et al.*, 1993). So far the selection of areas for conservation has been performed opportunistically and on the basis of expert knowledge, and sometimes through systematic scoring and ranking using different criteria to assess areas value for conservation (Margules & Usher, 1981; Margules, 1989). These approaches are useful, though there are risks associated with the allocation of limited economic resources to areas that may not be the key

areas for the conservation of species at risk (Pressey *et al.*, 1993). A new approach emerging since the 1980's and which is developing a very clear body of theory and practice is called "systematic conservation planning".

Margules & Pressey (2000) define systematic conservation planning as "the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values". The same authors define six main stages in which systematic conservation planning should occur: 1) data compilation, 2) definition of the conservation goal, 3) assessment of existing conservation areas, 4) selection of additional conservation areas, 5) implementation of conservation actions, and 6) maintenance of conservation areas.

As a first step for data compilation it is necessary to decide which elements of biodiversity and/or surrogates of these elements are the most suitable (Margules & Pressey, 2000). These elements may be, for example, biotic such as vegetation types, ecosystems, species, populations, *etc.* or abiotic such as, for example, climate variables, topography and soils, that are surrogates of biodiversity or for the processes responsible for the generation and maintenance of biodiversity. A further step is to gather together the selected datasets and decide if it is necessary to collect more data in the field (Margules & Pressey, 2000) and also whether this is feasible.

In a second stage, it is necessary to set explicit goals for representativeness and persistence where representativeness refers to the proportion of an element of biodiversity captured by a reserve network. Persistence denotes the capacity of the same network to protect in the long-term the selected elements of biodiversity. In general, the way the goals for representativeness and persistence are set is subjective, nonetheless their real value lies in the fact that they are explicit and that they may be revised and calibrated as part of an iterative planning process (Margules & Pressey, 2000).

In the third stage, is conducted a coverage or gap assessment of the predefined representativeness and persistence goals by existing conservation areas. Usually this evaluation is performed as a gap analysis, determining to which extent ecoregions, ecosystems and/or geographical patterns of species ranges are captured by reserve networks (Pressey *et al.*, 2002; Cowling *et al.*, 2003; Kerley *et al.*, 2003; Pressey *et al.*, 2003; Rodrigues *et al.*, 2004a; Rodrigues *et al.*, 2004b). In this sense, most evaluations have focused on biodiversity elements and not processes, which represents a limitation for planning highly persistent reserve networks (Margules & Pressey, 2000) since elements are a function of processes and the processes must be maintained in order to ensure the long term persistence of the resulting elements.

Results obtained from either the ecosystems/species gap analysis or the process gap analysis set the objectives for the fourth stage of the process (Margules & Pressey, 2000). Thus, area selection moves towards the completion of the proposed goals

for both representativeness and persistence, adding to the existing reserve network. For this purpose different species-level criteria have been used such as for example: rarity, endemism, vulnerability, irreplaceability and complementarity (Margules & Usher, 1981; Margules & Pressey, 2000). The first four are usually based on linear scoring techniques, while in the last one areas are selected to obtain the greatest combined richness in the selected biodiversity elements (Williams *et al.*, 1996; Margules & Pressey, 2000).

Once areas are selected for conservation, it is necessary to implement those in the field and to maintain them in the short, medium, and long-term, and these constitute the last two phases of systematic conservation planning. Ideally, the implemented network should match as closely as possible the planned network. However, there are many practical reasons that can make this impossible such as for example the land ownership, commercial interests, *etc.* (Margules & Pressey, 2000). Finally, the maintenance of each reserve area requires the identification of biodiversity indicators to monitor the achievement of the different goals and management strategies proposed (Margules & Pressey, 2000).

1.3.4. Justification for this research

Colombia is a megadiverse country with a high degree of endemism in which about 10% of the world's biodiversity is represented in less than 1% of the total land surface (Chaves & Arango, 1998; Baillie *et al.*, 2004). This megadiversity conveys a great responsibility and – at the same time – represents a great challenge for conservationists in the country, now and in the future. This is especially true when one considers the severity of the environmental and socio-political challenges facing the country due to poverty and political instability.

In spite of this remarkable need, the history of conservation in Colombia is very recent. It started in the 1960's, with the creation of the first national park, Los Guacharos National Natural Park (1960), in southeast Huila (Hilty & Brown, 2001). Since that time 45 more governmental protected areas have been created (Arango, 1998). Although the extent of the national reserve network has continued increasing in recent years, mainly through private reserves and a few more national reserves, these areas have been created rather opportunistically, as has been the case for several countries in the African tropics (De Klerk *et al.*, 2004). This type of “*ad hoc*” reserve selection is invaluable and effective as a first approach for conservation. However, looking forward – especially within the context of climate change – it is desirable to implement more innovative approaches that use analytical methods to systematically assess the national reserve network from complementary points of view.

Limited economic resources make it necessary to prioritise inventory and conservation decisions in a country of mega-diversity and large expanses of poorly studied intact

natural ecosystems. In this context of data paucity, the use of secondary sources of information such as biological collections becomes of primary importance to study biodiversity distribution. During 2002–2005 Project BioMap was conducted and aimed to increase biodiversity knowledge in Colombia through repatriation of bird data held in museums worldwide. As a main output, BioMap compiled an outstanding database with nearly 220,000 georeferenced accessions (the so-called Darwin–Hernandez Database). This provides a basis for analysis and modelling of bird diversity in the country in order to better understand the distribution of species and of diversity as well as the potential impacts of climate change upon it. Such analyses can assist systematic conservation planning in the country, and help inform policy makers using sound science to facilitate the adequate conservation of biodiversity (and its associated environmental services) in the long term. This kind of study contributes to the first objective of the national strategy for bird diversity conservation in Colombia (Renjifo *et al.*, 2001), which is to develop an information system to study and monitor bird diversity in the country. Such a system would increase the quality and quantity of research related to all aspects of Colombian bird biology and help to identify key conservation areas for Colombian birds, especially for threatened, endemic and migratory species. In this thesis, we improve and then use the Darwin–Hernandez Database to better understand the geographical distribution of bird species and diversity in Colombia with a view to understanding optimal conservation strategies under current and future climates.

1.4. Aim of the thesis

To model, spatially, bird diversity distribution in Colombia under current and future climate scenarios, thereby assisting the effective conservation of bird diversity through the development of sound biodiversity science for improved conservation planning for the country.

1.5. Objectives

1.5.1. To revise and correct coordinates attached to each one of the localities included in the Darwin–Hernandez Database from Project BioMap, making them suitable for geographical GIS–analyses, and producing estimates of georeferencing uncertainty for each coordinate.

1.5.2. To use the Darwin–Hernandez Database and GIS to map Colombian bird diversity at different taxonomic levels using several methodologies, and to explore new non–taxonomic (ecological) measures of diversity that may better represent elements of biodiversity, which are not well represented by taxonomic measures.

1.5.3. To assess the spatial variability of sampling effort and to evaluate any correlations between bird richness and sampling effort in the datasets extracted from the Darwin–Hernandez Database and used to model avian diversity.

1.5.4. To validate diversity maps produced under current climatic conditions using the Darwin–Hernandez Database against maps generated using other databases such as the WHDBD Database and ProAves Foundation field surveys.

1.5.5. To project avian diversity in West Colombia under future climate scenarios and evaluate the potential impact of climate change on it, assessing its spatial patterns and differences to diversity modelled under current climate conditions.

1.5.6. To select potential refugia of bird diversity in West Colombia under future climate–change conditions using a threefold criterion trying to highlight areas where projected diversity is high, the difference in diversity between future and current conditions is minimised and diversity projections are most robust.

1.5.7. To evaluate coverage of the potential avian diversity refugia in West Colombia by the National System of Protected Areas (SINAP) and a selection of private reserves, and discuss the implications for conservation strategy in the country and the SINAP.

1.6. Theoretical framework in brief

According to the classical niche concept, the niche may be visualised as a hyper-volume of n - dimensions of conditions and resources under which a species may survive and reproduce (Hutchinson, 1978; Begon *et al.*, 2006). Additionally, biological interactions such as mutualism, competition, predation, and parasitism also make part of the dimensions that define the niche. A species' geographical range is the projection of the niche on the environmental conditions on the ground defined by the spatial and temporal distribution of different abiotic and biotic environmental factors (Brown, 1995). In this context, changes in important climatic conditions such as temperature and precipitation may affect the spatiotemporal distribution of a species geographical range and by combining impacts on many species, thus affect local and regional biodiversity.

Tropical ecosystems are often thought of as having been very stable during the Quaternary climatic changes. However, palynological records have highlighted important shifts in the distribution of mountain vegetation zones. Nevertheless, today it is known that mountain vegetation has not remained stable and has changed markedly in specific composition and distribution during the last 30,000 years due to changes in climate (Flenley, 1979). According to Flenley (1979), glacial periods were thought to have resulted in increased rainfall in tropical latitudes rather than significant changes in temperature, while vegetational belts shifts remained in the order of

500m in mountain zones. Contrastingly, although during the last 33,000 years BP (before present) vegetation types remained similar in general terms, there has been considerable oscillation in the altitudinal limits for each vegetation type. Vegetation bands reached their lowest limits of distribution about 18,000–15,000 years BP some 1,000–1,700 m below the present limits, which were first reached around 3,000 years BP. In the northern Andes the tree line descended approximately 1,200–1,500 m during the Last Glacial Maximum (LGM), from 3,500 to 2,000 m of elevation (Van Der Hammen, 1974). These shifts were consequence of changes in temperature, and in this sense Van Der Hammen (1974) has estimated that temperatures fell by about 6–7 °C or more in the highlands and about 3 °C in the lowlands. The same author considers climatic changes had profound effects on regional evolutionary processes, and evidence suggests significant modifications in composition due to immigration from both Boreal and Austral vegetational components as well as replacement of taxa elevationally due to local adaptation, speciation and extinction.

Continuing this flow of ideas, it is expected that accelerated climate changes under human induced causes may produce alterations in species geographical ranges and therefore in total local and regional biodiversity. In recent years, evidence has accumulated showing potential shifts in the geographical ranges of different taxa in several regions of the globe (Peterson *et al.*, 2001b; Iverson & Prasad, 2002; Walker *et al.*, 2002; Root *et al.*, 2005; Walther *et al.*, 2005; Harrison *et al.*, 2006; Thomas *et al.*, 2006; Thuiller *et al.*, 2008). Moreover, changes are expected to affect more severely those species with their centres of abundance in high latitudinal and altitudinal zones, such as for example polar and high–mountain restricted species (Parmesan & Yohe, 2003; Ellis *et al.*, 2007; Virkkala *et al.*, 2008; Grabherr, 2009). In addition, climate change may have potential negative impacts on entire mountain ecosystems that depend on a very specific climate such as for instance the fragile mountain cloud forests and the paramos (Foster, 2001; Hooghiemstra & Van Der Hammen, 2004; Brown *et al.*, 2007).

This research uses the Darwin–Hernandez Database from Project BioMap and MAXENT (Phillips *et al.*, 2006), a machine learning modelling technique that generates a unique probabilistic distribution indicating the suitability of any particular combination of environmental variables based on the maximum entropy principle (Jaynes, 2003), to model potential bird habitats and geographical ranges in Colombia at high order taxonomic levels under current climatic conditions. Additionally, results are projected under expected climate conditions generated by the HadCM3 model, scenarios A2A and B2A for the years 2020, 2050 and 2080 (Nakicenovic *et al.*, 2001) assuming no limitations in dispersal capabilities and movement in response to climatic drivers rather than shifting vegetation systems. Based on the described theoretical framework we expect that under projected future climatic conditions bird geographical ranges in Colombia may shift, affecting the geographical distribution of bird diversity in the country and hence the conservation landscape.

CHAPTER 2

A REVIEW OF THE CONCEPTS OF BIODIVERSITY AND THE NICHE

Summary – Biodiversity, the diversity of life forms, has been defined in many different ways by different authors. Different definitions come from several fields of biology and most of them embrace the same basic idea about the variety of life. Further, operational definitions translate diversity from a concept to a measurable quantity, which is a requirement when trying to prioritise its conservation. This chapter develops three main subjects that are necessary to understand the approach taken in this thesis. First, it contains a brief revision of the values assigned to biodiversity and some of the approaches available in the literature to measure it. In this context, in this study we use taxonomic, functional and morphological measures, or a combination of the three, as a means of advancing our knowledge of the distribution of different components of bird diversity at national scale. Secondly, this chapter briefly reviews the general patterns of biodiversity observed in nature as well as the main hypotheses explaining biodiversity, as a general background to understanding geographical variability and its role in explaining bird diversity patterns in Colombia. Finally, we revisit the niche concept to establish a connection between the main body of theory developed in the field with some of the implications of the concept in ecology and biogeography, especially within geographical range and habitat suitability modelling, where it plays a central role.

Introductory note – Nowadays, biological diversity or “biodiversity” and its conservation are considered of great importance. However, biodiversity is not a new subject in ecology and biogeography and it has been the subject of intense research in the past 200 years in both disciplines. From the times of A.R. Wallace and A.P. De Candolle in the 1800’s, ecologists and biogeographers have tried to explain the distribution and patterns of biodiversity (Colwell & Lees, 2000). From those days to present, many explanations and mechanisms related to different ecological, historical and/or climatic causes have been proposed to account for the variation in the distribution of elements biodiversity, predominantly species richness (Lyons & Willig, 1999; Whittaker *et al.*, 2001). More recently, during the 20th century, the attention of ecologists was directed, among other subjects, towards describing the patterns of abundance of species, the development of diversity indices and during the last 20–30 years exploring the relationships between biodiversity and other characteristics of the communities and ecosystems that maintain this biodiversity (Gaston, 1996b; Ghilarov, 1996). In the 1990’s biodiversity took on a global socio–

political context because of the Convention on Biological Diversity (CBD), held as part of the United Nations Conference on Environment and Development (UNCED) in Rio de Janeiro in 1992. According to Ghilarov (1996), the recent popularisation of the term biodiversity has resulted from the connection it has had with politics since it was coined, aided by scientists who probably also contributed, aiming to improve the chance of funding for their research programmes.

2.1. Biological diversity “biodiversity”

2.1.1. Definition

Since the term “biodiversity” was coined in the 1980’s, it has been defined in different ways, which have tried to cover all the aspects related to the subject (Gaston & Spicer, 2004). Those definitions have stemmed from different fields of study and points of view, a fact that makes it particularly difficult to embrace all aspects considered of importance in one single definition (Noss, 1990). According to Gaston (1996b) all definitions may be encapsulated in three main categories in which either biodiversity is considered as a concept, a measurable entity or a social construct. When considered as a concept, biodiversity is treated as an abstract idea related to the diversity of life and in this sense the many different definitions proposed encompass expansions or contractions of this idea (Gaston, 1996b). For example, in its simplest form biodiversity may be defined as “the variety of life” (Gaston, 2000). Meanwhile, in a more complex way it may be defined as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (CBD, 1992). When referred to as a measurable entity, the conceptualisation made on the subject becomes operational, considering it a quantifiable quality that can be measured in different dimensions (Gaston, 1996b). In this sense, many of the advances made in this subject took place during the 1960’s and 1970’s, when most of the best well known indices to measure ecological diversity, based on principles taken from “information theory”, were developed (Gaston, 1996b; Magurran, 2004). More recently, research in biodiversity measures has moved towards new indices based on differences between constituent elements (Hector *et al.*, 1999; Izsák & Papp, 2000; Ricotta, 2005a). Despite these advances, to measure biodiversity in terms of complexity still remains a challenge, since it is not possible to capture or reduce a multidimensional quality such as biodiversity in one number (Roy *et al.*, 2004), and therefore this area still constitutes a fertile ground for future research.

Like the CBD definition, the definition proposed by the U.S. Congress Office of Technology Assessment (OTA) emphasises the systems approach. According to this

body, “Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity, these items are organised at many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis of heredity. Thus, the term encompasses different ecosystems, species, genes and their relative abundance” (OTA, 1987). Finally, in definitions in which biodiversity is regarded as a social construct it is considered in terms of its connection to conservation of nature (Gaston, 1996b). Thus, biodiversity does not constitute a neutral scientific concept but just a term in which a set of values arising from human societies concern for the loss of the natural environment is implicit (Gaston, 1996b; Aubertin *et al.*, 1998). This may be illustrated in part in the definition proposed by Reid & Miller (1989) “Biodiversity is the variety of the world’s organisms, including their genetic diversity and the assemblages they form. It is the blanket term for the natural biological wealth that supports human life and well-being. The breadth of the concept reflects the interrelatedness of genes, species and ecosystems.”

It is interesting to highlight that concepts of biodiversity have shifted focus during the last 50 years from a reductionist point of view to a hierarchical systems approach. In the reductionist view, biodiversity is seen as the variability in the elements that constitute a system and their proportions (*e.g.* genes of the gene pool of a population and/or species in a community, *etc.*). In this respect many of the indices to measure ecological and genetic diversity were developed under this framework (Futuyma, 1998; Magurran, 2004). The definition proposed by the OTA (1987) is a good example evidencing this. More recently biodiversity has started to be understood as a phenomenon of hierarchies interacting at different levels (Barbault, 1995). Therefore not just its elements and their variability are considered, but their levels of organization (*i.e.* genes, populations, species and ecosystems) and their interrelationships (Noss, 1990). The definition proposed by McNeely *et al.* (1990) evidences this change, it reads “Biological diversity encompasses all species of plants, animals and micro-organisms and the ecosystems and ecological processes of which they are parts. It is an umbrella term for the degree of nature’s variety, including the number and frequency of ecosystems, species, or genes in a given assemblage”

Irrespective of the approach, biodiversity has always been seen as a phenomenon constituted by different hierarchies. Whittaker (1972), referring to species richness, differentiates three levels at which biodiversity could be studied: alpha (α), beta (β) and gamma (γ). Thus, α diversity is defined as the diversity in a community, and therefore it is measured at local scale, β diversity is characterised by differences between communities in a spatial gradient (turnover), and γ diversity is the total diversity embraced in a regional context. In a similar way, in the definitions adopted

by OTA (1987), Reid & Miller (1989), McNeely *et al.* (1990) and the CBD (1992), three levels are mentioned (*i.e.* genetic, species and ecosystem). Genetic diversity is the genetic variability in a population or between populations of one species; species diversity is the variability in species in a defined area; and ecosystem diversity is the variety of different ecosystems in a regional context (Barbault, 1995; Zacharias & Roff, 2000; Gaston & Spicer, 2004). Noss (1990) further develops this concept based on the attributes of an ecosystem considered by Franklin *et al.* (1981). In his view, biodiversity is a system of nested hierarchies in which upper levels of organisation determine the processes occurring at lower levels. This author assigns three attributes that characterise biodiversity in five levels. The attributes are composition, structure and function; composition refers to the identity of each element, structure to physical organization of those elements in space, meanwhile function is related to the processes in which those elements are involved. The levels of organisation are genes, populations, species, ecosystems, and landscapes.

In this study, biodiversity is treated under the framework proposed by OTA and the CBD. Thus, on the one hand biodiversity is considered in many instances as a simple concept referring to the variety of life forms. On the other hand, the concept is made operational and treated as a measurable entity. In this sense, a series of different indices are developed to estimate bird diversity in Colombia. As it will be shown later in chapter 5, these measures are reductionists in its inception, although some of them, such as “functional diversity” try to incorporate a different level of community organisation in it.

2.1.2. Value of biodiversity

Conservation of biodiversity is a human construct that only acquires meaning in a social context. In this sense, Jepson & Canney (2001) have asserted that conservation is a social movement that is related to a set of values assigned to the relationship between humans and nature, and based on Ehrlich & Ehrlich (1992) have grouped those values in four categories: 1) cultural, 2) moral, 3) socio-economic, and 4) genetic. All the values we assign to nature in terms of its relationship to human societies are grouped in the first category. Culture may be defined as the way of life of a society, and this includes such diverse aspects as language, codes, behaviour and systems of belief (Jary & Jary, 2000), and in this context nature always has been an integral part of the “cosmovision” and development of these codes (Dussel, 1966; Townsed, 1992; Malaver-Rodríguez, 2001; Rojas, 2002). In this sense, many species, landscapes and phenomena are deeply rooted in human societies, to an extent that the distributions of certain species reflect the presence and movements of human civilizations (Jepson & Canney, 2001). In the second category lies a set of values that are purely metaphysical and are related both to ethics and/or compassion

(Jepson & Canney, 2001). On the one hand, it is sometimes considered that nature has the right to be respected and protected since it is part of a superior being, which permeates everything. On the other hand, respect for nature sometimes results from compassion for other beings, a unique virtue that is one of the traits of our identity as humans. In the third category are values linked to the fact that species, communities and ecosystems are closely interrelated to us. In this sense, nature and biodiversity represent an important array of services that if affected could compromise our own well-being and the social and economic development of our societies since nature provides important goods and services to us, without which we could not survive (MEA, 2005). Finally, in the last category are values allocated to nature regarding its importance as an impressive genetic reservoir from which humanity has satisfied its necessities historically and that could still contain many products that are waiting to be exploited for food, fibre and medicinal purposes (Wilson, 1992; Jepson & Canney, 2001).

In a slightly different way, Meffe & Carroll (1997) mention that values of biodiversity could be classified in two main sets: 1) instrumental values and 2) intrinsic values. In the first set, values are grouped in terms of the utility they represent to human societies and/or ecosystems. For example, goods or services such as food and water, spiritual enjoyment, or functions that facilitate natural processes in ecosystems. Intrinsic values are values that are independent of goods and services realised by humans and may be interpreted in terms of the “deep ecology” philosophy (De Jonge, 2003). Therefore, nature might be respected since it has a value in itself that is independent of the instrumentalist value assigned by human societies.

Ecosystem services are all the benefits and profits derived directly or indirectly from nature (MEA, 2005; Pereira & Cooper, 2006). MEA (2005) group ecosystem services into four different categories: provisioning services, regulating services, cultural services and supporting services. For MEA (2005) provisioning services are constituted by all products obtained from natural ecosystems, some of them obvious to us such as for instance the food we eat and the water, tea and coffee we drink every day. As well as some others less apparent such as fibres in our clothes, biochemical products in medicines, home and office furniture and paper made from wood, energy from coal, oil and gas, *etc.* Regulating services are those benefits that result from the autoregulation that ecosystems exert on different processes that occur at different levels from local to global scales. Some examples of those processes are: evapotranspiration, precipitation, water retention, runoff, soil formation and erosion, carbon sequestration, plant pollination and seed dispersion, pest control, *etc.* Cultural services refer to all of those activities related to the enjoyment of nature, from which we benefit in a social context. In this category we include the importance that nature represents in spiritual and philosophical realms for different people, the potential

that it represents for recreation (*e.g.* ecotourism, bird watching, hiking), inspiration for artists (*e.g.* poets, painters, musicians), and its value as an important part of the cultural heritage to which any society is attached. Finally, supporting services are those services that sustain the production of other ecosystem services and refer mainly to those processes that sustain communities and ecosystem functioning, such as for instance photosynthesis and primary production, oxygen production, decomposition, nutrient cycling, soil formation, natural selection and evolution, *etc.* Relationships between biodiversity and ecosystem services are unclear and the services provided by groups such as birds are perhaps less obvious than for instance those provided by mammals hunted for meat or insects which pollinate crops. Nevertheless, birds are a fundamental component of functioning ecosystems and thus responsible in part for ensuring the provision of services from the entire system.

2.1.3. Measures of biological diversity

Biodiversity means different things to different people, and consequently its definition and quantification varies in the different fields of biology. Harper & Hawksworth (1994) mention three general approaches to quantify biodiversity which they consider are alternatives to the most widespread used index of biodiversity, “species richness”: taxonomic, molecular and phylogenetic measures. In ecological research, the equitability of species population numbers in a community has received enormous attention. Thus, some of the most popular indices to measure equitability and thus “biodiversity” in the literature are for example: Simpson, Shannon–Wiener, Margalef and Brillouin for alpha and gamma diversity, and Whittaker, Jaccard, Morisita–Horn and Sorenson for beta diversity, among others (Magurran, 2004).

Furthermore, since the CBD it has become evident that if our purpose is to conserve biodiversity, we need to know more than just the number of species in a site (*i.e.* species richness). Trying to understand how populations, communities and ecosystems and their interactions work, and how processes integrate at different scales is equally important (Barbault, 1995). In this context, during the last 20 years the role of diversity in ecosystem function has been intensively debated (Schulze & Mooney, 1994; Grime, 1997; Hector *et al.*, 1999; Chapin III *et al.*, 2000; Schwartz *et al.*, 2000; Wardle *et al.*, 2000; Hector *et al.*, 2001; Loreau *et al.*, 2001; Giller & O’donovan, 2002; Srivastava & Vellend, 2005; Balvanera *et al.*, 2006). As part of this debate, a relatively new concept has emerged in ecology, that of “functional diversity” (FD). According to Tilman (2001), FD is defined as “those components of biodiversity that influence how an ecosystem operates or functions”. In spite of evidence in favour or against biodiversity as an important characteristic of communities for the maintenance of stability and resilience, it has become more accepted that the effects of diversity in an ecosystem are related to the actual constituent elements and the type of interactions

between them (Hooper *et al.*, 2005) rather than as a property *per se* of biodiversity, measured as the number of species of the ecosystem (Diaz & Cabido, 2001).

Ecological indices focus mainly on species, and therefore are probably not appropriate to measure FD, at least if used in their conventional form. Thus, in recent years other ways of using existing indices and/or new indices have been proposed for the measurement of different features of communities (or ecosystems) related to FD (Ricotta, 2005a). When ecological indices are used in its conventional way it is often assumed that FD is correlated to species diversity, which Diaz & Cabido (2001) believe is not always the case. According to these authors, this can only be assumed if occupation of niches in the community is random or regular, which apparently is not what occurs in natural communities. In its simplest form, FD may be estimated as the number of functional groups present in a community. In this way, a set of functional groups are defined *a priori* and then each species is assigned to one of them, then the “functional richness” is defined as the number of functional groups present (Hector *et al.*, 1999). Otherwise, multivariate–clustering techniques could be used as a more complex approach to measure FD (Ricotta, 2005a). To estimate FD in this way, first a matrix of functional traits for the species present is defined (*i.e.* m_{ij} rows = i = species, and columns = j = traits), and then groups are clustered using multivariate analysis (Ricotta, 2005a). A similar approach to measure FD, based in multivariate analysis, uses the trait matrix m_{ij} and estimates an index based on the trait divergence between species, which basically corresponds to the sum of the total pair–wise distances between the different species (Ricotta, 2005a). It is noteworthy to highlight that the majority of the new indices are based on Euclidean distances between the species of the community and/or ecosystem considered, and may or may not consider the equitability in population numbers for the species present (Izsák & Papp, 2000; Roy *et al.*, 2004).

In this study, several measures of bird diversity are explored for Colombia. Starting with the widely used species richness index and moving later to taxonomic measures at genus and family levels, and finally to more complex measures of FD investigating the equitability of avian ecological guilds in the community (Chapter 5, section 5.2.4.4).

2.1.4. Patterns of biological diversity in space and time

From the times of the early biogeographers, such as A.P. De Candolle, J.C. Prichard, W. Swainson and A.R. Wallace, more than 100 different hypotheses and mechanisms have been proposed to explain the observed patterns in the distribution of biodiversity (Lyons & Willig, 1999). However, this task has proved to be a difficult one, as the large number of different explanations that still exist suggests. According to Gaston & Williams (1996) there are three main reasons why the mechanisms explaining the

distribution of biodiversity are not completely clear. First, usually explanations are based on simple processes or hypotheses, which do not include the complete array of possible mechanisms involved. Second, factors correlated to biodiversity usually exhibit collinearity between them, which makes it difficult to clarify the ultimate factors which determine biodiversity. Furthermore, since correlation does not imply causation many studies cannot prove causation. Third, there are different processes acting at the microevolutionary and macroevolutionary time scales which are not easy to integrate within the static observational picture of the present, but that are necessary to obtain a complete understanding of biodiversity patterns.

To understand biodiversity fully, first it is important to understand its patterns of distribution and second to understand the different processes, both biotic and abiotic, that affect it at different scales and how those interact (Huston, 1994). At present there are four main geographical patterns that have been described in relation to the distribution of biodiversity: 1) the latitudinal gradient, 2) the altitudinal gradient, 3) the species–area relationship, and 4) the successional changes (Huston, 1994).

2.1.4.1. The latitudinal gradient

From the early 1800's A. Von Humboldt was proposing a method to measure the relative richness of certain families of plants across latitudinal and altitudinal gradients. A.R. Wallace also highlighted in several of his works how some groups exhibit high richness in the tropics but low richness in the arctic regions (Wallace, 1871, 1876).

Since then, it has been demonstrated that for major groups of terrestrial plants and animals diversity is lower at the poles and it increases towards the tropics (Rosenzweig, 1995). Stevens (1989), Huston (1994) and Hawkins *et al.* (2003) mention 143 different published studies on the latitudinal gradient of species richness, of which 28 were conducted on plants, 49 on invertebrates and 66 on vertebrates. Nonetheless, this pattern is not unequivocal in all groups, and there are even groups for which contrary gradients have been reported, such as for example some lichens, marine benthic organisms, soil nematodes, parasitic wasps and sea birds (Huston, 1994 and references therein). In this sense, Huston (1994) and Stevens (1989) mention 16 different studies, of which two were conducted on plants, nine on invertebrates and five on vertebrates.

2.1.4.2. The altitudinal gradient

Similarly, to the latitudinal gradient, the altitudinal gradient is a pattern also documented since the early days of biogeography by authors such as A. Von Humboldt

and A. Bonpland in their “*Essai Sur la Geographie des Plantes*” published in 1807. Since that time, naturalists have realised the correspondence existing between physical conditions and the distribution of life (Huston, 1994). Altitudinally, the “environmental lapse rate”, which is the decrease in air temperature with increasing elevation, changes by 6.5 °C for each 1,000 m of elevation (Briggs & Smithson, 1997). As expected, this change in climatic conditions creates a change in species ranges and thus biodiversity.

There is evidence over several groups and areas of the globe that biodiversity decreases with elevation, reaching low levels at higher elevations (Grytnes, 2003; Wake, 2004; Aubry *et al.*, 2005; Jacquemyn *et al.*, 2005; Grytnes *et al.*, 2006; Fu *et al.*, 2007), mirroring the latitudinal gradient. According to Rahbek (1995), this generalisation came from two classic studies in tropical birds in Peru (Terborgh, 1977) and New Guinea (Kikkawa & Williams, 1971). This same author considers also that the relationship has been considered historically to be a simple analogy of the latitudinal gradient and in this sense biodiversity decreases monotonically with altitude due to a decrease in temperature and thus primary productivity. Nonetheless, he points out that in a review of 163 examples from 97 papers in which the relationship is mentioned, he found evidence supporting declines, but that these were not necessarily monotonical. Some evidence shows that this relationship may be expressed as a humpback-shaped curve in which higher levels of biodiversity are exhibited at mid elevations (Rahbek, 1995; Navas, 2006). Nonetheless, the exact shape may vary due to factors such as the group under study, size of the study area and sampling effort, which must be taken explicitly into account to model accurately this relationship and thus get a better understanding of the processes and mechanisms involved (Rahbek, 1995; Sanders, 2002; Kattan & Franco, 2004). In this study, we make no assumption about the altitudinal gradient in bird diversity, choosing instead to measure it.

2.1.4.3. *The species–area relationship*

The nature of biodiversity increase with sample area is known as the species–area curve (Huston, 1994). This was probably first documented in the late 1700’s by J.R. Forster, who was appointed as the naturalist in charge during Captain J. Cook’s second expedition (Quammen, 1996), who quoted “...Islands only produce a greater or less number of species as their circumference is more or less extensive...”. Later in the mid XIX century and the early XX century the pattern was recognised in works of A. De Candolle (1855) and P. Jaccard (1901, 1908), and finally formalised mathematically in two forms (Equations 2.1.4.3.1 and 2.1.4.3.2) by O. Arrhenius (1921) and H.A. Gleason (1922) (Williamson *et al.*, 2001; Scheiner, 2003).

$$\log S = \log C + z(\log A) \quad (\text{Equation 2.1.4.3.1})$$

$$S = \kappa_0 + \kappa_1(\log A) \quad (\text{Equation 2.1.4.3.2})$$

Where:

S = number of species

C = constant

z = rate of change of the number of species in function of the area (slope of the relationship)

A = area

$k_0 = C$

$k_1 = z$

This relationship has been tested for very different groups including vascular and flowering plants, molluscs, arthropods, birds and mammals (Huston, 1994). Results of those studies have shown that the relationship in most cases fits better to the Arrhenius form than the Gleason form (Williamson *et al.*, 2001). Furthermore, modelling of the relationship for different geographical areas and taxonomic groups has shown that the shape of the curve may vary a great deal, which suggests that different processes are involved in regulating diversity for different taxa under different conditions (Williamson, 1981, 1988; Huston, 1994; Mutke *et al.*, 2001).

In both forms, the rate at which the number of species increases with the area (z in Arrhenius and k_1 in Gleason) and the shape of the curve have been related to a wide array of different mechanisms explaining the relationship. The most important are: 1) sampling artefacts, 2) the effect of area and its isolation, and 3) the effect of habitat heterogeneity (Huston, 1994). In the first case, the relationship is produced due to the effect that the increment in area would have in the proportional sampling of a population in a relatively homogeneous space (Rosenzweig, 1995; Cam *et al.*, 2002). The second constitutes the basis of the “island biogeography” theory. Accordingly, the number of species present in an area results from the balance between processes of colonisation and extinction, which are in turn affected by the relative size and shape of the island and the separation from the source area from where propagules may disperse (Preston, 1962b; MacArthur & Wilson, 1963, 1967; MacArthur, 1972). Finally, in the third case the species–area relationship is the product of the increased habitat heterogeneity introduced when a bigger area is sampled, which is reflected in a greater number of sampled species typical from the different habitats included each time (Williams, 1964; Connor & McCoy, 1979; Boecklen, 1986; Brose, 2001).

2.1.4.4. Biodiversity over time

Biodiversity also varies in time, at scales lasting from days to millions of years, embracing a vast array of both microevolutionary and macroevolutionary processes (Huston, 1994). Huston (1994) considers also that there are two major processes that may affect biodiversity over time: first dispersal and migration and secondly succession.

Dispersal may be defined as the “...geographic translocation of individuals leading to changes in the distribution of populations and species across a range of spatial scales.” (Giller *et al.*, 2004), and it is a term that may be applied at different taxonomic and time scales, ranging from individuals moving in hours or days to locations nearby to complete taxa moving to different subcontinents over millennia (Wilkinson, 2001). Dispersal may be passive as occurs in plant seeds which are transported by water, wind and/or animals or active as takes place in animals whose locomotion capabilities permit them to move long distances, such as for example in birds (Wilkinson, 2001). Frequently, migration is considered as a synonym of dispersal (Wilkinson, 2001), although many authors just use migration referring to long distance annual return movements such as those observed between the tropics and the temperate zones for some butterflies, birds and bats (Begon *et al.*, 1996). On the other hand, some authors refer to dispersal as short movements made by individuals out of their sites of birth (Danthanarayana, 1970; Gill, 1995; Hockey *et al.*, 2003).

Independently of the apparent confusion existing in the literature, dispersal and migration have been considered important processes in ecology and biogeography, since through them individuals move to colonise new areas (Begon *et al.*, 1996; Brown & Lomolino, 1998; Wilkinson, 2001). For instance, after a disturbance event, different organisms move—in progressively to colonise the area, changing biodiversity (Huston, 1994 and references therein). In this sense, much of the potential effect that dispersal and migration may exert on biodiversity depends on the organisms’ dispersal rate and the time and distance over which dispersal takes place (Huston, 1994).

Change in biodiversity after disturbance occurs as part of a process of succession in which organisms and communities become replaced over time due to the modification in the physical conditions. Disturbances may be infrequent and massive or frequent and less severe (Huston, 1994). Infrequent–massive disturbances relate to succession over long periods of time, so-called “evolutionary succession”. These include catastrophic events causing massive extinctions such as for example volcanism and extraterrestrial impacts (Ryskin, 2003; Sephton *et al.*, 2005; White & Saunders, 2005; Becker *et al.*, 2006; Retallack *et al.*, 2007), as well as the expansion and retreat of ice sheets during glacial and interglacial periods (Johnson & Baarli,

1999; Ravazzi, 2002; Falcon–Lang, 2004; Magri *et al.*, 2006; Ray *et al.*, 2006). After such events populations of existing taxa go extinct or expand and retreat their ranges according to variation in the physical conditions, leading to vicariance and radiation events and thus to an exchange in taxa assemblages at higher scales in space and time (Rosenzweig, 1995).

Frequent–less severe disturbances are conducive to succession over short periods of time, so–called “ecological succession”. This case includes forest gaps and clearings opened during storms, hurricanes and logging events (Attiwill, 1994; Peng *et al.*, 2003; Walker *et al.*, 2003; Martins *et al.*, 2004; Hill *et al.*, 2005; Quiñones–Nadler *et al.*, 2005; Smith & Nichols, 2005; Kariuki *et al.*, 2006; Shure *et al.*, 2006), areas affected by fires (Calder *et al.*, 1992; Gracia *et al.*, 2002; Nadeau & Corns, 2002; Letnic *et al.*, 2004; Buhk *et al.*, 2006; De Luis *et al.*, 2006; Nikonov *et al.*, 2006), and zones perturbed by human activities such as agriculture and cattle grazing (Aide *et al.*, 1995; Parrotta *et al.*, 1997; Tucker & Murphy, 1997; China, 2002; Kozłowski, 2002). After which different species assemblages gradually colonise the perturbed area during several successional stages that may last from years to centuries (Begon *et al.*, 1996).

Human–induced sources of perturbation such as land use and climate change might lead to succession over a continuum of time scales. In this sense, land use might favour ecological succession processes, while climate change might have more profound effects on biodiversity, leading to evolutionary succession processes. In fact, although it is suspected a synergistic effect between both types of perturbations, potential impacts on biodiversity are largely unknown and in need of research.

2.1.4.5. Other patterns of biodiversity

Some other common patterns described for biodiversity distribution are zonation and radial patterns. Zonation probably was one of the first patterns studied in ecology and biogeography and was the one that indirectly stimulated the description and research of the latitudinal gradient (Huston, 1994). Species are arranged in zones or bands and usually in each one of these there are particular elements of biodiversity characteristic and/or dominant of the zone (Huston, 1994). This concept has been applied at different scales. Some examples of it are the marine intertidal and subtidal zones (Wulff & Webb, 1969; Chavanich & Wilson, 2000; Henry, 2002), mangrove zonation (Tomlinson, 1986; Ball, 1988), the global biomes (Olson *et al.*, 1983; Prentice *et al.*, 1992; Olson *et al.*, 2001), and the vegetation life zones system (Holdridge, 1947; Thornthwaite, 1948; Holdridge *et al.*, 1971). The radial pattern refers to an increase or decrease of biodiversity in all directions from a central location as distance from it increases (Huston, 1994). For instance, some mountain related taxa exhibit radial

patterns, declining in diversity as distance increases from the altitudinal centre of their ranges (Huston, 1994). In addition, the patterns of richness observed in the Amazon basin, explained through the Pleistocene refuge hypothesis, agrees to a radial pattern; hence, richness decrease towards the Amazon periphery due to the hypothesised spatial distribution of forest refugia during the last glacial maximum nearly 21,000 years ago (Haffer, 1969; Prance, 1982; Huston, 1994).

2.1.5. A review of the main theories explaining biological diversity

Since the early 1800s more than a hundred explanations have been invoked to account for the variation in diversity (mainly species richness), based primarily on historical and ecological causes (Lyons & Willig, 1999; Gaston, 2000; Tilman, 2000). Fraser & Currie (1996) and Whittaker *et al.* (2001) mention seven main categories that group most of these hypotheses (Table 2.4.1): 1) historical factors, 2) available energy, 3) area, 4) biological/ecological interactions, 5) environmental stress, 6) environmental stability, and 7) disturbance. In general, historical factors are related to processes responsible for the generation of new biodiversity, while ecological hypotheses are associated to processes that contribute to maintain biodiversity. The next sections will present a brief summary of the main historical (1) and ecological (2, 3, 4) hypotheses.

Table 2.4.1. Main general hypothesis explaining diversity.
Based on Fraser & Currie (1996) and Whittaker *et al.* (2001).

Hypotheses group	Summary	Key references
Historical	Macroevolutionary processes such as vicariance, speciation, extinction and the history of the geographical regions (e.g. emergence of mountains, glaciations, etc.) play an essential role in determining diversity.	(Haffer, 1969; Prance, 1982; Ricklefs & Schluter, 1993; Colinvaux, 1998; Moritz <i>et al.</i> , 2000)
Energy	Available energy in the environment limits the maximum diversity that could be generated at the macroscale.	(Wright, 1983; Turner <i>et al.</i> , 1988; Lennon <i>et al.</i> , 2000; O'Brien <i>et al.</i> , 2000; Hawkins <i>et al.</i> , 2003)
Area	Diversity patterns either are the result of sampling artefacts or aggregated environmental heterogeneity, or for islands the balance between area size, isolation and colonisation and extinction rates.	(Huston, 1994; Rosenzweig, 1995) (Preston, 1960, 1962b, a; Terborgh, 1973) (MacArthur & Wilson, 1963, 1967)
Biological interactions	Microscale ecological processes such as competition and predation determine biodiversity directly at local scales and indirectly at higher scales.	(Hutchinson, 1961; MacArthur & Levins, 1967; Janzen, 1970; Shmida & Wilson, 1985)

Environmental stress	Environmental extreme conditions constrain diversity since just few species may adapt physiologically.	(Begon et al., 1996)
Environmental stability	Extreme variability in environmental conditions constrains diversity since just few species may adapt physiologically.	(Connell & Orias, 1964)
Disturbance	Medium levels of disturbance prevent competitive exclusion without eliminating a major part of the community.	(Hutchinson, 1961; Connell, 1978; Hubbell, 1979)

2.1.5.1. Historical explanations

This group of explanations claims that the main factors accounting for current biodiversity are the geological history of the earth and the evolutionary history of the existent taxa. In this sense, biodiversity results from events acting over long periods, such as for example glaciations and catastrophic events, which may trigger evolutionary succession processes. These types of disturbances may induce vicariance and radiation events leading to differential rates of speciation and extinction from place to place and in time, finally promoting also a differential exchange in existing taxa assemblages at higher scales in space and time (Huston, 1994; Rosenzweig, 1995).

One hypothesis that has generated particular interest is the Pleistocene refuge hypothesis (Haffer, 1969; Prance, 1982). According to this hypothesis, the high biodiversity observed in the tropics resulted from fragmentation of the geographical ranges of existing species during this glacial period as surviving forms retreated to refugia in the Amazon basin and diversified due to allopatric speciation. However, recent evidence shows that most of existing groups diverged long before the Pleistocene glaciation period (Moritz *et al.*, 2000; Smith, 2007) and that forests apparently were not fragmented in the exact way suggested by the refuge hypothesis (Colinvaux *et al.*, 1996a; Colinvaux *et al.*, 1996b; Colinvaux *et al.*, 1997; Colinvaux, 1998). This suggests diversification in the Amazon basin did not result from the changes proposed by the refuge hypothesis.

2.1.5.2. Ecological explanations

Explanations of this type affirm that causes defining biodiversity are related to the abiotic and biotic conditions present, and their spatial heterogeneity and interrelations. Three main general hypotheses have been of special interest in ecological biogeography: the first one is related to the environmental available energy, the second is linked to biological interactions inside communities, and the third is based on spatial heterogeneity.

Available energy. This is one of the hypotheses that has received most attention in ecology and to date a large amount of literature regarding the subject has been published, most of which supports the notion that current climate constrains species richness at the macroscale (Wright, 1983; Hawkins *et al.*, 2003). The general idea behind this hypothesis is that the amount of “available energy” limits diversity in a system (Whittaker *et al.*, 2001) and/or that energy availability generates and maintains taxonomic richness gradients (Hawkins *et al.*, 2003). This hypothesis appeared initially as a reformulation of the theory of “Island Biogeography”. In his seminal work Wright (1983), studying the plant richness of different islands, used the averages of the actual evapotranspiration (AET) and multiplied them by the area of the islands producing a new model, which has been the basis of many other studies investigating the same relationship to date (Whittaker *et al.*, 2001).

This hypothesis is also known as the productivity hypothesis and since its original formulation several surrogates of primary productivity have been used to investigate its relationship to both plant and animal richness, such as for instance temperature, rainfall, potential evapotranspiration (PET), *etc.* (Huston, 1994; Rosenzweig, 1995; Whittaker *et al.*, 2001). In most cases the relationship found between richness and energy has been positive increasing continuously or exhibiting a humpback shape, although in some few cases the relationship reported has been negative (Huston, 1994).

In North America, the relationship has been studied for different groups of organisms showing either a monotonic or unimodal relationship (Huston, 1994; Rosenzweig, 1995). For example, it has been found that species richness of seed-eating ants and rodents is positively correlated to mean annual precipitation (Brown, 1973, 1975; Brown & Davidson, 1977; Brown *et al.*, 2001). On the other hand, Owen (1990) studying all mammal, bat and rodent richness in Texas found a negative correlation to precipitation and AET. Other studies conducted investigating the relationship between richness and energy for small mammals in Chile (Meserve & Glanz, 1978), rodents in Israel (Abramsky *et al.*, 1985; Abramsky, 1988) and tropical mammals in Australia (Rosenzweig & Abramsky, 1993) have suggested unimodal tendencies.

Currie (1991) studying the richness–energy relationship for the major groups of vertebrates in North America found strong correlations between richness and the annual PET (Huston, 1994). Their results showed a relationship that tends to be logarithmic in all cases, although for amphibians and reptiles it is clearer than for birds and mammals. For these last two groups the relationship may be interpreted as a second order polynomial relationship, in which after some point increments in energy are matched by a decrease in richness.

O’Brien (1993, 1998) and O’Brien *et al.* (2000) have reformulated the productivity hypothesis. These authors, studying woody plant richness in South Africa have produced a simple model based on the dynamics of water and energy, which they

consider important for understanding the variation in photosynthetic activity and thus in the total capacity for taxonomic richness (Whittaker *et al.*, 2001; Field *et al.*, 2005). In their view, liquid water exists within a narrow range of temperature conditions and its dynamics can be described as a parabolic function of energy. Hence, increasing initially as energy increases and later reaching a maximum point at optimal energy conditions to finally decline at high values of energy, as more water passes to its gaseous state. Furthermore, they believe this relationship determines biological activity at other levels, such as for example, photosynthetic activity, since it depends on water and energy as primers to fix carbon. They described the relationship with the following equation:

$$P = W + (E - E^2) \quad (\text{Equation 2.1.5.2.1})$$

Where,

P = photosynthesis

W = water

E = energy

The same authors believe photosynthetic activity set the limits for richness and thus the variation in terrestrial diversity. In this sense, they summarize the described relationship in a simple “capacity rule” (*sensu* Brown, 1981). Accordingly, “whatever the geographical pattern of variation in water–energy dynamics, it will tend to be matched by the geographical pattern of variation in the amount and duration of chemical energy production, in biological dynamics and thus (over geological time) in the capacity for taxonomic richness.” (O’Brien *et al.*, 2000).

In Britain, Turner *et al.* (1988; 1996) and Lennon *et al.* (2000) found a strong correlation between butterfly and bird richness and the environmental temperature (Whittaker *et al.*, 2001). Similar to other studies which have used PET, but different to those using AET, they conceive available energy as a solar energy measure and not as productive energy (*sensu* Evans *et al.*, 2005), and therefore considering all energy available for the system rather than just the portion that may be converted into biomass. Their view deviates from *the most common formulation of the energy hypothesis*, in which richness is controlled by the energy entering and flowing through biological systems and food chains (Hawkins *et al.*, 2003); affecting indirectly resource levels and biological interactions, which in turn reflects in population sizes and the risk of extinction (Lennon *et al.*, 2000). Conversely, Lennon *et al.* (2000) consider that although temperature may act as a measure of energy, it directly controls richness through simple effects on the energy budgets of organisms. Thus, areas with low temperatures impose higher thermoregulatory expenditures, decreasing the amount of energy organisms allocate for growth and reproduction, finally reflected in smaller population sizes and a higher risk of extinction (Lennon *et al.*, 2000).

Evans *et al.* (2005) in a thorough review on the mechanisms acting at the macroscale in the energy– richness relationship identifies a total of nine causal formulations of the energy hypothesis. The authors assessed the assumptions, predictions and the evidence available supporting each one of them, concluding that they do not necessarily exclude each other, although some are unlikely to act synergistically. These mechanisms are: 1) sampling, 2) *increased population size*, 3) dynamic equilibrium, 4) niche position, 5) niche breadth, 6) more trophic levels, 7) consumer pressure, 8) range limitation, and 9) diversification rate. From this list they identify increased population size, niche position and diversification rate as those that may act as general promoters of the energy– richness relationship at the macroscale, and that at present time have better theoretical and empirical support. Explanation of each one of them is not intended here in this thesis and for further details see Evans *et al.* (2005).

Biological interactions. Hypotheses grouped here are principally focused on the effect that interactions between the organisms present in a community may have on biodiversity. Since the times of C.R. Darwin, diversity theories related to biological– interactions have centred on the description and understanding of competition and predation as the main processes that determine the structure of communities. In this sense, in general terms, most of them have relied on those processes to explain how species share available resources and/or how those processes affect the spatial distribution of organisms. Although such interactions occur at the local scale affecting α diversity, it is thought their effects extend indirectly to β and γ diversity (Huston, 1999).

The exclusion principle (Gause, 1934, 1935) and the competition and predator–prey theories (Lotka, 1925; Volterra, 1926) set the arena in which some of the most important theories related to biodiversity were postulated. Since coexistence was observed in nature, although theoretically it was not possible if species were competing for the same resources, then to understand the factors governing competition and how species avoid it became a central theme in order to understand biodiversity (Huston, 1994). Thus, Hutchinson (1961), trying to explain why so many species of plankton can coexist in an apparently homogeneous environment, proposed that environmental heterogeneity was the key for understanding coexistence, since it prevented equilibrium and thus competitive exclusion. MacArthur & Levins (1967) and MacArthur (1972) developed a theory of coexistence of species based on the maximum limits of similarity set by competing species. In this sense, much of their work focused on building a mathematical framework to understand the maximum overlap that related or competing species packed in a community may exhibit in resource use and yet maintain coexistence. Furthermore, Janzen (1970) proposed another explanation to understand the spatial distributions and biodiversity in tropical forests, making reference to the effect that competition and predation of seedlings have on population recruitment.

According to Whittaker *et al.* (2001), biological interactions are the explanation for biodiversity that has received most attention. In a revision of the mechanisms acting at the local scale to determine α diversity in New Zealand vegetation, Wilson (1990) mentions 12 different such mechanisms of biological interaction (Table 2.1.5.2.1) considered of importance and discussed previously in detail by Connell (1978) and Shmida & Ellner (1984).

Environmental heterogeneity. Living organisms inhabit a world that is spatially and temporally heterogeneous (Stewart *et al.*, 2000). Heterogeneity is not a new concept to ecology, being recognised from times of A. Von Humboldt and related since that time to a wide variety of subjects such as for instance plant and animal ranges, plant dispersion, population dynamics, *etc.* (Wiens, 2000). Heterogeneity may be defined in different ways, and in its simplest form it may be conceptualised as the variability in conditions, either spatial or temporal. Within a biological framework, some authors have defined heterogeneity making an explicit connection between this simple concept and the responses of organisms to it as well as their interrelations (Stewart *et al.*, 2000). In this sense, Milne (1991) defines it as “the complexity that results from interactions between the spatial distribution of environmental constraints and the differential responses of organisms to the constraints.” (Wiens, 2000). In a further step, Rees *et al.* (2000) proposed a highly operational definition and define heterogeneity as “any factor that can cause variation in individual demographic rates, and which may have a biotic or abiotic origin.”.

Heterogeneity may be generated at different levels and in very different ways in the environment (Wiens, 2000). The most intuitive form of heterogeneity is the one that may be found in abiotic environmental conditions, such as for example the variation in topography, solar radiation, temperature, precipitation, soil acidity, soil salinity and soil nutrient levels, *etc.* The change in these conditions along gradients may have effects on the species present at different localities, α diversity, and thus in the turnover rate of species, β diversity (Begon *et al.*, 1996).

Other types of heterogeneity are produced by disturbances in the environment, which according to White & Harrod (1997) may change physiochemical properties as well as the structure of the environments (Stewart *et al.*, 2000). Some events that may cause disturbances and consequently succession processes are: the generation of forest gaps and clearings opened during storms, hurricanes and logging, areas affected by fires, and zones perturbed by human activities such as agriculture and cattle grazing.

In addition, organisms themselves may modify the structure and the physiochemical properties of the environment (Wiens, 2000). In this sense, Huston (1994) applies a very simple classification to better understand the function of different species in the environment. In his view, species are either structural or interstitial. Structural species are those that generate a physical structure that becomes part of the environment,

Table 2.1.5.2.1. Main mechanisms cited in the literature to explain diversity through biological interactions (Connell, 1978; Shmida & Ellner, 1984; Wilson, 1990).

Mechanism	Summary	Key references
Niche diversification	Biological interactions such as competition and predation lead to characters divergence and niche specialisation.	(Mayr, 1963; MacArthur, 1972)
Pest pressure	Predators, parasites and diseases reduce population sizes of their prey and therefore intense competition is relaxed.	(Connell, 1970; Janzen, 1970)
Equal chance	Species are ecologically equivalent in terms of their dispersal, competitive and resilience abilities and therefore diversity is determined by the combination of species in the regional pool and their local abundances.	(Goldberg & Werner, 1983; Shmida & Wilson, 1985; Hubbell & Foster, 1986; Schafale & Christensen, 1986)
Gradual climate change	Change in environmental conditions occurs at a rate that prevents competitive exclusion.	(Hutchinson, 1961; Huston, 1979; Shmida & Wilson, 1985)
Intermediate–timescale disturbance	Medium levels of disturbance create enough heterogeneity to prevent competitive exclusion without eliminating a major portion of the entire community.	(Connell, 1978; Hubbell, 1979)
Life history differences	Subtle differences in life history strategies prevent competitive exclusion of functionally equivalent species.	(Fagerstrom & Agren, 1979; Shmida & Ellner, 1984; Crawley, 1986)
Initial patch composition	Random differences in abundance of species in a patchy landscape may determine exclusion of one or another in different patches if interspecific competition is higher than intraspecific competition.	(Levin, 1974)
Spatial mass effect	Some populations do not go extinct in non–adequate habitats due to the continuous input of propagules from nearby adequate areas from which individuals disperse.	(Shmida & Ellner, 1984; Shmida & Wilson, 1985; Pulliam, 1988; Kumin, 1998)
Circular competitive networks	Competitive ability is not absolute, but relative to species biology and the specific competitive mechanisms involved in each interaction. Thus at equilibrium, coexistence is possible since some species may exhibit excellent competitive abilities in relation to other species, while they may show low competitive abilities in comparison to others.	(Jackson & Buss, 1975; Harper, 1977; Connell, 1978)

<p>Cyclic succession</p>	<p>As in circular competitive networks, here competitive ability is not absolute and may be mediated by complex catalytic and inhibitory relations. In general, this mechanism is understood to involve particular species and not the whole community.</p>	<p>(Armstrong & McGehee, 1980; Shmida & Ellner, 1984)</p>
<p>Aggregation</p>	<p>Aggregation resulting from low dispersal abilities or other biological attributes of a species may slow down competitive exclusion and thus permit coexistence in a patchy landscape.</p>	<p>(Silvertown, 1987; Czarán & Bartha, 1989)</p>
<p>Stabilising coevolution</p>	<p>Natural selection favours niche divergence in a community, but within a continued process of coevolution where communities exhibit balanced competitive abilities among the assembled species. Coexistence is possible even in cases where species share a major part of their niche due to differences in their overall ability to preclude exclusion.</p>	<p>(Pimentel, 1968; Aarssen, 1983, 1985)</p>

while interstitial are all of those that use or fill the heterogeneous space created by the structural species. Moreover, structural species are usually sessile organisms and among some of the most typical examples are: bushes and trees, reef-forming corals, multicellular algae, oysters, mussels, *etc.* On the other hand, interstitial species are usually highly mobile and some examples are: microbes and fungi, insects and other arthropods, and major vertebrate groups. The presence or absence of certain structural organisms may change completely the conditions that other species experience and therefore affect the diversity of interstitial species. Additionally, species present in an environment may exert a direct effect on its physicochemical conditions. For example, big herbivorous mammals that graze in grassland habitats can induce changes in soil properties (Wiens, 2000 and references therein), and certain plants that produce allelopathic compounds can change soil conditions inhibiting germination of seeds of other species (Begon *et al.*, 1996).

A further biodiversity hypothesis considers that heterogeneity (irrespective of how it is produced and the form that it may take) is fundamental for the generation and maintenance of biodiversity (Huston, 1994). Wilson (2000) proposed two mechanisms for the relationship between richness and environmental heterogeneity. In the first of them, spatial heterogeneity, is said to generate a greater number of species' niches, thereby producing highly diverse communities (Rosenzweig, 1995). In the second mechanism, different organisms specialise in particular environments, and thus so heterogeneity encourages coexistence of many specialist species and thus β diversity along environmental gradients (Grime, 1994).

To date most of the evidence supporting the richness–heterogeneity hypothesis has been accumulated in favour of the first mechanism, which constitutes an *ad hoc* argument of the biological–interactions hypothesis since it focus on biotic interactions, especially competition. According to Huston (1994), at the local scale, heterogeneity may have an important effect on the number of functional types. In his view, since different functional types arise by competition and character divergence (*sensu* Mayr, 1963), thereby avoiding competition, a more heterogeneous environment offering more variability in resources will promote speciation and therefore higher richness of functional types. Thus, heterogeneity increases the diversity of functional types, which then use different resources or use the same resources in different ways.

The seminal work of R. MacArthur related to interspecific competition in warblers in North America represented a major advance for understanding the importance of heterogeneity in the maintenance of biodiversity. MacArthur (1958) studied five different species of warblers of the genus *Dendroica* in the northeastern coniferous forests of the U.S., which are usually found together during the breeding season. The species are very similar in several aspects of their ecology such as size, shape and diet, which rendered differences permitting coexistence in the context of the

competitive exclusion theory quite elusive (MacArthur, 1958). He found that warbler species exhibit differences in the feeding position they occupy in a tree, feeding behaviour and nesting date, factors that combined with slight differences in habitat preferences and territoriality to reduce competition between them. Thus, in terms of the competitive exclusion theory, coexistence was permitted since intraspecific competition was higher than interspecific competition (Huston, 1994).

In the following years MacArthur & MacArthur (1961) and MacArthur (1964, 1965) used concepts from information theory to calculate a series of indices (H') to describe bird and plant foliage diversity (Magurran, 2004), finding a very strong and linear relationship between bird and foliage diversity in forests and deserts of the U.S. (Rosenzweig, 1995). Other studies conducted on bird diversity in Australia (Recher, 1969), Panama and Puerto Rico (MacArthur *et al.*, 1966) found very similar results; while yet others, using different measures of habitat complexity found evidence for the same relationship in lizards and rodents in the U.S. (Pianka, 1967; Rosenzweig & Winakur, 1969; Stinson, 1978). Since this early research, the same relationship has been proven extensively for other groups of terrestrial and aquatic interstitial organisms (Huston, 1994 and references therein).

At the landscape level, the environment is constituted by a mosaic of resources in patches of different types of ecosystems and/or land uses, which often vary in space and time (Huston, 1994). Under such conditions, populations are subject to higher order spatial processes and not just to the biological interactions inside each patch.

A metapopulation may be defined as a “population of populations” that is constituted by smaller units or subpopulations spread throughout a landscape and interconnected by the dispersal of individuals between them (Levins, 1969; Levin, 1976). At the landscape scale, metapopulation theory and patch dynamics constitute *ad hoc* arguments for the biological–interactions hypothesis, and play a determining role in the understanding of higher order processes governing biodiversity.

Patch dynamic theory centres on the variability and changes in conditions that make patches in the landscape suitable or unsuitable at different times for colonisation by particular organisms (Fahrig, 1992; Amarasekare & Possingham, 2001; Ellner & Fussmann, 2003; Thomas *et al.*, 2004; Wilcox *et al.*, 2006). Since heterogeneity in the environment is also produced by structural organisms (Huston, 1994), the theory offers a framework for understanding better the particular contributions that organisms make to heterogeneity at the landscape level (Pickett *et al.*, 2000). Pickett *et al.* (2000); discuss five main recent developments in patch dynamic theory contributing to a general theory of heterogeneity (Table 2.1.5.2.2).

At the beginning of the 1990's, ecologists turned their attention once more towards understanding the relationship between local and regional biodiversity and the processes generating them (Ricklefs, 1987; Cornell & Lawton, 1992; Ricklefs &

Schluter, 1993). In this context, contrary to the traditional view that biotic interactions control local biodiversity, it has been proposed that higher scale processes acting at the regional level may be more important in determining local biodiversity and not *vice versa*, since regional processes set the limits and characteristics from which local assemblages may be constituted (Caley & Schluter, 1997). Cornell & Lawton (1992), proposed that the theoretical relationship between local and regional richness may be positive and monotonic, increasing linearly (type I), or unimodal reaching a plateau after which there is no increment (type II). If the relationship is of type I, it is assumed that local communities are unsaturated and diversity is principally defined by regional diversity. In consequence, processes acting at the local scale such as biological interactions do have a minor role in defining local diversity. On the contrary, if the relationship is of type II, it is assumed that local communities are saturated and that processes acting at local scale may have a strong influence in the determination of local biodiversity.

Table 2.1.5.2.2. Main points from patch dynamics theory contributing to a general heterogeneity theory (Pickett *et al.*, 2000)

Point	Brief explanation
1) Patch dynamics are spatially explicit.	Configuration and location of patches is an important aspect that determines the overall dynamics in the landscape. In this sense, for instance, the invisibility of a particular patch may be affected by its position, size, orientation, etc.
2) Patches may have different origins.	Patches may be originated from disturbances, both natural or human induced, stress and the effects of engineering organisms. Engineering organisms are those organisms that directly or indirectly modulate the availability of resources to other organisms (Jones <i>et al.</i> , 1994).
3) Patches have complex structure.	A patch that may seem relatively homogeneous, at finer scales may be constituted by sub-patches that, at a lower hierarchical level, may present their own sub-dynamics. Moreover, boundaries are usually not strictly defined but may represent a gradation in conditions. Otherwise, in time complexity may be created by long lasting effects of a previous disturbance or from the resilience of the structural components and/or the engineering organisms in the patch.
4) Patches are not functionally isolated from their context.	Functionality of a patch depends not just on the matrix that surrounds it but also on its neighbours and their properties and dynamics.
5) Patch connectivity depends on the nature of the flux through the mosaic of which patches are part.	Connectivity between patches is not guaranteed in a simple manner by established corridors and boundaries but by the nature of the dispersal of individuals through the patches. In this sense, some approaches advancing this point have been percolation theory (Gardner <i>et al.</i> , 1989) and the consideration of the dispersion of propagules between patches in a non-uniform fashion.

It is interesting to note that different community structure models make different predictions about the saturation of local communities (*i.e.* if communities have reached its ecological equilibrium). For example, models based on niche and resource partitioning and limited dispersal capabilities may result in saturated communities, while spatio-temporal heterogeneity models tend towards non-saturated or over-saturated communities (Cornell & Lawton, 1992; Caley & Schluter, 1997). Regardless of predictions of theory, to date a large number of studies suggest that non-saturation is probably the most common state in nature (Cornell & Lawton, 1992; Caley & Schluter, 1997; Hugueny *et al.*, 1997; Heino *et al.*, 2003). Nevertheless, some empirical evidence shows that this pattern is not definitive and for some groups of plants and animals it has been found that local communities are indeed saturated (Westoby, 1985; Aho & Bush, 1993; Westoby, 1993; Srivastava, 1999; Winkler & Kampichler, 2000).

Some authors believe that methodologies implemented to test the local-regional diversity relationship are not adequate, and therefore potentially misleading. According to Hillebrand (2005), the criticisms are either statistical, associated with local *vs.* regional scale definitions or related to the effects of different local interactions at higher spatial levels. Moreover, the same author suggests abandonment of traditional regression methods and replacing them with methods including regional processes and dispersal limitations, which may be more suitable to understanding the relationship. Regarding scale, Huston (1999) considers that most of published analyses have failed to measure biodiversity at appropriate scales to detect the influence of local processes such as for instance competition. Caley & Schluter (1997) carried out a pivotal study conducted at continental level, which compared 23 different taxa of plants and animals at different scales from 2,500 km² to 250,000 km², showing a strong relationship of type I between richness at local and regional levels. Furthermore, the authors argue that spatial heterogeneity, although not explicitly assessed in their model, is the most plausible explanation for their results. Contrary to their view, Huston (1999) suggests that the scale at which local biodiversity was measured in that study is not appropriate to measure the effects of local processes on regional ones, and that their local scale aggregates sufficient environmental heterogeneity to confound the processes underlying the relationship.

A new set of ideas that correlate biodiversity to geodiversity (a measure of environmental heterogeneity) at the macroscale has arisen recently (Barthlott *et al.*, 1996; Barthlott *et al.*, 2005; Kier *et al.*, 2005; Küper *et al.*, 2006). In this context, geodiversity is defined as "...the spatial heterogeneity of atmospheric and geospheric conditions (*e.g.* petrography, soils, topography and associated climate)..." (Braun *et al.*, 2002). Thus, several authors have mapped phytodiversity at continental to global scales, refining the initial 25 centres of diversity and endemism ("hotspots") formerly acknowledged by Myers *et al.* (2000). For instance, Küper *et al.* (2005)

found that for sub-Saharan Africa their proposed “hotspots” overlap with Myers *et al.* (2000) by about 48%, while they include 10% more species and 15% more range restricted species. Furthermore, as part of their studies, they have also pointed out that all the identified “hotspots” are related to highly “geodiverse” areas. The reasoning underlying the relationship between biodiversity and geodiversity is that highly geodiverse areas promote mechanisms such as allopatric speciation, and these in turn result in high levels of biodiversity (Küper *et al.*, 2005). Among the evidence in favour of this relationship, Mutke *et al.* (2001), studying the vascular plant diversity of Africa, found a correlation between the centres of high species richness and geodiversity, and produced a first map of topodiversity. Their study also showed that biodiversity was correlated to the annual sum of NDVI, the number of dry months and the water balance. Similarly, Mutke & Barthlott (2005), studying global phytodiversity, established plant diversity was well correlated to the length of the thermal vegetation period and to water availability. More recently, Kreft & Jetz (2007) examining 1,032 regions worldwide found that plant species richness was correlated to potential evapotranspiration, the number of wet days per year and topographical and habitat heterogeneity. Furthermore, combining these variables the same authors produced a series of Simple Linear – and Generalised Linear Models to predict global plant richness, which exhibited relatively good predictive power ($\approx 65\text{--}70\%$). Their results strongly suggest that water–energy dynamics are an important control of plant species richness, and that the several hypotheses used to explain variation in species richness are not necessarily exclusive, but might interact synergistically to produce the observed distributional patterns.

2.2. The niche

Few concepts in the ecological literature are so commonly used and at the same time are so ambiguous as the “niche” concept. During nearly 100 years, it has been central in ecological research and used widely in very different contexts to address several species’ properties such as occupied habitat, function or role in a community, and minimum requirements and ecophysiological limitations. The concept also has influenced ecological thought importantly and guided the research programs of population biology and plant ecophysiology. In recent years, it has received renewed attention due to impending global climate change and its potential effects in global biodiversity. In this sense, to understand clearly the concept and its utility for modelling species geographical ranges has regained great relevance. The next sections will describe briefly the main concepts used to date, the main implications of the concept and its connection to another elusive concept – the geographical range. A deep understanding of these issues is necessary to comprehend the species range modelling undertaken here.

2.2.1. A review of the niche concept

Few ecologists would disagree concerning the important role the niche concept has played in ecology in the recent past and present (Leibold, 1995). The high proportion of publications that use the term evidences this. According to Chase & Leibold (2003), in the journal “Ecology”, during the 1960’s and 1970’s the word “niche” was mentioned in about 25% of papers published. Nonetheless, the popularization of the term and its use in different contexts had created confusion (Whittaker *et al.*, 1973).

Despite a great deal has been learnt through the extensive body of theory developed to study the concept, it remains ambiguous. Classically, the niche has been interpreted either as the habitat occupied by a species, the role of a species in a community, or the requirements (both abiotic and biotic) that a species needs to survive (Leibold, 1995). Modern revisions to the concept have tried to amalgamate those different points of view in diverse and innovative conceptual models (Vandermeer, 1972; Patten & Auble, 1981; Leibold, 1995; Chase & Leibold, 2003; Leibold & Geddes, 2005). Recently, some authors have proposed to reevaluate completely the concept and its whole implications in the ecological theory (Hubbell, 2001), while others still believe the concept may be reinterpreted in new ways leading to more robust explanations to different phenomena in the field (Chase & Leibold, 2003).

Classical concepts. Modern sources from the literature point to J. Grinnell as the first who used the term “niche” formally to refer to the habitat of the California Thrasher (*Toxostoma redivivum*) in 1917 (Brown, 1995; Leibold, 1995; Leibold & Geddes, 2005). A detailed revision of his ideas is important as a basis to understand the development of the concept from its inception. In his seminal paper Grinnell (1917) examined the “niche–relationships” of the California Thrasher. The author takes two distinct perspectives to describe the “niche–relationships” of the species. First he focuses on the factors that he believes limit the geographical range of the species and second he describes in detail the habitat preferences of the species, its behaviour and diet.

Grinnell (1917) believes two main factors control the restricted geographical range of the California Thrasher. On the one hand, “zonal” and “associational” factors (referring to habitat and habitat use), while on the other hand “faunal” factors (referring specifically to atmospheric humidity). Thus, in his paper he examines the habitat occupied by the species as a means of understanding the “critical conditions” that he expected limited the geographical range of the species. First, he refers to the close correspondence existing in the ranges occupied by the “Upper Sonoran Division (Austral Life–Zone)” and the Thrasher. Addressing in some detail locations of “chaparral”, vegetation where the species is present, and highlighting its absence from “transition” vegetation. Furthermore, he considers that to the south, the

geographical range is less sharply defined by the presence of “chaparral” vegetation and that the species may occur also in the Lower Sonoran Division, but only where “associational” factors permit. To exemplify, Grinnell lists several locations where the congeneric Leconte’s Thrasher (*Toxostoma lecontei*) is present and where in consequence the California Thrasher is absent and confined to the Upper Sonoran Division. It is interesting to note that the author considers the Leconte’s Thrasher the “associational homologue” of the California Thrasher in the Lower Sonoran Division; referring explicitly to competitive exclusion. Otherwise, regarding the zonal factors, Grinnell believes the zonal diagnosis correlates well to temperature, being the variable that ultimately controls the geographical distribution of the California Thrasher.

Furthermore, Grinnell (1917), describes in good detail the habitat preferences, behaviour and diet of the California Thrasher, and calls these “associational preferences” and “habitat relations”. According to this author, the California Thrasher is a very shy bird, strongly associated to the “chaparral” vegetation, where it forages mainly on the ground or on low bushes and branches. The species is omnivorous, which includes in its diet beetles, ants and seeds taken from the ground, and also, but not often, a few berries and seeds taken from upper levels. Its nests are usually located in dense foliage at approximately 0.5–2 m above the ground. Additionally, Grinnell (1917) in his account makes some notes on the morphology and behaviour of the species, but these are not relevant here.

In a second place, Grinnell (1917) identifies “faunal” factors as those relating to the dependence on atmospheric humidity. In this sense, he asserts the California Thrasher is present in conditions that are not extremely arid and gives a list of locations that fulfil those conditions to exemplify his point. Moreover, the author believes that, although of little importance to limit the range, the “faunal” factors are critical in defining intra-specific variation and shows how the three different geographical races of the species (*T. r. pasadenense*, *T. r. sonomae*, *T. r. redivivum*) occupy areas of different precipitation regimes.

According to Patten & Auble (1981), in that seminal publication Grinnell (1917) referred to the niche in three different ways worthy of highlight: 1) as synonym of habitat, 2) as a constituent part of a major whole, such as the community, and 3) as a unique property of the species that cannot be occupied by two species in the same community, thus leading the way to the “competitive exclusion principle” later proposed by Gause and widely attributed to this author (Gause, 1934). Additionally, in a subsequent publication Grinnell (1928) referred to the niche as “the ultimate distributional unit, within which each species is held”, which suggests the niche as a unit of geographical distribution (Patten & Auble, 1981). Although it is clear that Grinnell makes some emphasis on the geographical distribution and the habitat, I believe differently to the opinion of other authors (Vandermeer, 1972; Brown, 1995;

Leibold, 1995) that in his first publication he considers the niche is also related to function and role of the species in the community. This is evident in the second half of his paper where he describes in some detail microhabitat preferences, behaviour and diet. This view agrees with that expressed by Whittaker *et al.* (1973), according to which Grinnell referred to the term niche as a concept that merged both the ideas of habitat and niche ideas.

Contemporarily to Grinnell, the ecologist C. Elton (1927) proposed a definition of niche focusing on the role and position of the species in a community, particularly referring to its relationships to other species. This author defined niche as the “status of an animal in its community”, also referring to it as the place an animal occupies in its biotic environment, especially regarding its relations to food and enemies (Whittaker *et al.*, 1973). Patten & Auble (1981), draw attention to four main implications from Elton’s concept of niche: 1) it is equated to a role or function, 2) it is delimited in relation to the other species in the community, 3) the concept implies the niche is part of a structured system, and 4) the niche is a preset unit accomplished in different systems. The authors conclude the last two points from the fact that C. Elton considered in his book that the comparative study of niches was a useful tool to reveal common principles of organization (3), as well as to bring up the parallelism existing between niches in separated and distanced communities (4). Similarly, other authors such as Leibold (1995) believe Elton (1927) presented in his book a strong case for the niche as a “role” or “function” in the community.

The revolution. By the 1950’s, other authors developed similar concepts to that one of C. Elton, basing their definitions on the functional role of a species in a community or ecosystem. Among some of them were L.R. Dice, E.P. Odum, G.L. Clarke as well as many others (Whittaker *et al.*, 1973 and references therein). Nevertheless, the concept did not stabilise (Whittaker *et al.*, 1973), but on the contrary by the end of 1950’s the ecologist G.E. Hutchinson made a reinterpretation of the concepts in use at the time and propose some new ideas that changed the way the niche was seen in the field.

Thus, G.E. Hutchinson (1957, 1978) defined first an environmental hyperspace of n -dimensions both abiotic and biotic, which represent all variables limiting existence of a species, that is variables that because of the species particular genotypic and phenotypic traits limit its survival and reproduction. Secondly, the set of points given by the coordinates in which a species may be found can be used to draw up the boundaries of an imaginary hypervolume of n - dimensions of environmental conditions and resources within which a species may survive and reproduce or persist indefinitely in the absence of competition. Hutchinson called this hypervolume the “fundamental niche”. Otherwise, very often, a species cannot occupy the whole volume delimited by the “fundamental niche” and may be excluded from some

portions because of competition. In such cases, Hutchinson called the remnant volume “the realised niche”.

Whittaker *et al.* (1973) brought into attention three points worthy of mention here from the seminal “concluding remarks” paper of Hutchinson in 1957, from where the hypervolume niche concept was derived: 1) within the hypervolume defining the niche there is a differential probability of survival, presenting an optimum in some region and suboptimum values near the boundaries, 2) the hypervolume assumes a linear ordering of all environmental variables affecting the species, which is impossible in practice, and 3) the concept represents a snapshot in time and consequently the consideration of time as another variable is important in defining the niche, such as for example for species similar in other variables but differing in the time during which they are active (*e.g.* day and night, alternating each other, *etc.*).

The “fundamental niche” and the “realised niche” are properties of different levels or hierarchies of biological organisation *sensu* Noss (1990). In this sense, it is important to highlight first that the niche is a biological property and not a property of the environment, and therefore the idea of a “void niche space” or “niches to fill” in the environment is not correct (Brown, 1995). Otherwise, the “fundamental niche” constitutes a unique property of the taxon involved, which is defined by the genotypic and phenotypic traits that determine the taxon physiology, tolerances, *etc.*, when exposed to particular conditions that it may or may not experience (Patten & Aule, 1981). The “realised niche” constitutes a unique property of the community or the ecosystem, which is defined by the genotypic and phenotypic traits that determine each taxon’s behavioural responses, life history strategies, *etc.*, when exposed to the biological interactions occurring between them in their own ecosystem (Patten & Aule, 1981).

Agreeing with Whittaker *et al.* (1973) the Hutchinsonian concept of niche merges both habitat and niche ideas. On the one hand, the “fundamental niche” is defined by limiting factors and ecological requirements (Leibold, 1995), which are mostly abiotic and that clearly have very specific spatial connotations. According to Whittaker *et al.* (1973 and references therein), Hutchinson was not the first to use the multidimensional definition of the habitat and other authors including himself and others already had used different techniques for this purpose, among those applying population measurements to define the habitat of different species. On the other hand, the niche concept that is well rooted in the Malthusian law of population growth and in Gause’s competitive exclusion principle (Brown, 1995), was developed by Hutchinson in the context of explaining the ecological requirements of species as well as their coexistence within biotopes perceived as “relatively homogeneous” (Whittaker *et al.*, 1973). As consequence Hutchinson gave a disproportionate importance to competition as the only biological interaction included in his concept,

as other authors have highlighted (Leibold, 1995; Chase & Leibold, 2003). In that sense, according to Whittaker *et al.* (1973) the most important contribution of Hutchinson concept lies in the fact that it applies the multidimensional view to explain the coexistence of taxa within biotopes and diversity in ecosystems. In addition, it is particularly interesting to note that from Hutchinson's concept emerge two possible states to the niche: one state defined by limiting environmental factors and *a priori* to any biological interaction and a second state, *a posteriori*, accomplished after biological interactions have been completed. Vandermeer (1972) called those states pre-interactive and post-interactive and believes this differentiation was possibly Hutchinson's major contribution to the field.

Although the value of the Hutchinsonian niche concept been accepted for long time, as is expected the concept is not applicable and universal to all sorts of ecological situations, and therefore there are several criticisms made of it. As highlighted before, the niche is a property of the species (Brown, 1995), the operative taxonomic unit (OTU) for Vandermeer (1972), or the operative biological hierarchy (OBH). Moreover, if we consider that each one of the environmental variables, factors or dimensions limiting the niche potentially represent a filter of natural selection, the most important contribution of the concept lies probably in the fact that it provides means of formalising the relationships between those filters and any microevolutionary changes affecting the niche (Brown, 1995). The concept possesses high heuristic value, although many researchers still debate its utility in practical situations, because of the difficulty in capturing and measuring all variables affecting the persistence of a species in space-time (Brown, 1995).

Furthermore, Whittaker *et al.* (1973) considers that the use of the niche concept *sensu* Hutchinson confuses both habitat and niche ideas, leaving undefined one of the most important concepts in community theory and makes no differentiation between processes happening inside communities *vs.* between them. In that context, these authors mention at least four undesired consequences of a concept merging both features (habitat+niche): 1) it obscures the importance of the niche as "role" or "function", and thus as an aspect of community organisation; 2) it alters the central ecological idea of niches being adaptive responses to competitive interactions at the interior of communities and the competitive exclusion principle (Gause, 1934), since a) it raises the possibility of coexistence of species that have different habitat+niche but cannot coexist in the same community because have the same niche, and b) it raises the possibility of related species with different niches that may have also different habitat and therefore have not met ever in the same community and had competitive interactions; 3) evolutionary relationships and consequences resulting from different processes are merged and confused, such as for example α and β diversity, which result from adaptation to biological interactions inside the community and as a response of different communities to habitat gradients, respectively; and 4) creates

semantic and operative confusion in measuring different intra- and inter-community properties, such as niche breadth and habitat amplitude, which sometimes have been defined and measured as interchangeable by some authors, when in reality they represent different attributes.

Patten & Auble (1981), considers the Hutchinsonian niche concept loses generality and also is unrealistic because it is non-dynamic. According to those authors, the concept loses generality in a systems framework because it does not include non-living subsystems and limits the definition to one viability criteria for the populations (*i.e.* persistence), while other viability criteria may be useful in other circumstances such as for example biological fitness. Additionally, it is clear that being a biological property the niche is not static, but dynamic, changing over time (Brown, 1995), limiting its explanatory power regarding microevolutionary processes.

The Hutchinsonian niche concept revitalised research programmes in plant and animal ecology and the way old ecological questions were seen. Since times of A. Von Humboldt and A. Bonpland, in their “Essai Sur la Geographie des Plantes” published in 1807, naturalists have realised the correspondence existing between physical conditions and the distribution of life (Huston, 1994). Also, A.P. De Candolle in his “Essai Elementaire de Geographie Botanique” recognised the study of the spatial distribution of plants as part of plant physiology, as well as the connection existing between the present ranges of plants and external environmental factors (De Candolle, 1820). Nonetheless, during that time early ecologist and biogeographers were more interested in describing the range of life forms than in understanding the environmental factors delimiting those. Near the end of the 19th century, in 1896 the publications of “Lehrbuch der Okologischen Pflanzengeographie” by E. Warming and the “Deutschlands Pflanzengeographie” by O. Drude were the first to explore the physiological relations between plants and their environment and also the biotic interactions inside the assemblages described and classified by earlier plant geographers (Jax, 2001). In the early 19th century, in animal ecology the publications of J. Grinnell and C. Elton, mentioned previously, were dealing with different aspects of niche relationships either focusing on factors defining habitat or the role of a species in a community. However, from that point and just prior to Hutchinson (1957), still the interaction between both was not clear and the definition of niche not very intuitive (Maguire, 1973). In that sense, the Hutchinsonian concept made a bridge between both viewpoints when defining the “fundamental niche” based on requirements and the “realised niche” based on biological interactions. That permitted the reformulation of old ecological questions trying to examine aspects of the relation between an organism, the abiotic environment, and other organisms this time focussing on the organism (Maguire, 1973).

Brown (1995), similarly to Hutchinson (1957), recognises the difficulties in assessing thoroughly the niche of a species. However, he believes that answering some of the following questions can help: 1) why the species is restricted to certain habitats or regions?, 2) why the abundance of the species varies over space–time?, and 3) how many and which environmental factors impose the primary limits to the range and define the abundance of the species?, do these affect equally all stages of its life history? In answering those questions, physiological ecologists have been successful in studying factors that limiting the survival and reproduction of organisms and thus the physical conditions that limit their ranges.

Continuing with the strong legacy of the competitive exclusion principle (Gause, 1934, 1935) and rooted in Hutchinson's niche concept and Lotka–Volterra models (Lotka, 1925; Volterra, 1926), MacArthur, Levins and others designed a series of field experiments and theoretical models to investigate the factors that permitted coexistence, the maximum number of coexisting species and also the maximum possible similarity within species in a given community (MacArthur, 1958; MacArthur & Levins, 1967; MacArthur, 1972). This led to the development of related concepts such as niche breath, niche partitioning, niche overlap, and niche assembly, as well as much research directed towards measuring those properties in natural communities (Chase & Leibold, 2003 and references therein).

Modern concepts and synthesis. Recently, several authors have reviewed the Hutchinsonian concept and proposed re–interpretations of it. For example, in the early 1970's, Vandermeer (1972) proposed a dynamic theoretical framework, in which the environment modify populations and *vice versa*, which is a more realistic framework than the original concept. The author also extended the ideas of the fundamental and realised niches proposing the idea of “partial niches” that lie in a continuum from the fundamental niche to the partial niche. He also discusses environmental grain and the way organisms move between different habitats, niche breath and populations' response in different habitats, as well as the possible “shapes” that a niche may have and its implications.

Other authors such as Whittaker *et al.* (1973), as mentioned before, criticised the concept on the grounds that it merges ideas of both habitat and niche, confusing intra– and intercommunity properties and the mechanisms operating on each. In the same publication, they suggest decoupling both ideas from the concept, keeping niche to indicate the role of a species in a community and propose the term “ecotope” to indicate both habitat+niche, apparently used at the time as equivalent of habitat, biotope, microlandscape, and biocenose. On the other hand, although the authors do not see major problems in interchangeably using the terms habitat and biotope, they state that is preferable to follow Udvardy (1959) and apply habitat to refer to the environment of the species, while biotope to the environment of the community. The

major points that summarise their view are the following: 1) the habitat of a species is an imaginary hypervolume of m - dimensions of environmental abiotic conditions; 2) the niche is an imaginary hypervolume of n - dimensions of environmental biotic conditions in a community, n' - when applied for all communities in a landscape; 3) the “ecotope” of a species is an imaginary hypervolume of $m + n'$ - dimensions that make part of an $m + n'$ - dimensional hyperspace of environmental abiotic and biotic conditions combined; 4) habitat, niche and “ecotope” may be described based on the species’ populations response to the particular conditions within each hypervolume, expressing them as a population measure; and 5) habitat, niche and “ecotope” are complementary concepts that can be visualised as part of a simplified three-dimensional system, in which habitat and niche are axes, the “ecotope” is the plane formed by them and the population measure define a third axis (Figure 2.2.1.1).

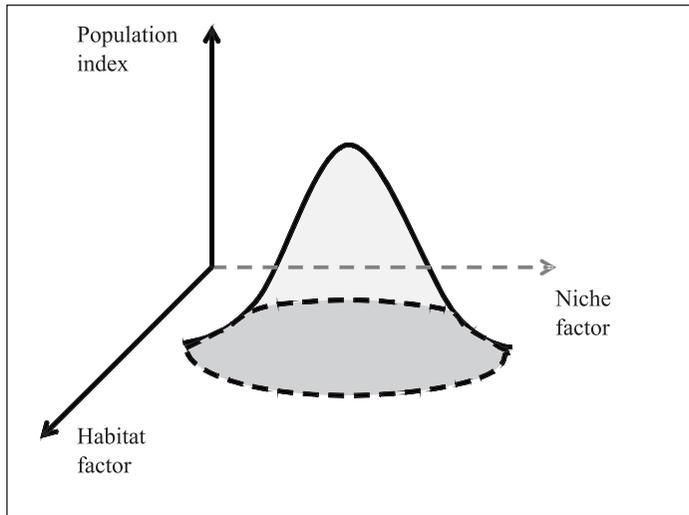


Figure 2.2.1.1. Representation of the ecotope and its relations to habitat and niche, for explanation see text (after Whittaker *et al.*, 1973).

In a different approach, Maguire (1973) reflects on the Hutchinsonian concept from a systems theory point of view. In his opinion, any type of system has a response (*i.e.* change, dissolution) to each possible combination of conditions in its own environment. In this context, the niche is defined as the “genetically (evolutionary) determined capacity (range of tolerance) and pattern of biological response of and individual, a species’ population, or the whole species to environmental conditions.” The author defines different patterned responses depending on the biological hierarchy studied. Thus, for instance, for an individual some possible responses are

in terms of growth rate, maturation rate, potential reproductive capacity, fitness, territorial establishment, dispersal and migration, home range and activity, *etc.* For a population, some possible responses are birth, death, and growth rates, type and magnitude of effects on the environment such as depletion of resources, production of metabolites, *etc.* For species, one possible response is the geographical variation in population responses. Finally, the relationship between patterned response and the environment may be applied to study other ecological and evolutionary processes such as population growth, competition, prey–predator dynamics, succession, geographic variation, population genetics and adaptation, among others.

Leibold and collaborators (Leibold, 1995; Chase & Leibold, 2003; Leibold & Geddes, 2005), have reinterpreted the Hutchinsonian niche concept elaborating further on Maguire’s (1973) ideas. They believe the concept should make explicit reference to the response of the organisms to their environment and the effect they exert upon it. In that sense, they define two different components of the niche: “requirements” and “impacts”, in which the authors believe, it is possible to synthesise most of previous approaches. They identify as “requirements” all limiting environmental factors, both abiotic such as temperature, salinity, *pH*, *etc.*, and biotic such as specific resources, resource levels, *etc.* On the other hand, as “impacts” are included all the effects that organisms produce on other organisms and the abiotic environment such as for example, competition, predation, resource depletion, production of metabolites, *etc.* Agreeing with the authors, the first component embraces the Grinnellian niche and the Hutchinsonian “fundamental” niche concepts, while the second is compatible with the Eltonian niche and the Hutchinsonian “realised” niche concepts, as well as with the niche concept used by R. MacArthur and collaborators.

Chase and Leibold (2003) define the niche in two ways. First, the niche is “the joint description of the environmental conditions that allow a species to satisfy its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of *per capita* effects of that species on these environmental conditions.” Second, the niche is “the joint description of the zero net growth isocline (ZNGI) of an organism along with the impact vectors on that ZNGI in the multivariate space defined by the set of environmental factors that are present.” The authors consider the first definition merges both historical concepts and it is used as a pivotal point to produce the second definition, which is made operational through several mechanistic models to study a wide array of ecological phenomena building further from work developed by Leibold (1995).

2.2.2. Implications of the niche concept

As we saw previously the niche concept has had a central role in the development of both ecology and biogeography and, broadly speaking, there are three main areas

of interest in which the niche concept has been fundamental in explaining observed patterns (Brown, 1995). The first is related to the limits of geographical species ranges, the second to geographic patterns of diversity and the third to the role of the environment on macroevolutionary processes. It is interesting to highlight that those different implications are focused on different niche concepts. The first is inclined towards the habitat and/or the habitat+niche concepts, which corresponds to the Grinnellian and Hutchinsonian niche concepts. The second and the third focus more on the niche as a role in the community that corresponds more to the Eltonian niche concept.

The limits to the geographical range of any species are expected to occur where there is a particular combination of ecological factors that lie out of the species niche hypervolume, under which the species may not survive or sustain a population. In this sense, the particular combination of abiotic and biotic factors found in those sites may reduce survival or reproduction, preventing the establishment of individuals and the viability of populations (Brown, 1995). Abiotic factors, such as climate, impose limitations on species ranges and control their geographical spread. Especially for vegetation, there is a good deal of empirical evidence supporting the importance of climate in defining range limits at high latitudes; particularly in terms of how low temperature affects on survival (Woodward, 1987). Physiological stress diverts metabolic energy that may be used in reproduction towards survival, reducing competitive abilities and overall fitness (Woodward, 1987). Otherwise, the presence of some species in areas with extreme conditions may indicate either that the phenotypes have a certain degree of plasticity to tolerate extreme conditions or that the organisms have developed special adaptations to deal with them (MacArthur, 1972). This is true for example, for the Frailejon (*Espeletia* spp. and *Espeletopsis* spp.) and the giant African rosettes (*Lobelia* spp. and *Dendrosenecio* spp.) in tropical regions, as well as some other Paramo and Alpine types of vegetation, which have special morphological and physiological adaptations to resist low-freezing temperatures as well as cacti (Family Cactacea) and other desert and desert-scrub type vegetation in subtropical regions, which have special adaptations to resist low-moisture conditions.

Nevertheless, climate alone cannot account for limits in geographical ranges. A particular good example of this are the many exotic species transplanted successfully between continents where originally they were absent (Brown, 1995). As we move towards the equator temperatures increase, becoming in this sense less and less a limiting factor for geographical spread (Woodward, 1987) and this suggests that at these latitudes besides climate, other factors also might be involved in determining ranges boundaries. Particularly for plants, other abiotic factors such as soil may have a strong influence. Otherwise, biological interactions and especially competition and competitive exclusion have been considered the key factors involved in determining

range boundaries in the tropics (MacArthur, 1972 and references therein). More recently other mechanisms such as the “mass effect”, the “rescue effect” and “metapopulations dynamics” have been invoked to explain how population dynamics may affect species range boundaries (Gaston & Blackburn, 2000). Otherwise, besides ecological factors, historical factors may have influence in determining geographical range limits. This is especially true for the effect of physical barriers on geographical spread. Thus, when a physical barrier has prevented a species from a potential habitable area, current ranges can also be the result of past geologic and oceanographic conditions (Brown, 1995).

From a classical view, the boundary of a geographical range may shift given two cases (Brown, 1995). In the first case, the boundary may move if a particular unsuitable combination of ecological factors in a site or several sites changes and becomes inside the species niche hypervolume. While in the second case, the boundary may move if the species niche hypervolume evolves in a direction in which it embraces a new or several new combinations of ecological factors, unsuitable previously for the species. There are a third and a fourth possibilities in which a species may move its range boundaries, but these are not considered by Brown (1995). In the third, similarly to the first case, the niche is considered non–dynamic. However, differently in this case the boundary may move if a particular suitable combination of ecological factors in a site or several sites changes and become outside the species niche hypervolume. Finally, in the fourth as in the second case the niche is considered dynamic. Nonetheless, in this case the boundary may move if the species niche hypervolume evolves in a direction in which it excludes a particular or several combinations of ecological factors, suitable in the past for the species.

Nevertheless, the definition of the boundaries of the niche and its projection on the boundaries of the geographical range is not as straightforward as it seems at first glance. According to MacArthur (1972) one option is to define the boundary in the farthest point where an individual has been recorded in a particular direction. However, that approach can have several caveats, mainly because individuals may be present also in areas with conditions that lie out of their usual range for different reasons, such as for example vagrants. Another option presented by the same author is to define the boundary in the farthest point where a reproductive population or colony is recorded. Nonetheless, this definition has the problem that any population may go extinct at any point by pure chance, climatic change or random extreme events, and therefore not be included. A final option offered is to define the boundary in the farthest point where there is a drastic reduction on the abundance or density of the species, such as for instance when the abundance or density goes below $1/20^{\text{th}}$ of the maximum values. This final approach has the problem that it is extremely subjective. Furthermore, the literature is not clear about what is understood by geographical range and its

size (Gaston & Blackburn, 2000). According to Gaston (1991, 1994), there are two general ways in which the geographical range of a species can be defined: “extent of occurrence” and “area of occupancy”. The “extent of occurrence” corresponds to the area that embraces the farthest points of occurrence of the species. Nonetheless, species occupancy of its “extent of occurrence” is not continuous in space–time due to pure chance, local extinctions, vagrant individuals and biological interactions (*e.g.* competition), which can prevent a species from occupying the whole extent. Thus, the “area of occupancy” corresponds to the area over which the species is actually present. Geographical ranges presented in field guides usually represent “extent of occurrence”, while ranges presented in more detailed atlases represent often the “area of occupancy” (Gaston & Blackburn, 2000). Both “extent of occurrence” and “area of occupancy” are influenced by different factors and are dynamic changing in space and time. The “extent of occurrence” fluctuates as the species’ niche boundaries and its projection on range limits change, while the “area of occupancy” fluctuates as species’ populations colonise new areas or become locally extinct in others (Gaston & Blackburn, 2000).

Several authors believe current geographic patterns of diversity reflect current environmental conditions as well as the earth past history (Rosenzweig, 1995). Brown (1995), suggests that a high α diversity reflects current conditions that satisfy the niche requirements of many species, as well as evidence the existence of past conditions that permitted high levels of immigration/colonisation and speciation. On the other hand, high β diversity and consequently high turnover rates indicate high rates of environmental variation. As another example, MacArthur & Levins (1967) and MacArthur (1972) developed a theory of diversity based on the idea that coexistence of species is defined by the maximum limits of similarity of the niche set between competing species. Similarly, other explanations based on biological interactions refer to the niche as for example the stabilising coevolution hypothesis, according to which natural selection favours niche divergence within a continued process of coevolution in a community, where the assembled species exhibit balanced competitive abilities (Pimentel, 1968; Aarssen, 1983, 1985).

As mentioned before, massive changes in environmental conditions may conduce to succession processes over long periods (see section 2.1.4.4). These changes may be produced by catastrophic events, which cause massive extinctions such as for example volcanism and extraterrestrial impacts, or being the result of regular events such as the expansion and retreat of ice sheets during glacial and interglacial periods. Under those massive modifications, populations of existing taxa may go extinct completely or colonise and become locally extinct in different areas of their geographical ranges according to the variation in the environmental conditions. Leading to cycles of extinction and radiation, and thus to an exchange in taxon assemblages at higher scales in space and time (Rosenzweig, 1995).

2.2.3. *Niche modelling*

Despite the general limitations of secondary sources of information (see Chapter 3, section 3.2.2 and Chapter 4, section 4.1), museum specimen records have been increasingly used to model species geographical ranges. Thus, a wide array of different types of algorithms and modelling techniques using either presence-only or presence-absence records has been used in the last 20 years to investigate different questions in ecology and biogeography. Some examples of the most commonly used techniques in the literature are for instance BIOCLIM (Nix, 1986), DOMAIN (Carpenter *et al.*, 1993), GARP (Stockwell & Noble, 1992; Anderson *et al.*, 2002a; Anderson *et al.*, 2002b; Stockwell & Peterson, 2002; Anderson *et al.*, 2003), MAXENT (Dudik *et al.*, 2004; Phillips *et al.*, 2004; Phillips *et al.*, 2006), and Logistic Generalised Linear Models (GLM) and General Additive Models (GAMs) implemented in GRASP (Pearce & Ferrier, 2000; Guisan *et al.*, 2002; Lehmann *et al.*, 2002, 2003), *etc.* Among those methodologies, the Genetic Algorithm for Rule Set Prediction “GARP” is the most extensively used. For example, it has been used to test the theory of niche conservatism in evolutionary time for several groups of animals (Peterson *et al.*, 1999), predict change in animal distribution due to climate change in Mexico (Peterson *et al.*, 2001a; Peterson *et al.*, 2002; Parra-Olea *et al.*, 2005), to test competitive exclusion and competitive release in mice in northern South America (Anderson *et al.*, 2002b), and assess possible routes and areas that invasive species may occupy (Soberon *et al.*, 2001; Peterson, 2003; Peterson *et al.*, 2003; Soberon & Peterson, 2004), among other subjects. Additionally, it has been applied to prioritise biodiversity inventory (Soberon *et al.*, 2003) and conservation areas selection (Chen & Peterson, 2002; Velasquez-Tibata & Lopez-Arevalo, 2006; Martinez-Meyer *et al.*, 2007).

However, more recently some newly developed techniques have shown better results than previously “traditional” approaches. Elith *et al.* (2006) provide the most complete comparison to date, using 16 different methods to model geographical ranges of 226 species in six regions of the world, demonstrating better performance of some novel community models and machine-learning techniques over relatively well-established methodologies such as BIOCLIM and GARP. The best performing novel models include methodologies such as Multivariate Adaptive Regression Splines – Communities (MARS-COMM), Boosted regression Trees (BRT), Generalised Dissimilarity Models – Species (GDM-SS) and Maximum Entropy (MAXENT), with mean AUC statistic (Area Under the Curve statistic estimated from the Receiver Operating Characteristic plot) values higher than 0.72, while techniques such as BIOCLIM and GARP exhibited mean AUC values lower than 0.69. Moreover, although in general terms a reduction in model performance with reduction in sample sizes for different modelling techniques has been proven

(Peterson & Cohoon, 1999; Dudik *et al.*, 2004), MAXENT proved to make good predictions with even few presence records. Thus, Pearson *et al.* (2007) studying the geographical range of several species of endemic geckos in Madagascar showed that MAXENT still performs well with samples as small as 5 presence localities, which is half of the number of localities reported previously for GARP to obtain accurate predictions near 90% (Stockwell & Peterson, 2002). This consideration may be particularly important, as demonstrated in the case of the bird atlas of Mexico and the analyses performed by Stockwell & Peterson (2002) using GARP. Pearson *et al.* (2007) highlight that if analyses would have been performed using a modelling methodology such as MAXENT instead of GARP, the number of modelled species would augment in about 23%, representing nearly 88% of the total bird species from Mexico.

MAXENT is a general methodology based on the Maximum Entropy Principle developed by Jaynes in 1957, according to which a unique probability distribution, indicating the suitability of any particular combination of environmental variables, is estimated from incomplete information, assuming that the least biased distribution is the one that maximises information entropy (Jaynes, 2003). This concept has been introduced recently to habitat suitability and niche modelling using presence-only data, obtaining promising results and showing a better performance compared to other modelling techniques, as mentioned earlier (Elith* *et al.*, 2006; Phillips *et al.*, 2006). In this sense, having a space X (*i.e.* study area) and some features f that characterise each point x in X (*i.e.* geovariables), MAXENT estimates the maximum entropy (H) of the probability distribution (p) as $H(p) = -\sum_{x \in X} p(x) \ln p(x)$, that represents the most uniform distribution, based on the assumption that the empirical average, throughout a total of m points ($x_1, x_2, x_3, \dots, x_m$) sampled from X , for each evaluated feature f_j is close to the expected value under the estimated distribution – *i.e.* $\tilde{p}[f_j] = \hat{p}[f_j] = \frac{1}{m} \sum_{i=1}^m f_j(x_i)$ (Phillips *et al.*, 2004).

It is interesting to note that much of the confusion generated in relation to the niche concept seems to have permeated the field of niche modelling. In that sense, it is noticeable in the literature how several techniques addressing similar questions in ecology and biogeography have received different names such as habitat suitability/selection models, habitat/species distribution models, resource selection functions, ecological niche models and gradient analyses, among others (Hirzel & Le Lay, 2008 and references therein). Also, regardless of the evident connection with the niche concept and niche theory, most models produced using these techniques have been poorly connected to the main body of theory (Guisan & Thuiller, 2005; Hirzel & Le Lay, 2008). Several conceptual ambiguities as well as uncertainties in both data used and methodologies remain (Araujo & Guisan, 2006).

Araujo & Guisan (2006), consider that there are several challenges in the field of species distribution modelling that need to be addressed in order to increase certainty in model results. Among them are to clarify the niche concept and to improve the modelling process in general. Aiming for better sampling design for data, more complete model parameterisation and evaluation using independent datasets, and an enhanced selection of best predictors and models. They believe that although in general terms most modellers will interpret their work within the Hutchinsonian niche concept, the true meaning of results and what the models really represent is still disputed. Thus, while some authors consider their models as a representation of the fundamental niche, others believe they are a representation of the realised niche. Araujo & Guisan (2006) think the disagreement has its cause in Hutchinson's original formulation of both niche concepts. In that sense, they criticise the excessive importance given to competition and the exclusion of other interactions in defining the realised niche of a species. Furthermore, they suggest that the differentiation between both niche types for modelling is not necessary, and propose the adoption of a Grinnellian view of the niche as a solution.

Other authors such as Hirzel & Le Lay (2008) although seeing models as linked with the niche concept and niche theory use the name "habitat suitability models" rather than "niche models", which in my opinion is more appropriate. The niche concept relates the environment to the fitness of a species, while the "habitat suitability models" relate the environment to the probability of occurrence of a species. Moreover, they found that most of the literature related to "habitat suitability models" has contributed to unravelling niche characteristics, although other related subjects such as niche interaction, community processes and niche evolution is increasing in importance for research. Thus, if we assume niche characteristics and ecological requirements of species are parallel, we can suggest as an extension that most of these studies adhere to the definition of the Grinnellian niche or the Hutchinsonian fundamental niche. Under the usual scale at which "habitat suitability models" work (1–50/ km), that fact may represent at least two advantages for models developed within that framework. First, it avoids clashes with the competitive exclusion principle, since coexistence may be allowed by environmental heterogeneity in space–time (Araujo & Guisan, 2006). Second, it offers better agreement between the mechanisms and processes studied and the scales used. Since biological interactions occurring under the Eltonian niche and realised niche concepts tend to exert their effects at more local scales, centred on the community, scales at which "habitat suitability models" are produced are not adequate to study those particular community properties (Hirzel & Le Lay, 2008).

These arguments firmly suggest that most models produced under the umbrella of "niche models" are definitely not niche models but habitat models. First, most of

them do not investigate or produce as results relationships between the environment and measurements of fitness or reproductive capacities or other estimators of similar population properties. Second, agreeing with Whittaker *et al.* (1973), both the Grinnellian niche and the Hutchinsonian fundamental niche concepts are related to the habitat, which puts models and results produced under those views as models of the habitat hypervolume (*sensu* Whittaker *et al.*, 1973). On the other hand, some authors argue models are representations of the Hutchinsonian realised niche, since datasets used to generate models are taken from ranges that are constrained by non-climatic factors too (Araujo & Pearson, 2005; Araujo & Guisan, 2006). However, species are not unequivocally present in adequate habitats or absent from unsuitable ones as consequence of biotic factors such as competition, and patterns in area occupancy may change depending on dispersal capabilities and metapopulations dynamics (Pulliam, 2000). Furthermore, models may represent the Eltonian niche or the Hutchinsonian realised niches only in applications where they explicitly address the role of the species in the community and the interactions with other taxa, which most techniques fail to do. In general, niche theory and habitat suitability modelling will be better served by making a clear separation of concepts and regarding models produced within this framework as related to the habitat hypervolume, and only to the niche hypervolume if the roles and interactions between species are explicitly stated in models.

Despite of the advance reached in novel habitat suitability and niche modelling techniques, their applicability is still geographically limited. Thus, for birds, these models continue being applied at national or regional level and most studies researching biodiversity at global scales have used as an input geographical ranges representing the extent of occurrence (Orme *et al.*, 2005; Orme *et al.*, 2006; Storch *et al.*, 2006; Davies *et al.*, 2007a; Davies *et al.*, 2007b; Gaston *et al.*, 2007; Olson *et al.*, 2009). Furthermore, the lack of explicit modelling of some processes such as dispersal, population dynamics in the edges of ranges, biotic interactions and the relationships between the effects of land use and climate change still constitute significant challenges in habitat suitability and niche modelling (Thuiller *et al.*, 2008).

At national level in Colombia, biodiversity has been studied increasingly using GIS and habitat suitability and niche modelling approaches during the last 10 years. Moreno-Ballesteros (2000) used geographical ranges obtained from Hilty & Brown (2001) and GIS to study bird richness and rarity spatial distribution and its environmental correlates. Similarly, Verhelst (2004) studied bird richness spatial distribution and its environmental correlates using GIS, but instead of range maps used secondary museum information from the first versions of the Darwin–Hernandez Database (see Chapter 1, section 1.3.4). On the other hand, Jarvis (2005) using GIS studied the controls on tree species diversity in lowland and montane forest, while Armenteras

(2003) developed a climatic envelope technique to model habitat suitability based on Mahalanobis distances as a proxy to study tree distribution in the country with a selection of three species. More recently, novel machine learning techniques such as GARP and MAXENT have been used in research related to the definition of conservation priorities in parrots – Family Psittacidae – (Velasquez–Tibata & Lopez–Arevalo, 2006) and in studying the factors involved in determining range limits in the Andes for 70 range restricted bird species (Graham *et al.*, 2010).

CHAPTER 3
STUDY REGION AND METHODOLOGY

Summary – This chapter has two main parts, in a first section, the main features of topography, climate and vegetation for each geographical region of Colombia are described as a framework to understanding the general conditions in which bird diversity exists in the country. In a second section, the chapter describes the general methodological strategy used in the whole thesis and gives a brief account of the datasets and analyses used to model and explore bird diversity distribution in the country using the Darwin–Hernandez Database produced by Project BioMap. Colombia is usually divided in five main geographical regions that reflect very marked differences in topography, climate and culture. Topography and climate in the northern and western parts of the country is complex, while in the east and southeast it is relative flat and homogeneous. In this particular study, bird diversity was modelled as taxa richness from a significantly improved Darwin–Hernandez Database at family and genus hierarchies using two approaches. First, using DIVA–GIS point–to–grid tools, richness was estimated as simple counts of taxa at different grain sizes. Second, richness was estimated overlapping habitat suitability models (at ≈ 1 km resolution) produced for all taxa using MAXENT. A great deal of effort was put into producing improved and filtered versions of the Darwin–Hernandez Database retaining the most accurate georeferences. For this purpose, the whole list of site localities and coordinates was revised carefully several times to correct errors in georeferencing. In addition, the uncertainty attached to each georeference was estimated. Thus, all records with localities holding low precision georeferences were filtered out from the database. All taxa available with more than 5 localities were modelled, and for taxa with more than 15 localities model performance evaluated using 30% of available data to estimate the AUC statistic; other parameters were set to default values. Furthermore, to produce habitat suitability models, heavily collected areas in the country were resampled to reduce sampling effort bias. Thus, grid cells (≈ 120 km in dimension) with a density of localities higher than 60 sites were resampled at random to a maximum of 70 localities, with further data excluded. A first series of correlation analyses between richness and effort were produced using Equal Elevation Interval Bands (EEIBs) and later Approximate Equal Surface Interval Bands (AEQSIBs), which permitted the elimination of both effort bias and the richness–surface area relationships to understand better changes in bird

diversity with elevation in Colombia. Finally, methodologies that offered the best results were fine-tuned to make final predictions of bird diversity distribution under current climatic conditions, and generate projections under future climate-change scenarios. At this point, georeferencing was again revised and corrected, with special emphasis on rivers and streams, and producing new estimates of error. Thus, two new filtered datasets were generated: one dataset holding accessions with high precision georeferencing, and a second dataset extracted from the first one retaining just accessions collected after the year 1950 inclusive. The second generation of habitat suitability modelling exercises used a three-factor ANOVA experiment to test the effect of training sample size, number of replicates and grain size on model performance. Results were used to define criteria which were then used to run final habitat suitability modelling exercises (25 replicates each time at 3 km resolution) for family and genus taxonomic levels for all taxa available and at species hierarchy for hummingbirds (family Trochilidae) and tyrant flycatchers (family Tyrannidae). All taxa available with more than 5 localities were modelled, and for taxa with more than 12 localities model performance was evaluated using 30% of available data to estimate the AUC statistic; other parameters were set to default values. Presence/absence potential geographical ranges were generated from models using the “equal test sensitivity and specificity” logistic probability threshold, and consensus maps were produced based on models exhibiting the highest accuracy. Furthermore, other biodiversity measures such as the “weighted endemism score” were estimated, and to advance knowledge on functional diversity distribution in the country two new indices of ecomorphological diversity were proposed, and tested for hummingbirds and tyrant flycatchers. All richness maps were cross-validated using independent data obtained from field surveys conducted by ProAves Colombia (<http://www.proaves.org>) and with the “Western Hemisphere Digital Bird Distribution Database” (<http://www.natureserve.org/getData/birdMaps.jsp>). Finally, consensus potential ranges derived from model projections for future climate scenarios produced by the HadCM3 climate model were used to predict potential refugia of bird diversity given future climate-change conditions for different subsets of the Colombian avifauna, and to evaluate how the Protected Areas National System (SINAP) captures projected refugia.

3.1. Study region

3.1.1. Bird diversity

Colombia is widely recognised as one of the richest countries in the world in terms of bird diversity (Stiles, 1998). In the country 1,869 bird species have been registered to present, representing about 19% of the world bird diversity (Hernandez-Camacho,

1993; Salaman *et al.*, 2007b), and distributed among 690 different genera and 90 different families. The best-represented families in terms of species in the country are: Flycatchers, Tyrannidae (204); Hummingbirds, Trochilidae (162); Tanagers, Thraupidae (130), Typical Antbirds, Thamnophilidae (110); Ovenbirds, Spinetails and Woodcreepers, Furnariidae (109); and Emberizid Finches and Sparrows, Emberizidae (60). This high diversity is not equally distributed among the different natural regions in the country (Salaman *et al.*, 2007b). Thus, the Caribbean is the region with most species (711 species), followed by the Amazon (674 species), the Andes (650 species), the Pacific (539 species) and finally the Orinoco (420 species). Furthermore, it is worthy to mention that nearly 87% of the species are linked to forested habitats (humid forests: $\approx 77\%$ and dry forests: $\approx 11\%$), mainly in the lowlands below 1,000 m (Table 3.1.1.1) (Salaman *et al.*, 2007b).

Seventy species are recognised as endemic (range-restricted endemic) to the country, meanwhile 96 more are considered range-restricted species for which part of their distribution is shared with a second or a third country (Stiles, 1998; Salaman *et al.*, 2007b). Those species are distributed into 23 areas of endemism (Stiles, 1998). In this sense, the most important areas for endemics are the Sierra Nevada the Santa Marta (14 endemic species), followed by the Eastern Cordillera (11 endemic species), and the Pacific Slope and the Caribbean including the mid Magdalena valley (9 endemic species in each region). Moreover, four species are restricted to the high Magdalena valley, three to the Central Cordillera and just one to the Amazon. Otherwise, when considering range-restricted species the Pacific Slope is the most important region (46 range-restricted species), while the other regions show smaller numbers (Stiles, 1998).

Although birds are one of the best well-known biological groups in the country, still their diversity has not been completely assessed. Evidence of this includes the 174 new records for birds species not reported previously for Colombia since the first publication of “A Guide to the Birds of Colombia” by S.L. Hilty and W.L. Brown in 1986 (Hilty & Brown, 2001; Salaman *et al.*, 2001). As well as the several new bird species for science described during the last 20 years as result of new explorations in the field (Salaman *et al.*, 2007b) and the revision of museum material from Colombia. Among them: the Chiribiquete Emerald, *Chlorostilbon olivaresi* (Stiles, 1996); the Bogota Sunangel, *Heliangelus zusii* (Graves, 1993); the Gorgeted Puffleg, *Eriocnemis isabellae* (Cortés-Diago *et al.*, 2007); the Parker’s Antbird, *Cercomacra parkeri* (Graves, 1997); the Cloud-forest Pygmy-owl, *Glaucidium nubicola* (Robbins & Stiles, 1999); the Cundinamarca Antpitta, *Grallaria kaestnaeri* (Stiles, 1992); the Upper Magdalena Tapaculo, *Scytalopus rodriguezi* (Krabbe *et al.*, 2005); the Stile’s Tapaculo, *Scytalopus stilesi* (Cuervo *et al.*, 2005); the Chesnut-capped Piha, *Lipaugus weberi* (Cuervo *et al.*, 2001), the Antioquia Bristle-tyrant, *Phylloscartes lanyoni* (Graves, 1988); the Munchique Wood-wren, *Henicorhina negreti* (Salaman *et al.*, 2003); and the Choco Vireo, *Vireo masteri* (Salaman & Stiles, 1996).

Table 3.1.1.1. Species by ecoregions in Colombia.
Slightly modified from Salaman *et al.* (2007b).

Ecoregion	Total of species
Inter–Andean Valleys and the Caribbean	711
Widely distributed	164
Lowlands (Tropical Zone)	373
Magdalena River Valley	198
Cauca River Valley	117
Guajira Peninsula	62
Pelagic and Coastal	60
San Andres and Providencia and Other Caribbean Islands	36
Amazon	674
Widely distributed	310
Lowlands (Tropical Zone)	301
Subtropical	63
Andes	650
Widely distributed	140
Eastern Cordillera	348
Central Cordillera	298
Western Cordillera	189
Southern Massif	185
Serrania de Perija	86
Sierra Nevada de Santa Marta	55
Pacific	539
Lowlands	239
Subtropical Choco	65
Serrania del Darien	105
Gorgona and Malpelo Islands	5
Pelagic and Coastal	82
Orinoco	420

3.2. Methodology

3.2.1. Methodological strategy

Here we discuss the overall methodological strategy. Detailed methodologies for the different analysis are given in the relevant chapters. This research was developed as five sets of activities conducted consecutively and iteratively (Figure 3.2.1.1).

First, both biological and environmental data were gathered and prepared for analysis. Each record from the Darwin–Hernandez Database was carefully revised and corrected; giving special attention to the georeferencing information attached to each one of the records in the database. Additionally, the uncertainty for each georeference in the database was estimated (objective 1). Second, bird diversity was mapped for Colombia at the national level (objective 2), and the relationship between bird richness, sampling effort and surface area was evaluated (objective 3). These two initial blocks of tasks were repeated iteratively using different filtered versions of the database aiming to eliminate the relationship between richness–effort–surface area and produce improved bird diversity maps. Next, the best performing methodologies were selected, and in a third step, bird diversity was projected for future climate–change scenarios. Finally, in a fourth stage, the maps of bird diversity developed were used to highlight potential refugia of bird diversity in the country under future climate–change scenarios (objective 4).

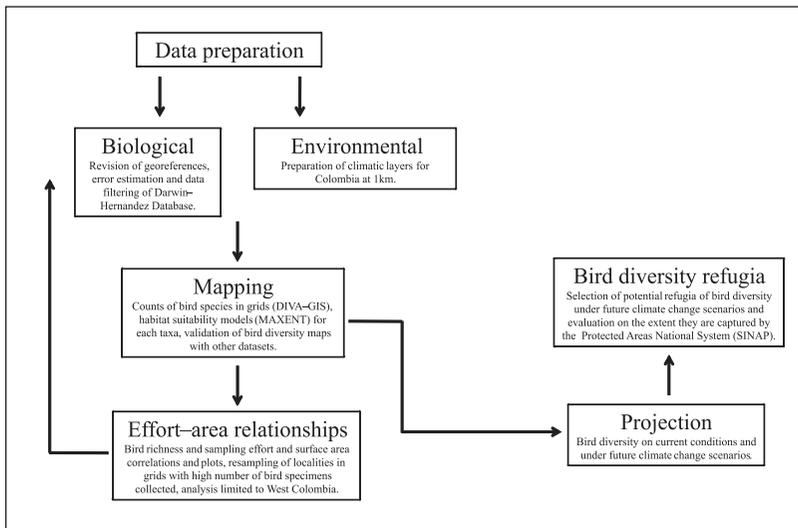


Figure 3.2.1.1. Flow chart of main tasks developed during this research.

3.2.2. Data preparation

Datasets were gathered from several sources, all of them freely available in the Internet. Bird distribution information was obtained from Project BioMap (Salaman *et al.*, 2007a), ProAves Foundation Colombia (Proaves, 2008) and the “Western Hemisphere Digital Bird Distribution Database” (Ridgely *et al.*, 2007), while environmental datasets were obtained from WorldClim (Hijmans *et al.*, 2007; Hijmans *et al.*, 2008), Mulligan (2006) and Jarvis *et al.* (2004). The bird and

environmental data received different treatments. Bird distribution information from project BioMap was received directly and afterwards revised, corrected and filtered. Geographical range maps from the “Western Hemisphere Digital Bird Distribution Database” were downloaded and processed to obtain range maps at genus and family levels. Environmental datasets were downloaded from the Internet in tiles, merged and masked to the outline of Colombia.

The BioMap Alliance invested a total effort of about 5,000 person–days, during project BioMap during 2002–2005. During that time, the BioMap team digitised, revised and compiled the information of all Colombian bird specimens placed in 90 of the most important natural history museums in Colombia, United States and Europe. As its main output the project made public the Darwin–Hernandez Database, a dataset of approximately 220,000 georeferenced accessions of Colombian bird specimens (Salaman *et al.*, 2007a). For each accession, the database contains fields related to the repository archive (*e.g.* museum name, acronym, contact, catalogue number, *etc.*), the taxonomy of the specimen (*i.e.* family, genus, species and subspecies), the collection event (*e.g.* locality, date, collector, field number, *etc.*) as well as age, sex, general notes and information about the existence of accessory data in the label (*i.e.* soft parts, DNA, gonads state, body measurements, weight and fat deposits).

Project BioMap is part of a recent wave of initiatives that are making herbaria and natural history collections data increasingly available. In spite of the undeniable importance of this type of data, the use that can be made of it is limited due to problems of locality georeferencing, determination of taxonomy and synonymies (Chapter 4, section 4.1). Moreover, data can be biased spatially and temporally (Boakes *et al.*, 2010), which is a direct consequence of the irregularity in which specimens deposited in natural history museums have been gathered. Usually data from such sources have been taken opportunistically in a time span of 100–300 years using a variety of methods. Thus, many collections were created during the 19th century when European expansionism was at its zenith. Explorations of new territories advanced by governments and private individuals and the growing interest of naturalists in describing the fauna and flora from these regions made possible the amalgamation of thousands of specimens shipped from all over the world in natural history archives in Europe (Rounds, 1990). In an outstanding example, Lord L.W. Rothschild by 1905 had sent hundred of collectors around the world and was assembling what later became the largest private bird collection (Rothschild, 1983). Most specimens held today in natural history collections were taken by shooting. Although most recently, during the last 30 years, other techniques such as mist–netting have been increasingly used.

Colombian specimens included in the Darwin–Hernandez Database were collected over a time span of about 250 years (Verhelst *et al.* unpublished data). However, many specimens did not have detailed information regarding the locality of collection and

therefore the oldest specimens were deleted during the filtering process and were not used as part of the dataset prepared for analysis and mapping of bird diversity in the country (see section 3.2.2.1 and Chapter 4, section 4.2). In this sense, the oldest information used in mapping exercises may have been taken over a time span of about 100 years, during several expeditions conducted by U.S. natural history museums (see chapter 6, section 6.2.2), and very likely most of them collected by shooting. It is difficult to make a precise account of the methodologies used since most metadata relating collection methods for each specimen are not available in the database. However, if we assume that just those specimens post 1970 could have been collected using other methods such as mist-netting, only a fraction from 30,590 specimens ($\approx 14\%$ from the total database) could have been taken by methods different to shooting (Verhelst *et al.* unpublished data).

WorldClim version 1.4 is a series of global climate datasets produced by interpolation at ≈ 1 km (0.008333 arc degrees) spatial resolution from monthly average point data, averaged over the period 1950–2000 from locations around the world (Hijmans *et al.*, 2005a, 2007). The authors used information from global, regional and country climatic databases, restricting data to the period 1950–2000 whenever possible. Point data was interpolated using the software ANUSPLIN and the Thin-Plate Smoothing Spline Algorithm with altitude as a covariable. For the purposes of this research, tiles were downloaded for the monthly total precipitation, the mean temperature and 19 bioclimatic (BioClim) variables covering Colombia.

WorldClim have also produced and made available future climate conditions simulated by several Global Climate Models or General Circulation Models (GCMs) at <http://worldclim.org>. GCMs are built based on complex mathematical equations describing the physical laws governing the redistribution of incoming radiative energy from the sun among major climate system components such as the earth's surface, the atmosphere and the oceans and its subsequent effects in climate (see Chapter 6, section 6.1).

Among the different models available in the WorldClim archive are some results from the Canadian Centre for Climate Modelling and Analysis (CCCMA) model, some results from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) model and some results from the Hadley Centre Coupled Model 3 (HadCM3). As expected, different global climate models have different results and they depend in general terms in the equations used and relations modelled, as well as the projected scenarios of emissions of greenhouse gases and aerosols (Hijmans *et al.*, 2008). On the other hand, due to mathematical complexity and machine memory limitations most GCMs have been developed at coarse resolutions between 100–250 km, making it necessary to downscale the projections when they are to be used at finer resolutions (Hijmans *et al.*, 2008).

For this research we decided to download projections from the HadCM3 model, SRES-scenarios² A2A and B2A for the years 2020, 2050 and 2080 (Hijmans *et al.*, 2008). According to Gordon *et al.* (2000) one of the main advantages of the HadCM3 model in relation to older versions of the same model and other models is that it does not need flux adjustments to alleviate the large climate drifts usually present in simulations of current conditions. In addition, the model produces stable and realistic sea surface temperatures and sea ice simulations and has improved resolution for the atmospheric and the ocean components. Moreover, it shows better compatibility between the heat budgets of atmosphere and ocean that, according to the authors, is possibly one reason for the improved simulations. The atmospheric component of the model has a resolution of $2.5^{\circ} \times 3.75^{\circ}$ latitude–longitude that roughly is equivalent to $417 \times 278 \text{ km}^2$ at the equator and that reduces to $295 \times 278 \text{ km}^2$ at 45° of latitude both north and south (IPCC–DDC, 2008). Results were downscaled by Hijmans *et al.* (2008) comparing the absolute and relative differences of model predictions both in current and future conditions to the current climate conditions baseline of WorldClim, the so-called delta methods.

Finally, current rainfall and elevational datasets were downloaded from Mulligan (2006). The rainfall data was originally produced by the Tropical Rain Measurement Mission (TRMM) satellite, which uses the combined algorithm 2B31 and data from the TRMM Microwave Imager (TMI) and the Precipitation Radar (PR) to produce the best possible estimate of instantaneous rainfall (NASA, 2007). Mulligan (2006) processed the information during the period 1997–2006 to produce an annual and monthly rainfall climatology at $\approx 1 \text{ km}$ resolution from the instantaneous values and made the data available through a Google Earth visualisation interface placed at <http://>

² These scenarios are part of four narratives, storylines or scenarios families defined by the Intergovernmental Panel on Climate Change (IPCC) in its third assessment report, Special Report on Emissions Scenarios – SRES, (Nakicenovic *et al.*, 2001), which describe the main factors responsible for global climate change and their expected impacts on climate conditions during the next 100 years. The four scenarios families (*i.e.* A1, A2, B1 and B2) represent two distinct groups of opposing patterns regarding economic development, population growth and the introduction of environmentally friendly – “green” – technologies (Nakicenovic *et al.*, 2001). Thus, the A1 and A2 families represent scenarios where there is an accelerated economic development. However, in the A1 family global population decreases after 2050 and global economy becomes more homogeneous, as well as are introduced rapidly “green” technologies. Contrastingly, in the A2 family global population continues increasing and economic development is directed regionally, increasing differences worldwide. Otherwise, the B1 and B2 families represent scenarios where are highlighted environmental values, and therefore there is expected a shift in economic structures towards environmental sustainability. Nonetheless, in the B1 family global population follows the same tendency as family A1, while the homogenisation of global economy permits the shift to highly (continues at bottom of next page) environmentally friendly development initiatives and technologies. Conversely, in family B2 global population continues increasing, although below levels of family A2, while economic development is directed regionally.

www.ambiotek.com/1kmrainfall/. For this particular study, tiles covering Colombia were downloaded for annual total rainfall. Furthermore, a Digital Elevation Model (DEM) dataset processed by Jarvis *et al.* (2004) and available from the Google Earth visualisation interface produced by Mulligan at <http://www.ambiotek.com/topoview> was also downloaded for Colombia. The authors processed the datasets from information originated by the NASA Shuttle Radar Topographic Mission (SRTM) at approximately 90 m resolution, and available at the National Map Seamless Data Distribution System (<http://seamless.usgs.gov/>). The authors produced vector contours, which were re-interpolated to a grid Digital Elevation Model to fill the void areas, improving the quality of the data (Jarvis *et al.*, 2004). The DEM at ≈ 90 m resolution was imported into Arc View 3.3 (ESRI, 2002) and aggregated at ≈ 1 km grain size using the spatial average function; the new map was permitted to expand if necessary and “no data” cells were ignored in calculations. A more detailed description of the mentioned datasets, their quality and metadata, may be found in the different electronic addresses cited in the previous paragraphs. In the next sections, we will describe in detail how each group of data was prepared for analysis.

3.2.2.1. Biological data

The Darwin–Hernandez Database was prepared for this thesis in three major phases. First, georeferencing was checked carefully to ensure localities were correctly placed within the boundaries of Colombia and to correct any obvious errors found in assigned localities and/or coordinates. Second, for each georeference an evaluation of its uncertainty using different measures of error was conducted. Finally, based on the estimated measures of error localities with a high degree of uncertainty were filtered out from the database, retaining the best quality information for posterior mapping exercises.

Revision and correction of georeferencing in BioMap database

The Darwin–Hernandez Database (Microsoft Access version *.mdb) was revised and corrected in two periods. First, in January–March 2007 and, second, in April–June 2008; investing a total effort of 4 person–months. During the first revision, localities and georeferences were imported into DIVA–GIS 5.2.0.2 (Hijmans *et al.*, 2005c) to check georeferences that were out of the limits of the country or outside of the first administrative unit recorded in the database, indicating a gross coordinate error. Whenever necessary, revisions and adjustments were made using all gazetteers available for Colombia (Paynter & Traylor, 1981; Paynter, 1997; ADL, 2007; NGA–GNS, 2007). Additionally, major errors in localities assigned to specific records were corrected as much as possible when evident. During the second revision, localities and georeferences were checked to correct “false precision” in the coordinates, which

was common in the database due to transformation of coordinates from degrees and minutes to decimal degrees. On the other hand, georeferences for records related to rivers and streams were revised, assessing consistency between the actual recorded altitude on the collection and the SRTM observed altitude at the location where the georeference lay and filtering out records where significant differences in altitude were to be found. More details on how the database was revised and improved can be found in Chapter 4, section 4.2.1.

Georeferencing error

A further step to improve the quality of the database included an evaluation of the accuracy of the georeferences assigned to each site. For this purpose, two different measures of error were estimated immediately after each revision period in 2007 and 2008. After the first revision period, the “minimum horizontal error” and the “slope-weighted horizontal error” were computed. The minimum horizontal error was calculated as the error derived from the precision of recorded coordinates, and was estimated using the equations suggested by Wieczorek *et al.* (2004); implemented in a simple model in a Microsoft Excel 2007 (Microsoft–Corporation, 2007) spreadsheet. The slope-weighted horizontal error combines the slope and the minimum horizontal error to measure the vertical elevational error for each site locality. This is important since even a small horizontal error, which yields a significant vertical error (*e.g.* in areas of steep terrain) can have significant impacts on habitat suitability and niche modelling where climate changes sharply with elevation. For this study, the slope-weighted horizontal error for each locality was calculated multiplying the minimum horizontal error by the average slope in an area around the locality defined by this minimum horizontal error. Calculations were performed running a simple cartographic model in PCRaster version 2001 (percalc update 2007 De Jong *et al.*, 2001).

In 2008, after “false precision” was corrected and georeferencing improved for a second time (Chapter 4, section 4.2.1), a further phase of correction was performed to estimate uncertainty based on the “minimum horizontal error” and the “collection–event horizontal error”. The minimum horizontal error was calculated again using the same methodology as previously. The collection–event horizontal error was estimated as the maximum distance at which the specimen attached to a particular accession could have been collected from the recorded georeference, according to the altitudinal range known for the species attached to the record and the range of elevations in the landscape around the coordinate recorded. This measure has the advantage that evaluates, according to the best expert knowledge regarding each species altitudinal range, if the particular species attached to an accession could have been collected within the limits of a set of predefined classes of distance. Thus, the error value is assigned as the upper limit of the class of distance where it was found

first any overlap between the known altitudinal range for the species and the elevations observed within each distance class. Calculations were performed in PCRaster using cartographic and dynamic modelling and small python scripts to develop part of the tasks necessary to complete mathematical operations. Results were exported to Excel where they were analysed and plotted.

These estimates of uncertainty were used to filter out highly uncertain localities from the database in order to prepare datasets for subsequent analyses and to determine the minimum grain resolution at which bird diversity maps should be produced to make best use of the true precision of the available coordinates. More details on georeferencing error estimation can be found in Chapter 4, section 4.2.2.

Filtering of the database

Once georeferencing was carefully revised and corrected all records that had inconsistencies or were otherwise incomplete were filtered out from the database. This was performed several times obtaining different filtered versions of the database that were used at different points for different mapping exercises trying to obtain a balance between the quantity and the quality of the information retained each time, since filtering sometimes cut out large numbers of records.

The database was filtered each time following six general steps. Firstly, records attached to highly uncertain localities were eliminated (*e.g.* highly non-specific localities such as Colombia, New Granada). In a second step, records with an incomplete taxonomy were deleted. Afterwards, in a third stage, records of non-continental localities were deleted. In a fourth step, the approximate elevation attached to the locality of each record from a DEM at ≈ 1 km grain size was extracted and in a fifth step those values compared against the known altitudinal distribution limits for the species attached to each record. This was used to filter out accessions for which the extracted elevation did not coincide with the known altitudinal range for the species. Finally, in a sixth step, all accessions with estimations of georeferencing error higher than 1 km and placed in areas with average slope higher than 5% were filtered out. This last step also was repeated after the second revision period of the database in 2008, but filtering out all accessions with estimations of error higher than 2 km and average slope higher than 5%. Eight different filtered datasets³ were generated retaining different number of accessions each time. More details on steps used to filter out low precision accessions can be found in Chapter 4, section 4.2.3.

³ BioMap-Fil500 (174,330 accessions); BioMap-FilDated (149,649 accessions); BioMap-FilDated700 (146,297 accessions); BioMap-BasicFil (195,090 accessions); BioMap-BasicFilHP (169,221 accessions); BioMap-BasicFilHP700 (126,914 accessions); BioMap-BasicFilHP_v2 (141,140 accessions); and BioMap-BasicFilHP_v2_1950 (69,059 accessions).

3.2.2.2. Biophysical data

WorldClim datasets

WorldClim data are available in 30°×30° tiles in ESRI ARC–ASCII format in geographical coordinates reference system (not projected). Tiles 23 and 33 were downloaded for the monthly total precipitation, the mean temperature and 19 bioclimatic (BioClim) variables (Table 3.2.2.2.1) for this research. For each one of the 21 geovariables the tiles were imported into DIVA–GIS and mosaiced. Then they were exported as ASCII files and imported into Arc View. Once in Arc View, layers were masked to Colombia’s boundaries and all clipped to the same display extent. Finally, all were exported in generic ASCII format for input to MAXENT version 2.3, which was used to generate the first habitat suitability models. Previously to run models a Principal Components Analysis (PCA) was conducted to select those bioclimatic variables explaining major part of the total variability and hence reduce the number of variables used in modelling (see Chapter 5, section 5.2.2 for details).

Table 3.2.2.2.1. WorldClim bioclimatic variables list.

BioClim code	BioClim variable name
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (P2/P7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max. Temperature of Warmest Month
BIO6	Min. Temperature of Coldest Month
BIO7	Temperature Annual Range (P5-P6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Additionally, for the second generation of modelling exercises downscaled results from the climatic projections generated by the HadCM3 model, scenarios A2A and B2A for the years 2020, 2050 and 2080 were used (Hijmans *et al.*, 2008). Thus, from the same WorldClim website, grids at ≈ 1 km resolution covering the whole world for the monthly total precipitation, the minimum temperature and the maximum temperature were downloaded. Grids were imported into DIVA–GIS and clipped to northern South America and Panama, and exported as ASCII files. Afterwards, ASCII files were imported into Arc View and projected to Lambert Equal Area Azimuthal [Equatorial] projection at 1 km resolution. All files were again exported as ASCII files and imported into PCRaster where they were processed to estimate several BioClim variables (BIO1, BIO2, BIO3, BIO12, BIO13, BIO14), defined according to a PCA as those variables explaining major part of the total variability (see Chapter 5, section 5.2.4.1 for details).

Other datasets

TRMM Rainfall data (Mulligan, 2006) are available in $1,000 \times 1,000$ km² tiles and elevational data is available in $5^\circ \times 5^\circ$ tiles both in ASCII format (Jarvis *et al.*, 2004). For this study tiles *sumrainmmy_5_4* and *sumrainmmy_5_5* for the rainfall and *srtm_21_10* to *srtm_21_13*, *srtm_22_10* to *srtm_22_13*, and *srtm_23_10* to *srtm_23_13* for the DEM data were downloaded. Datasets were prepared exactly in the same way as explained before for WorldClim datasets in the previous paragraphs.

3.2.3. Bird diversity mapping

Bird diversity mapping was conducted using different methodologies and datasets aiming to conserve as much information as possible in the dataset whilst in successive steps eliminating spatial sampling effort and area size biases. Initial tests focused on richness (number of taxa in a specific taxonomic level) to measure diversity. First, BioMap–Fil500 dataset was used in DIVA–GIS to explore species richness, calculating it at different grain sizes combining different techniques and richness estimators. This method proved to be inadequate, because of the highly concentrated nature of sampling for Colombia as represented in the Darwin–Hernandez dataset, which resulted in a strong correlation between richness measured in this way and sampling (expeditionary) effort (Chapter 5, section 5.3.2). Consequently, it was decided to generate habitat suitability models and potential geographical ranges at family and genus taxonomic levels using BioMap–BasicFilHP and MAXENT, and estimate richness by overlapping the maps produced. Finally, as part of a second phase of analyses, conducted after completing the second period of georeferencing revision and correction, error estimation, and once having prepared all necessary bird and environmental datasets, we performed an experiment to test the influence of

sample size, number of replicates and grain size on MAXENT model performance. Thus, for each taxon, 25 habitat suitability models were generated at 3km grain size and consensus potential range maps produced using the most accurate replicas (see Chapter 5, sections 5.2.4.1 and 5.2.4.2).

Once appropriate methodologies were finely tuned, other measures of diversity such as the “weighted endemism score” (Crisp *et al.*, 2001) and two new indices of ecomorphological diversity proposed and tested for hummingbirds and tyrant flycatchers (families Trochilidae and Tyrannidae respectively) were integrated to explore alternative measures of biodiversity related to the function species play in their communities. Final richness maps were cross-validated comparing them to richness maps elaborated using the geographical range maps from the “Western Hemisphere Digital Bird Distribution Database” (Ridgely *et al.*, 2007) and data obtained from field surveys conducted by ProAves at 76 sites distributed across the Colombian Andes and north and west of them (Proaves, 2008). More details on mentioned alternative biodiversity measures and the validation of generated maps can be found in Chapter 5, sections 5.2.4.3–5.2.4.5.

3.2.4. Bird diversity refugia under future climate change

During the second generation of modelling exercises, habitat suitability models built using MAXENT and the new filtered versions of the Darwin–Hernandez Database⁴ were projected onto future climate-change conditions predicted by the HadCM3 model, scenarios A2A and B2A for the years 2020, 2050 and 2080. Habitat suitability maps at family and genus levels were processed using the same methodologies to produce consensus geographical range maps and estimate richness and rarity (using the weighted endemism score) in Western Colombia. Furthermore, the differences in bird diversity between the several scenarios and current conditions were evaluated, exploring their spatial patterns in West Colombia as a whole and along the elevational gradient. In addition, diversity maps were used as the basis to apply an algorithm to select a series of potential refugia of bird diversity trying to maximise diversity, minimise the difference in diversity between predicted scenarios and current conditions and select the areas where modelling was most robust.

⁴ BioMap–BasicFilHP_v2 and BioMap–BasicFilHP_v2_1950

CHAPTER 4
DEVELOPING AND QUALITY CONTROLLING A SPATIAL
DATABASE OF BIRD COLLECTIONS

Summary – Secondary sources of information such as specimens deposited in natural history archives and herbaria around the world constitute an important resource to study biodiversity and are becoming increasingly accessible. Such information can be used in Geographical Information Systems (GIS) applications to model species geographical ranges based on a series of statistical techniques applied to accession points and continuous environmental data in order to inform conservation planning. However, there are still limitations to the use that can be made of most of the biological information available due to taxonomical misidentifications, synonymies and issues of data quality with the georeferencing of accessions. During 2002–2005 Project BioMap compiled for Colombia a database of approximately 220,000 georeferenced accessions of Colombian bird specimens from 90 of the most important natural history museums in Colombia, the United States and Europe. Modelling bird diversity in the country using this BioMap data and GIS techniques is important to advance our understanding of the spatial distribution of biodiversity and the potential impacts of climate change on it in the country. However, to do this accurately, first it is necessary to address the quality of the data. The objective of this particular chapter is to present the steps used to revise and improve the Darwin–Hernandez Database and account for uncertainties in georeferencing in the database when assessed using two different methodologies.

The database was assessed during 2007 and 2008 following three general steps: 1) data were carefully revised and georeferencing checked using GIS tools to correct major errors in the database, 2) georeferencing uncertainty was estimated using two different measures of georeferencing error each time, and 3) the error analysis results were used to filter out highly inaccurate accessions. Uncertainty in georeferencing was calculated using three different measurements of error, the latter two of which were developed specifically for this study: 1) the minimum horizontal error, 2) the slope-weighted horizontal error, and 3) the collection–event horizontal error. The first type of error is based simply on an assessment of the precision of coordinate measurements, whilst the second and the third are newly developed estimations of uncertainty of specific relevance to this study. The second measure integrates information on slope gradients around the accession in order to estimate the elevational precision of the record, since elevation is a critical factor in determining environmental conditions.

The third implements simple algorithms to evaluate the error based on the range of elevations in the landscape around the georeference *versus* the known altitudinal range of the particular species recorded in each accession. During the first revision period nearly 2,000 localities were revised because of the detection of a potential problem, and from those 1,000 localities were adjusted for being, for example outside of the limits of the country, outside of the respective first administrative unit recorded on the accession, *etc.* The high precision filtered dataset (minimum horizontal error $\leq 2\text{km}$) extracted from the database during 2008 was smaller than the dataset extracted during 2007 (minimum horizontal error $\leq 1\text{km}$) by some 50,000 records, evidencing a more stringent quality control of the database. The approach as a whole proved successful in producing purged datasets retaining the best quality information, although reducing drastically the number of accessions, sometimes by up to 70% of the original number of records in the database.

The retrospective georeferencing method, used for many of the accessions in Project BioMap, and very often for this type of data, is limited due to uncertainties related to the assignation of unique coordinates to locality names using ornithological gazetteers. In reality, most accessions are found some distance away from named features in gazetteers but no record is made of offset distances from the coordinates for the nearest place–name assigned. This renders a degree of uncertainty in the coordinates, which is likely greater for very rural areas where the named and georeferenced features are fewer and further apart. For these reasons, results from this chapter suggest the use of a minimum grain size of 3 km for habitat suitability and niche modelling applications when using datasets derived from the filtered versions of Darwin–Hernandez Database under current georeferencing.

4.1. Introduction

Developments during the last decade in information technology and machine computing power have made available to the scientific and public communities large amounts of data from secondary sources of information, such as for example data from specimens deposited in natural history archives and herbaria (Soberon *et al.*, 2000; Soberon & Peterson, 2004). This process began separately in many different organizations under initiatives to digitise and catalogue electronically their collections and advanced with changes in the willingness of the institutions for collaboration and data sharing. That, with the arrival of the Internet, made possible the sharing of exceptional quantities of information through the World Wide Web (Soberon & Peterson, 2004). One example, of the many initiatives in progress, is the one led by the Global Biodiversity Information Facility (GBIF), which offers free and open access to nearly 190 million data occurrences within 8,827 datasets from 309 different institutions to the scientific and public communities worldwide (GBIF, 2008).

However, there are still limitations to the use that can be made of most museum accessions mainly related to problems of taxonomy determination and synonymies and locality georeferencing (Soberon *et al.*, 2000; Wieczorek *et al.*, 2006). Common mistakes in the taxonomy include misidentifications which sometimes are not easy to detect without the participation of experts and use of outdated taxonomies, or even worse the blending of different taxonomies, which results in databases with a high proportion of synonymies (Soberon *et al.*, 2001). Most museum accessions and existing datasets have rarely been georeferenced and even when georeferenced usually lack metadata documenting the methodologies used, assumptions made in the process and thus the likely accuracy and precision of the coordinates (Wieczorek *et al.*, 2006). Wiecezorek *et al.* (2004) consider six main sources of uncertainty associated with georeferencing of this type of data: 1) the extent of the locality of collection; usually localities are referred to as points but in fact they may comprise an area around a base camp where the collector or collectors conducted their activities; 2) unknown projection and/or datum assigned to the georeference; 3) imprecision in offset distance measurements from a specified (named) locality (*e.g.* 10 km from Palmira); 4) imprecision in direction measurements from a specified locality (*e.g.* 10 km E of Palmira); 5) imprecision in coordinate measurements of named places and false precision due to conversion between coordinate types and retention of too many significant figures; and 6) issues of map scale. Additionally, error may be introduced by mistakes in transferring or typing data from original sources such as specimen tags or from the literature, and also from misinterpretations of locality descriptions in retrospective georeferencing of localities using published gazetteers (Graham *et al.*, 2008). Gazetteers are commonly used for georeferencing museum specimens and other secondary information sources for which georeferencing has not been taken in the field. To improve the utility of any dataset of accessions for use in habitat suitability and niche modelling these uncertainties must be rigorously addressed (Wieczorek *et al.*, 2004).

There are two main different ways in which the types of error and uncertainty discussed have been handled in the literature (Graham *et al.*, 2008). On the one hand, datasets and georeferencing are manually revised thoroughly to search for errors in data transfer, misinterpretations of locality descriptions and/or assigned coordinates. This process is time consuming and becomes a cumbersome task for databases with large numbers of accessions. Some authors have proposed several methodologies using GIS to assist the effective detection of some of those errors (Hijmans *et al.*, 1999; Hijmans & Spooner, 2001; Hijmans *et al.*, 2005b). Thus, for instance major errors such as localities placed in the middle of the oceans can be detected by visual inspection of all localities in a GIS against coastal boundaries. Through a semi-automated process conducted in a GIS, an algorithm can be implemented to perform multiple spatial queries and check for coherence between the administrative divisions

assigned to each accession in the revised dataset and the administrative divisions where the georeference assigned to the locality actually lie as defined by an independent administrative boundaries map. Later if any incongruence is found georeferences are checked and new coordinates assigned where possible. Highly uncertain localities or accessions with major errors that cannot be corrected are deleted from the database, although this may reduce model performance due to a reduction in sample size (Hernandez *et al.*, 2006; Graham *et al.*, 2008), although possibly it is better to have fewer, more accurate data than more data but of dubious accuracy.

Other authors advise to investigate more in depth uncertainties associated with georeferences. In this context, Wieczorek *et al.* (2004) propose the “point–radius method”, a more complex approach that addresses the type of uncertainty and also quantifies its magnitudes. Their method first provides a series of guidelines to assign for each locality a unique georeference as a point (*i.e.* a georeferencing method) and second offers a repeatable methodology to account for the magnitude of each one of the six different types of uncertainties mentioned above. This method has the advantage that it combines the different types of uncertainties in one value, the “maximum error”, which constitutes the radius of a circle that has as centre the assigned georeference and that denotes the maximum area around the georeference where the locality may lie according to the quantified sources of uncertainty (Wieczorek *et al.*, 2004).

Project BioMap was conducted during 2002–2005 and aimed to increase biodiversity knowledge in Colombia through a model of bird data repatriation. The project devoted a total effort of about 5,000 person days to compile, georeference and made public information of nearly 220,000 Colombian bird specimens (see Chapter 3, section 3.2.2). Modelling bird diversity in the country using BioMap and GIS constitutes a unique opportunity to advance our understanding on biodiversity in the country. A first step to achieve this must consider to assess the quality of the data in order to improve the utility of the information and thus to obtain maximum advantage from it. Thus, the objective of this particular chapter is to present the steps used to revise and improve the Darwin–Hernandez Database and account for uncertainties in georeferencing in the database when assessed using two different methodologies.

4.2. Methodology

The Darwin–Hernandez Database was prepared in three major phases. First, georeferencing was checked carefully to ensure localities were correctly placed within the boundaries of Colombia and to correct any mistakes found in assigned localities and/or coordinates. Second, each georeference was evaluated for uncertainty using different measures of error. Finally, based on the estimated measures of error, localities with a high degree of uncertainty were filtered out of the database, retaining the best quality information for the later habitat suitability modelling exercises.

4.2.1. *Revision and correction of georeferencing in BioMap database*

From the 10th of January to the 10th of March 2007 a first revision of the Darwin–Hernandez Database (Microsoft Access version *.mdb) was conducted. During this period, localities and georeferences were checked in a semi–automated way to prepare them for later analyses. First, the locality table from the database, which contains all sites and their georeferences, was exported as a *.txt file and imported into DIVA–GIS 5.2.0.2 (Hijmans *et al.*, 2005c) aiming to detect georeferences that were outside of the limits of the country and outside of the respective first administrative unit recorded in the database. When discrepancies were found, georeferences were carefully revised and the locality checked against the full description given in the field notes for each specific record involved. Revisions and adjustments were made using all gazetteers available for Colombia (Paynter & Traylor, 1981; Paynter, 1997; ADL, 2007; NGA–GNS, 2007).

A second and final revision of the Darwin–Hernandez Database (Microsoft Access version *.mdb) was conducted from the 4th of April to the 4th of June 2008. During this period, localities and georeferences were checked to correct “false precision” and to improve coordinates in general, especially those attached to linear (rather than point) features such as named rivers and streams. “False precision” is the overestimation of the precision, which results from the use of many decimals obtained after transformation of coordinates from degrees, minutes and seconds (DMS) to decimal degrees (DD) (Wieczorek *et al.*, 2006). The R. Paynter gazetteer coordinates, originally in DMS format, has a maximum precision of 1 arc minute, which is equivalent to 0.01666667°. Thus, the maximum precision in the coordinates from this gazetteer is expected to be in the order of 0.01°, which at Colombian latitudes represents ≈1,500 m. Other gazetteers such as ADL and NGA–GNS, with coordinates in both DMS and DD formats but retrieved in DD format, have most places georeferenced to the nearest arc minute. Though they include some places with coordinate precision to the nearest second (0.0001°), which suggests “false precision” may be less problematic for some places in those gazetteers than in R. Paynter gazetteer. For the Darwin–Hernandez Database 2,048 localities (≈53% of the total) documented from the R. Paynter gazetteer were transformed to decimal degrees format and therefore we assigned to them a precision of 0.01°. Coordinates from other gazetteers were revised manually and precision assigned accordingly to the number of different (non–recurrent) decimals. For example, a coordinate such as “4.0166667°” or “2.2622222°” were assigned a precision of 0.01°, while a coordinate such as “3.4372222°” received a precision of 0.001° and a coordinate such as “8.3125°”, truncated in the fourth digit and all of them different, was assigned a precision of 0.0001°. Precision was used later for estimation of uncertainty in georeferences (see next section).

Moreover, some linear geographical features such as rivers and streams usually have their georeferences placed at the mouth of the river or at its confluence with a major river, which does not necessarily coincide with the site of the collection events. To improve these type of georeferences, they were imported into Google Earth version 4.2 (*.kml) and the elevation recorded for the collection events at each particular location compared to the elevation obtained from Google Earth – based on the SRTM dataset; which has an absolute horizontal accuracy of 20 m and absolute vertical accuracy of 16 m (NASA, 2005). When there was agreement between compared elevations, the coordinates were left intact or replaced with higher precision coordinates from newer sources such as the ADL and NGA–GNS gazetteers. If not, the recorded elevation at which specimens were taken was used as a guide to place each georeference manually upstream from the confluence to a site where elevation approximated the collection event recorded value. Specimens without recorded elevation were marked for deletion during the posterior filtering process.

Although errors in the localities assigned to specific records were corrected as much as possible, that particular type of error still may be present in the database. In that sense, it would be possible to continue improving the Darwin–Hernandez Database, revising manually the coherence between the actual sites assigned and the locality notes of each accession, though this would take a great deal more time and effort with likely diminishing returns. It is expected that major errors of these type were detected in the following process of filtering information, which is described in the next sections.

4.2.2. Georeferencing error

After completing georeferencing and locality revision, a further step to improve the quality of the dataset included an evaluation of georeferencing accuracy. For this purpose, georeferencing uncertainty was estimated using two different approaches. As a first approximation, the “minimum horizontal error” and the “slope–weighted horizontal error” were estimated. In a second stage, after “false precision” was corrected and georeferencing improved, uncertainty was estimated based on the “minimum horizontal error” and the “collection–event horizontal error”. In both cases, estimation of error also permitted the definition of highly uncertain localities to be filtered out from the database in order to prepare datasets for later analyses and to determine the minimum grain resolution at which bird diversity maps should be produced.

4.2.2.1. Minimum horizontal error

The minimum horizontal error was calculated as the error derived from precision in coordinates. It was estimated using the equations suggested by Wieczorek *et al.* (2004) as follows:

$$MHE = \sqrt{LaE^2 + LoE^2} \quad (\text{Equation 4.2.2.1.1})$$

$$MHE = \sqrt{\left(\frac{\pi \times R \times LaP}{180}\right)^2 + \left(\frac{\pi \times X \times LoP}{180}\right)^2} \quad (\text{Equation 4.2.2.1.2})$$

Where:

MHE = minimum horizontal error (m)

LaE = latitude error (m)

LoE = longitude error (m)

LaP = latitude precision measured as a fraction of a degree (degrees)

LoP = longitude precision measured as a fraction of a degree (degrees)

R is the radius of curvature of the meridian at the given latitude, and is calculated using the equation:

$$R = \frac{a \times (1 - e^2)}{\sqrt{(1 - e^2 \times \sin^2(La))^3}} \quad (\text{Equation 4.2.2.1.3})$$

Where:

a is the semi-major axis of the reference ellipsoid, 6,378,137 m when using the WGS84 ellipsoid and datum

e is the first eccentricity of the reference ellipsoid, defined by the following equation:

$$e = \sqrt{2f - f^2} \quad (\text{Equation 4.2.2.1.4})$$

Where:

f is the flattening of the reference ellipsoid, 0.00335281067 when using the WGS84 ellipsoid and datum

X is the orthogonal distance from the specific point to the polar axis, and is calculated using the equation:

$$X = |(N \times \cos(La))| \quad (\text{Equation 4.2.2.1.5})$$

Where:

N is the radius of curvature in the prime vertical at the given latitude and is calculated by the equation:

$$N = \frac{a}{\sqrt{(1 - e^2 \times \sin^2(La))}} \quad (\text{Equation 4.2.2.1.6})$$

All equations to calculate the minimum horizontal error were implemented in a simple model in a Microsoft Excel 2007 (Microsoft-Corporation, 2007) spreadsheet.

4.2.2.2. Slope-weighted horizontal error

This type of error combines the slope gradient and the minimum horizontal error to measure the potential vertical error (difference in elevation) for each site locality. The error reflects explicitly the effect the slope gradient may have in the precision of the elevation of the exact site where the georeference is placed. It is important to evaluate since the same horizontal error has different implications for elevational accuracy in zones with different slopes. This effect is particularly relevant in Colombia due to the major importance of elevation for regional and local climate, and therefore vegetation life forms and associated fauna. In this sense areas with the same horizontal error in the Andean Region, where climatic conditions may change drastically in few kilometres, will have a greater slope-weighted horizontal error than those in the Orinoco and Amazon regions, where conditions are relatively homogeneous. For this study, the slope-weighted horizontal error for each locality was calculated as:

$$SWE = MHE \times \bar{S} \quad (\text{Equation 4.2.2.2.1})$$

Where:

SWE = slope-weighted horizontal error (m)

MHE = minimum horizontal error (m)

\bar{S} = average slope (%) calculated in a squared window where each side is equal to the double of the minimum horizontal error value and the cell for which the slope-weighted horizontal error is calculated is in the centre of the window. The side of the window is the MHE doubled to include values in either direction from the centre of the georeference.

To achieve this, an error table containing the minimum horizontal errors for each locality was imported into Arc View and converted to a⁵.shp file and afterwards to a grid⁵ at ≈ 1 km projected to Lambert Equal Area Azimuthal⁶ [Equatorial] projection. The grid file was exported as ASCII file and imported into PCRaster version 2001 (pcrcalc update 2007 De Jong *et al.*, 2001) and then using a very simple cartographic model script, equation 4.2.2.2.1 implemented to calculate the slope-weighted horizontal error. The slope map used was produced from an original DEM at ≈ 1 km grain size projected to Lambert Equal Area Azimuthal [Equatorial] in Arc View and exported to PCRaster using the PCRaster slope function. Maps produced in PCRaster were exported to Arc View and new values of the average slope and the slope-weighted horizontal error added to the error⁵.shp file using the Grid Analyst extension version 1.1 (Saraf, 2002).

⁵ All non-projected grids at ≈ 1 km specifications – projection: Geographic; cell size: 0.008333 decimal degrees

⁶ All projected grids at 1km specifications – projection: Lambert Equal Area Azimuthal [Equatorial]; spheroid: sphere; central meridian: -72.5333; reference latitude: 0; cell size: 1,000 m

4.2.2.3. Second-generation of error estimation

Following the second phase of georeference revision and correction in 2008, the minimum horizontal error was again calculated using the same procedures described before for all remaining accessions. This time, instead of producing the slope-weighted horizontal error to account for the vertical error, we estimated the collection-event horizontal error. The collection-event horizontal error assesses whether the range of elevations around the coordinate assigned to each record (the record coordinate included) overlaps with the known altitudinal range for the species in the record. The error is evaluated in a predefined set of classes of distance and assigned as the upper limit of the first class of distance for which it was found an overlap in both ranges. Thus, the error represents the maximum distance at which the specimen could have been collected from the georeference assigned within the first class of distance where it could have been possibly taken. For this purpose, the locality table from the database, which contains all sites and their georeferences, was exported as a *.txt file and a short Python version 2.1 (Python-Community, 2001) script written to read the list of localities and write each one of them in a separated *.txt file formatted for PCRaster. Afterwards several batch files were written to run different PCRaster scripts aiming to import each locality file as a new map, cover the non-data areas around with zero values and calculate continuous distance maps for each new locality map (operators “map2col”, “cover” and “spread”). Also, distance maps were reclassified in nine distance classes: 1) 0–1.5 km, 2) 1.5–2 km, 3) 2–3 km, 4) 3–5 km, 5) 5–10 km, 6) 10–25 km, 7) 25–50 km, 8) 50–100 km, and 9) > 100 km, and converted to ordinal type data (operators “if then else” and “ordinal”). Additionally, several area operations were conducted for the DEM for Colombia and its derived slope using the reclassified distance maps for each locality, and results reported to *.tss files. Thus, the DEM area-minimum, DEM area-maximum and the slope majority (*i.e.* mode) for each one of the area classes contained in the locality maps were calculated (operators “areaminimum”, “areamaximum”, “areamajority” and “report”). Finally, a short Python script was written to read the original locality *.txt file and each one of the *.tss reported files and append one by one in separate columns the calculations obtained from the area operations. In this way, three different files for : minimum DEM values, maximum DEM values and slope majority were produced; each file containing the locality ID number, the X and Y coordinates and nine additional columns having the results from the area operations for the noted nine distance classes. It is important to note that slope majority was calculated reclassifying the original continuous slope range (0–61%) into 12 classes at 5% intervals: 1) 0–5%, 2) 5–10%, 3) 10–15%, 4) 15–20%, 5) 20–25%, 6) 25–30%, 7) 30–35%, 8) 35–40%, 9) 40–45%, 10) 45–50%, 11) 50–55%, and 12) 55–61%. This was necessary to reduce the high variability in values and permit majority calculations, which were not possible with the original (scalar) data. The files produced were imported into Excel and used as reference tables

to compare the known altitudinal distribution for the taxon attached to each record to the range defined by the minimum and maximum values for the DEM in each distance class using the function “vlookup” and several conditional statements (functions “and”, “or”). Accordingly, the collection–event horizontal error was assigned as the upper limit of the first distance class where both elevational ranges overlapped, if the accession is well within the known elevation range then the resulting horizontal error is low, else it is potentially high. Procedures were conducted in a similar way as described for the filtering process conducted to delete records with attached taxa out of their known altitudinal distribution range, but in this case increasing the altitudinal distribution range by 300 m in both the lower and upper limits (see next section for more details). All calculations within the second generation were performed on maps at 1 km resolution projected to Lambert Equal Area Azimuthal [Equatorial] projection.

During the two revision periods, when georeferences included offset distances and directions (*e.g.* 10 km E of Palmira) coordinates and uncertainty were estimated using the georeferencing calculator of Project MaNIS (<http://manisnet.org/gc.html>), which implements Wieczorek *et al.* (2004) “point–radius method”. Accordingly, the error was calculated adding the different sources of uncertainty defined by these authors (see introduction).

4.2.3. Filtering of the database

Once georeferencing was revised and uncertainty assessed, all records that had inconsistencies, were incomplete, or were highly uncertain were filtered out of the database. This step was performed several times obtaining different filtered versions of the Darwin–Hernandez Database that were used at different points for different mapping trials or analysis exercises trying to obtain a balance between the quantity and the quality of the information retained each time. For each analysis the version and characteristics of the database used is specified.

In the first phase in 2007, after uncertainty estimation, the original database constituting 217,659 accessions, was exported as a *.txt file, imported into Arc View and then filtered in consecutive steps until it was reduced to a new database of 174,330 accessions. Firstly, records attached to highly uncertain localities were eliminated. Thus, accessions without any georeference, records approximated to the first administrative unit, and trade skins from Bogota, Medellin, Cartagena and Popayan were deleted. Trade skins were identified manually making searches in the database helped by key words related to that kind of specimen, such as trade, trade skin, Bogota skin, uncertain, uncertain locality, incierta, localidad incierta, native, native skin. In a second step, records with an incomplete taxonomy (*i.e.* accessions not identified to species) were deleted. Afterwards, in a third stage, records of non–continental localities (*i.e.* islands in the Caribbean Sea or the Pacific Ocean) were

deleted. In a fourth step, the database was split in six parts, which were used to extract the approximate elevation of the locality attached to each record from the SRTM DEM at ≈ 1 km grain size using the Grid Analyst extension version 1.1 (Saraf, 2002). Then each part was exported to Excel and using the function “vlookup” and a complete list of the species in the database with their lower and upper altitudinal distribution limits, two new columns were added showing those limits for the species attached to each record. Altitudinal distribution species limits were set up according to Stotz *et al.* (1996), and to Hilty & Brown (2001) for species not listed by the first authors. Afterwards, using the function “and” a last column was added to evaluate if the DEM extracted altitude was inside the interval (I) 500 m below the lower limit (lol) and 500 m above the upper limit (upl), that is “ $I = lol - 500 \text{ m to upl} + 500$ ”, records that did not fall inside the specified range were deleted. This filter roughly eliminated records in which the attached species did not coincide with the known altitudinal distribution buffered by two 500 m altitude bands implemented to account for possible altitudinal extensions of the known distribution. Finally, retained records were brought together in a *.txt file and imported again into Arc View and DIVA-GIS as a *.shp file. This first filtered version of the database (BioMap-Fil500) was used for the first tests performed to map bird diversity as richness and collection effort using DIVA-GIS (see Chapter 3, section 3.2.3). Finally, estimations of error were used to filter out all accessions with highly uncertain coordinates. After the first revision period, accessions holding values for the slope-weighted horizontal error higher than 1 km and placed in areas with an average slope higher than 5% (extracted from a DEM at 1km grain size) were eliminated. This later filtered version of the database (BioMap-BasicFilHP) was used during the first generation of habitat suitability modelling exercises conducted to map bird diversity as richness using MAXENT and collection effort using DIVA-GIS (see Chapter 3, section 3.2.3).

During the second phase in 2008, roughly a similar process was followed to filter out highly uncertain accessions. However, it is important to highlight that this time overlap between the known altitudinal range of a species in a record and the elevation extracted for the georeference was evaluated in a far more complete approach, including the landscape around, while the assessment was integrated within the process of estimation of error (section 4.2.2.3). In addition, criteria to define each species’ range altitudinal limits were more stringent. Reducing the range of elevations within possible extensions of the known altitudinal range where accepted in 200 m, in both the upper and lower known limits of each range (section 4.2.2.3). Moreover, the same final step was repeated, but filtering out all accessions that held a collection-event horizontal error greater than 2 km and placed in areas with an average slope greater than 5%. We thus retained accessions with only the highest precision in steeplands and those that may have had higher uncertainty than the specified error thresholds but were in relatively flat areas.

Is important to note that the several filtered versions of the Darwin–Hernandez Database were produced aiming to understand better the advantages and limitations of different datasets drawn from the original database. Although, each filtering attempt in the first and second phases of revision repeated roughly each one of the mentioned steps, retained accessions varied enormously each time.

4.3. Results

4.3.1. Revision and correction of georeferencing in the BioMap database

During the first period of revision in 2007, it was found that from a total of 3,862 sites 906 were located with coordinates outside of the limits of the country, meanwhile for a further 935 localities the first administrative unit in the database did not match the unit extracted from the coordinates assigned (Figure 4.3.1a). Two hundred and six (206) sites with coordinates outside of Colombia could not be better georeferenced, while for another 700 sites it was possible to improve the precision of the existing coordinates or assign new coordinates. On the other hand, for 244 sites for which the respective first administrative unit did not match the one expected, coordinates and/or the administrative unit were corrected using all the information contained in the accessions and gazetteers to determine the reason for the mismatch (Figure 4.3.1b). Another 691 more sites did not need any modification in their georeference since mismatches were caused by typographical errors in the locality administrative units in the database.

During the second period of revision in 2008, a total of 1,094 localities were revisited; 683 related to linear features such as rivers or streams and 411 linked to other (point) geographical features. From those, coordinates were changed for 471 localities, whilst for 206 more localities precision in coordinates was adjusted. Moreover, a further 389 localities were highlighted to be deleted due to unavoidably high uncertainty in locating the georeference (*e.g.* for long rivers, mountain ranges, *etc.* where the coordinate associated with the named location could extend over a significant area) and 5 new localities were added to the database. Some records were split from the original erroneous localities and added to the correct ones accordingly. Of the 166 localities remaining without a georeference, some 40 localities were assigned coordinates.

4.3.2. Georeferencing error

First phase of revision. Results obtained for the minimum horizontal error calculations, estimated as the error in precision in coordinates, showed that about 70% of accessions exhibited an error lower than 1.5 km, and that approximately 25%

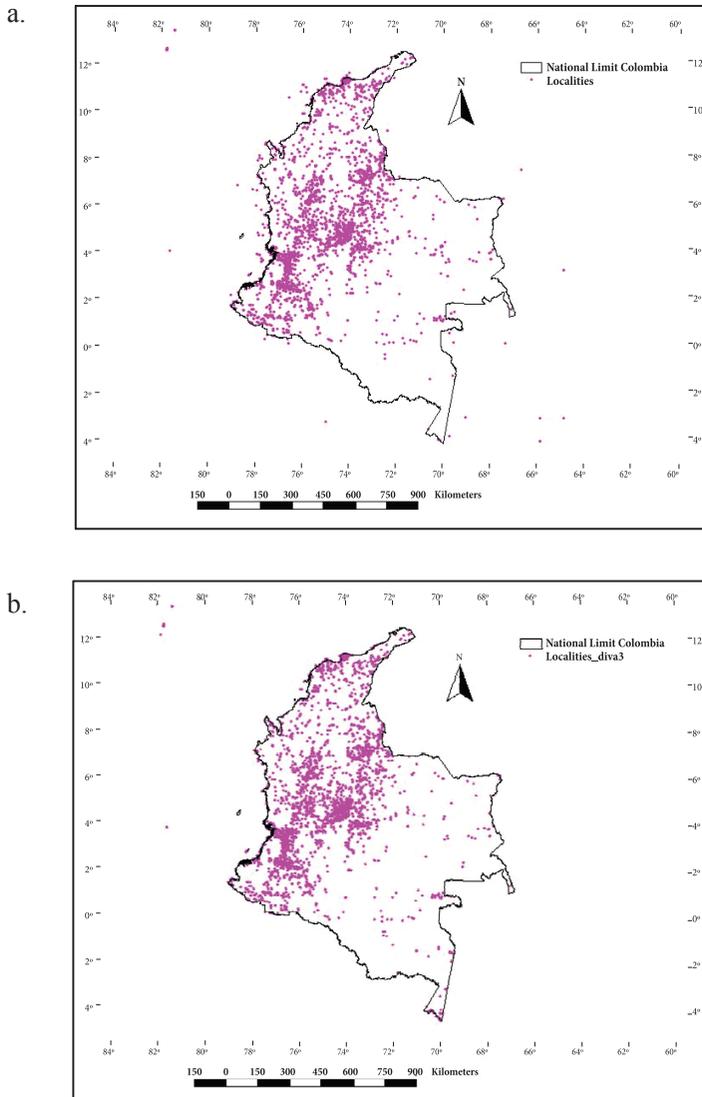


Figure 4.3.1. Darwin–Hernandez Database site localities placement according to original coordinates assigned by Project BioMap (a.) and after georeferencing revision and correction (b.). About 23% of localities fell out of the country limits, meanwhile 24% out of the respective first administrative unit. For about 24% of localities georeferencing was improved or corrected (see text for details). Localities out of limit in (b.) correspond to insular territories.

more presented values that varied between 5–25 km (Figure 4.3.2.1). The latitude and the longitude error components showed slightly different behaviour, reflected in their different frequency distributions (Figure 4.3.2.2).

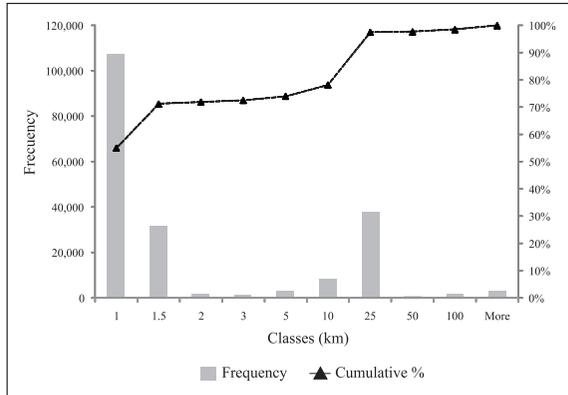


Figure 4.3.2.1. Frequency distribution for the minimum horizontal error in the Darwin-Hernandez Database. First period of revision and error estimation in 2007.

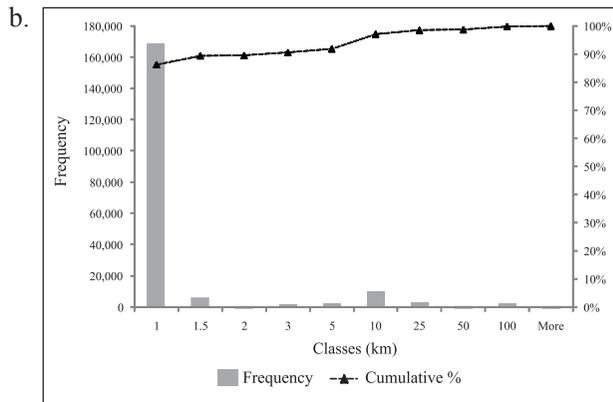
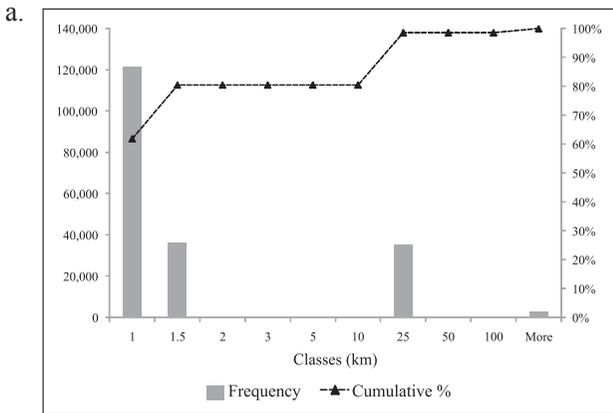


Figure 4.3.2.2. Frequency distribution for the minimum horizontal error in the Darwin-Hernandez Database. Latitude (a.) and longitude (b.) components treated separately. First period of revision and error estimation in 2007.

Results regarding the slope-weighted horizontal error, calculated as the product of the minimum horizontal error and the average slope of a squared area with each side equal to double the minimum horizontal error, showed a frequency distribution similar to that for the minimum horizontal error (Figure 4.3.2.3). About 60% of the accessions exhibited slope adjusted error values lower than 1 km. The slope-weighted horizontal error is considered here as a surrogate of the error in elevation that is produced by the average slope of the area under consideration, in which case errors above 1 km in steep areas as the Andes may be significant.

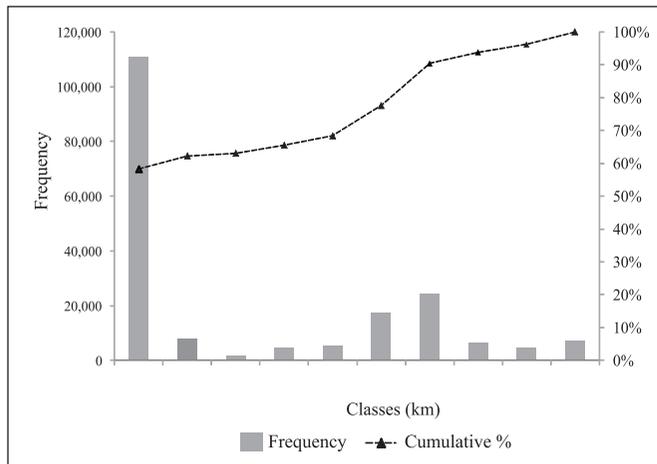


Figure 4.3.2.3. Frequency distribution for the slope-weighted horizontal error in the Darwin-Hernandez Database. First period of revision and error estimation in 2007. This type of error was calculated multiplying the minimum horizontal error (km) by the average slope (percentage) in the area around the georeference (for details see text).

During the second period of error calculations in 2008, nearly 89% of accessions exhibited a minimum horizontal error lower than 1.5 km and about 10% more presented error values between 1.5 and 2 km (Figure 4.3.2.4). These results represent an increase of about 20% in the proportion of accessions with values of error lower than 1.5 km in relation to results from the first phase in 2007. In addition, it was recorded an increment of nearly 10% in the proportion of accessions with error values in the interval 1.5–2 km. Accessions in intervals of error higher than 2 km just added up about 0.5% of the total, decreasing in more than 25% in their frequency in relation to 2007. Indicating a significant filtering and cleansing of the database over its previous version. Similarly, for the collection-event horizontal error more than 90% of accessions had values lower than 1.5 km (Figure 4.3.2.5). However,

differently to the minimum horizontal error the next interval of error (1.5–2 km) held a very low number of accessions.

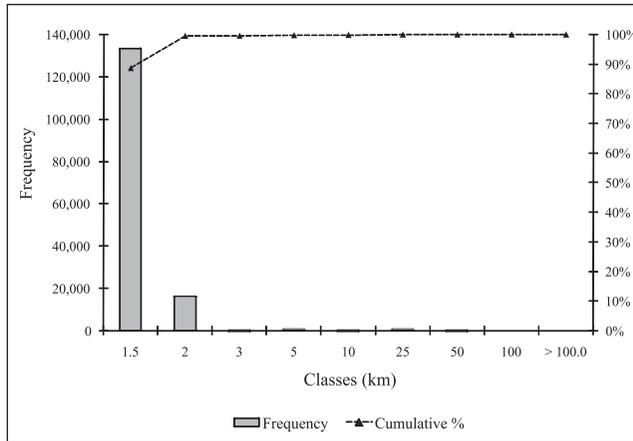


Figure 4.3.2.4. Frequency distribution for the minimum horizontal error in the Darwin–Hernandez Database. Second period of revision and error estimation in 2008.

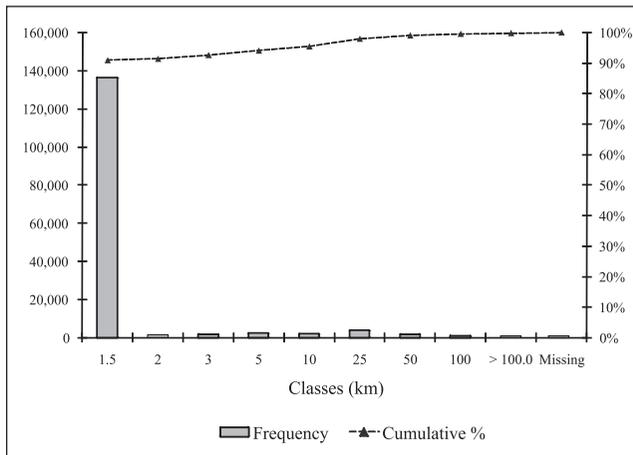


Figure 4.3.2.5. Frequency distribution for the collection–event horizontal error in the Darwin–Hernandez Database. Second period of revision and error estimation in 2008.

4.3.3. Filtering of the database

As result of the filtering process, eight different filtered versions of the database were produced (Table 4.3.3.1), six during the first revision period in 2007 and two more

during the second period in 2008. Although during the second period, some filtering criteria were relaxed, especially in terms of the error threshold selected to filter out accessions, filtered datasets in the second period retained fewer accessions than those produced in 2007, which we believe reflects overall an improved assessment of georeferencing uncertainty and more stringent quality controls of the information.

Table 4.3.3.1. Different datasets produced during the filtering process of the Darwin–Hernandez Database. Datasets are organised as they were produced chronologically.

Year*	Dataset name	Accessions retained	Filtering process details
2007	BioMap–Fil500	174,330	Deleted records with uncertain and non–continental localities, incomplete taxonomy, and attached species out of 500 m buffered altitudinal distribution known range
2007	BioMap–FilDated	149,649	Deleted records without complete date of collection, uncertain and non–continental localities and incomplete taxonomy
2007	BioMap–FilDated700	146,297	Same as BioMap–FilDated plus deleted records with attached species out of 700 m buffered altitudinal distribution known range
2007	BioMap–BasicFil	195,090	Deleted records with uncertain and non–continental localities, and incomplete taxonomy
2007	BioMap–BasicFilHP	169,221	Same as BioMap–BasicFil plus deleted records with localities in areas with average slope > 5% and slope–weighted horizontal error > 1 km
2007	BioMap–BasicFilHP700	126,914	Same as BioMap–BasicFilHP plus deleted records with attached species out of 700 m buffered altitudinal distribution known range
2008	BioMap–BasicFilHP_v2	141,140	Same criteria as BioMap–BasicFil plus deleted records with localities in areas with average slope > 5% and collection–event horizontal error > 2 km
2008	BioMap–BasicFilHP_v2_1950	69,059	Same as BioMap–BasicFilHP_v2 plus deleted accessions with incomplete recorded date of collection or collected before 1950

* Year when was generated the particular dataset.

4.4. Discussion

At the beginning of this study from 3,866 localities present in the Darwin–Hernandez dataset, 714 ($\approx 18.5\%$) had not been georeferenced. This represents a relatively minor proportion of the localities, if compared to similar projects such as Project MaNIS (Mammal Networked Information System). Project MaNIS compiled information of 17 different natural history archives in North America and at its initial stage about 260,536 localities were not georeferenced, $\approx 90\%$ of the total (Wieczorek *et al.*, 2004). Furthermore, for the same project, from those localities already georeferenced about 28,382 ($\approx 80\%$) had no documentation regarding the methodologies used in the georeferencing process, the assumptions and the uncertainty attached to them (Wieczorek *et al.*, 2004). Moreover, globally it has been estimated that just about 1% of more than one billion biological specimens held in natural history archives and herbaria have been georeferenced, which represents a major limitation to use of this information in spatial analyses and geographical range modelling of species (Guralnick *et al.*, 2006 and references therein). Similarly, to project MaNIS, Project BioMap had most accessions without any georeference at the start of the project. In this sense, when the database was compiled a list of 8,135 localities existed. This initial list had many duplicates, errors in coordinates and approximately 50% of localities lacked a georeference. Project BioMap revised and curated the database, reducing it to a list with 3,866 localities with metadata regarding coordinates sources (Verhelst *et al.*, unpublished data).

However, although documentation and metadata regarding the georeferencing process in BioMap was relatively accessible for this thesis, still the dataset lacked an explicit assessment of the uncertainties attached to each georeference. In that sense, this study constitutes a first approximation to estimate georeferencing uncertainty for the database based on three different measurements of error: 1) the minimum horizontal error, 2) the slope–weighted horizontal error, and 3) the collection–event horizontal error. The first type of error is based simply on precision in coordinate measurements (Wieczorek *et al.*, 2004), whilst the second and the third are newly developed estimations of uncertainty, which integrate information about the slope to estimate elevational precision and elevation in the landscape to estimate errors on the basis of known elevational limits for the species in each accession.

These georeferencing uncertainty estimations were later used to filter out records with imprecise locality from the database, retaining only accessions with the highest elevational precision. This is particularly important for habitat suitability and niche modelling, since elevational errors may render models useless where climatic gradients with elevation are very well marked, thus locational errors contributing to overestimate the real range of the modelled species. Conversely, insufficient records or an uneven distribution of records within the real species range may produce underestimations

of the modelled range. This study has built upon methodologies used previously by other researchers. First, to revise extensively georeferencing using GIS tools and thus filter out geographical outliers (Hijmans *et al.*, 1999; Hijmans *et al.*, 2000; Hijmans & Spooner, 2001; Hijmans *et al.*, 2005b); and second, in using an explicit assessment of georeferencing uncertainty to filter out records with high error and hence select the most accurate information for posterior habitat suitability and niche modelling exercises (Graham *et al.*, 2008).

Although the approach used in this study was useful to improve information quality, there are still several other sources of uncertainty that still may affect georeferencing in the database, which were not assessed explicitly here. From the different sources of error mentioned by Wieczorek *et al.* (2004), for all georeferences assigned in this study the datum used was documented, since most georeferences were taken from well-known gazetteers. When offset distances and directions were specified, coordinates and error were estimated using the georeferencing calculator of Project MaNIS (<http://manisnet.org/gc.html>). In those cases, it was not possible to address directly the precision of distance measurements, since the means of measurement was usually not documented. The georeferencing calculator was used for just 74 localities with complete offset distance and direction out of 145 ($\approx 51\%$) that had a description of offset distance, representing less than 2% of the total localities in the database.

Map scale may affect georeferences taken from some gazetteers, in cases where georeferences have been taken originally from maps. Therefore, this possibly may be another source of uncertainty for georeferences found in the Darwin–Hernandez Database. In this sense, the most important resources used in this study, Paynter’s (Paynter & Traylor, 1981; Paynter, 1997) and NGA–GNS’ (NGA–GNS, 2007) gazetteers, use as primary source the information listed by the United States Board on Geographic Names (USBGN). According to Wieczorek *et al.* (2006) the error from maps produced by the USBGN at the lowest scales handled by this institution (1:250,000 and 1:1’000,000) are ≈ 695 ft and 2,777 ft, equivalent to ≈ 212 m and 846 m, respectively. In addition, if we assume a chart accuracy of 1 mm for maps produced by “Instituto Geografico Agustin Codazzi” (IGAC) in Colombia, as recommended by Wieczorek *et al.* (2004), the maximum error in the smallest scale IGAC maps (1:500,000) used should be ≈ 500 m. According to the same authors, this precision is equivalent to three times the minimum graphical error detectable, and therefore is reasonable for application to most maps. Project BioMap used IGAC maps to georeference 18 localities, but those were replaced by new or improved precision coordinates in this study; with just two localities remaining georeferenced from maps at a scale of 1:200,000 (maximum error ≈ 200 m).

It is important to notice that probably the most important source of uncertainty not addressed in this study is the extent of the locality. All localities in BioMap

were georeferenced using the point method. This method has the advantage that it is not highly demanding computationally, since each georeference is assigned only a single pair of coordinates. Nonetheless, this has the disadvantage that it considers the collection event occurred in a single site (and thus altitude and climate), when often it may have occurred within an area around a base camp (Wieczorek *et al.*, 2004). In this sense, it may be worth trying to address the extent of the locality in which the collection event occurred, even if there is no explicit information about it in the original specimen tag. Moreover, this is particularly relevant if we consider that in many cases the georeference assigned to a locality does not correspond to the exact description of the locality in the tag, but the seat either of the county or municipality or the third or fourth administrative division (*i.e.* corregimiento, vereda), as is the case for many localities in the Darwin–Hernandez Database. This situation was documented for at least 659 localities ($\approx 17\%$ from the total), which were approximated to the nearest site and 108 ($\approx 3\%$ from the total) more approximated to the first administrative unit. This situation may be particularly important for Andean municipalities where elevational differences within a municipality can be significant. In this region, about 76% of the municipalities are smaller than 500 km², and certainly have irregular shapes. However, if we visualize this area as a regular shape it may represent a square with sides of ≈ 22.4 km or a circle with a radius of ≈ 12.6 km. In both cases, such dimensions will introduce a relatively high uncertainty to the georeference since the real location may be located anywhere within ≈ 12.6 – 15.8 km, which represents a distance over which environmental conditions in the Andes may change rapidly. Despite this, if we consider that usually collectors conducted their activities in relatively accessible areas, near towns and/or main roads, it may be expected that most of the approximated localities may be close to the town main square (where usually is located its seat), or the third or fourth administrative division seat (*i.e.* corregimiento, vereda) assigned in each case, rather than at the extremes of the municipality. However, in reality, it may be not possible to estimate in detail for each accession this type of error, depending of the amount of information contained in the original description of the locality. It is important to also note that the boundaries of municipalities can change over very long time periods such as those represented within the Darwin–Hernandez Database. An analysis of the variability of elevation within each municipal unit would indicate the municipalities for which this type of error will have significant effects on the analysis.

A preliminary examination in changes in the mean temperature and precipitation within concentric areas around the localities in the database evidenced that averaged climatic conditions are relatively constant at distances lower than 10 km (Figure 4.4.1). However, patterns are different between the two climatic variables and, as expected, they exhibit contrasting tendencies regionally. The Andean region showed the highest dispersion in temperature values and a drastic increase in the average temperature

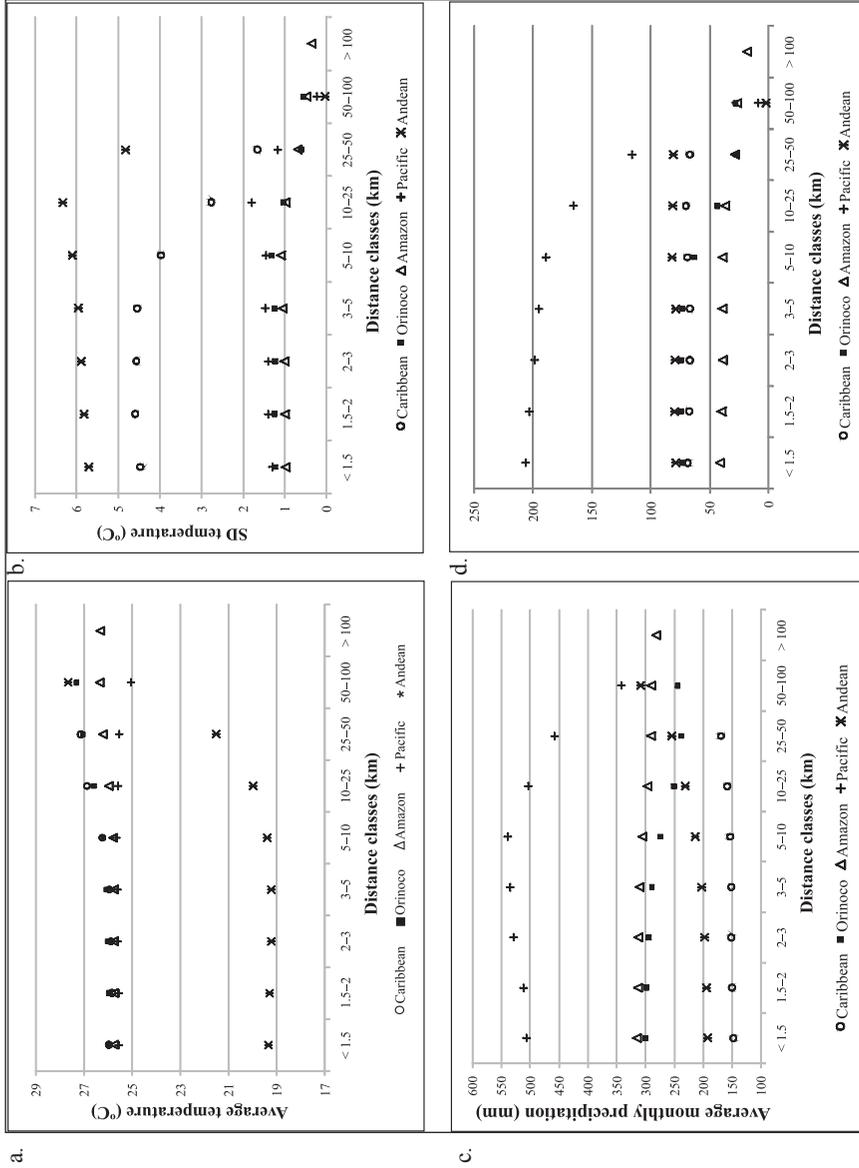


Figure 4.4.1. Changes in average monthly temperature (a.) and monthly precipitation (c.) and data values dispersion (b. and d.) with increments in distance from localities of collection (see text for explanation).

at distances higher than 25 km, while the Pacific region exhibited both the highest averages and dispersion values for the average monthly precipitation. Furthermore, it was noticeable a slight increase in the variability of temperature values with increments in distance, particularly in the Andean region. Contrastingly, in the Pacific region it was noticed a decrease in the variability of the monthly precipitation values. In addition, the dispersion in temperature values in the Caribbean region exhibited a similar pattern to that observed in the Andean region, which very likely is caused by the presence of the Sierra Nevada de Santa Marta. Overall, these results suggest that georeferencing uncertainty may have a higher impact in habitat suitability and niche models performance for taxa occupying the Andean, Pacific and the Sierra Nevada de Santa Marta in the Caribbean than for taxa occupying the Amazon and Orinoco. Nonetheless, the generation of models at higher grains averaging climatic conditions may contribute to dilute effects of these errors.

During the first revision period, false precision in coordinates constituted an important source of uncertainty. Wieczorek *et al.* (2006) defines “false precision” as the overestimation in precision that results from the use of many decimals obtained in coordinate transformation. In the Darwin–Hernandez Database, most georeferences were converted from degrees and minutes to decimal degrees, and hence it was expected many georeferences to include that particular type or error. This was the case for at least 2,048 localities documented as drawn from Paynter’s gazetteers (Paynter & Traylor, 1981; Paynter, 1997). Other localities georeferenced from more recent gazetteers that use as a primary source of information the listings published by the United States Board on Geographic Names (ADL, 2007; NGA–GNS, 2007) are less likely to present this problem. The maximum precision of gazetteers such as Paynter’s is 1 minute, equivalent to 0.01° , which at the latitudes Colombia is placed represent $\approx 1,500$ m. In fact, when this source of error was corrected during the second revision period in 2008, a major portion of georeferences showed a minimum horizontal error close to this value.

In addition, misplaced georeferences for linear named features such as rivers and mountains comprised another source of uncertainty. In those cases, gazetteers usually assign coordinates at the mouth of the river or the top of the mountain that in many cases may be far from the actual site of collection, especially for long rivers or large mountain systems. During the second revision period in 2008 683 localities related to rivers and streams were revised (*i.e.* “rio”, “río”, river, “quebrada”, “caño”). From that pool of localities, for 165 localities coordinates were changed to NGA–GNS’ gazetteer (NGA–GNS, 2007) locations improving their precision. Independently of this, for a total 241 localities coordinates were adjusted manually using Google Earth combined with the altitude information recorded on the accession. Moreover, 112 localities referring to rivers and streams were highlighted to be deleted since

uncertainty in locating the georeference was very high. On the other hand, for the 92 localities linked to mountain systems (*i.e.* “sierra”, “serrania”, “cuchilla”, “cerro”) it was not possible to make many changes since the best georeference was already in place, usually the approximate geographical centre, as recommended by Wieczorek *et al.* (2004) and not good enough for this analysis.

Wieczorek *et al.* (2004) identify three types of descriptive localities that in any case must not be georeferenced or used: 1) dubious localities, 2) localities not possible to locate, and 3) demonstrably inaccurate localities. Those types of localities were not georeferenced in this study, or when previously georeferenced as was the case for some dubious localities or localities approximated only to the first administrative division level, the type of assumption made was documented. In all cases, those types of localities were considered in the filtering process to be deleted systematically and thus not used in subsequent analyses.

At the outset of this study, some still unresolved synonymies were found in the taxonomy table of the Darwin–Hernandez Database. However, most of these synonymies were attached to old records from the “Bogota trade skins”, accessions that were filtered out from the database since they had highly uncertain localities. Moreover, in the first year, accessions with a slope–weighted horizontal error higher than 1 km and placed in an area with a slope greater than 5% were filtered out, whilst in the second year accessions with a collection–event horizontal error higher than 2 km and placed in an area with a slope higher than 5% were filtered out. Differences in retained accessions between these years resulted from differences in the way slope was calculated each year. Thus, during the first year it was estimated as the neighbourhood average, whilst in the second year it was calculated as the neighbourhood majority (*i.e.* mode) within areas defined by the different type of error used each time. As a central tendency measure, the average is greatly affected by extreme values, resulting in this case in associated slope values with a highly positively skewed frequency distribution (Figure 4.4.2a). On the other hand, the use of the slope majority reduced the effect of extreme values, reflecting better the predominant topography of the area demarcated by the error; although exhibiting still a positively skewed frequency distribution (Figure 4.4.2b) and permitting a more accurate filtering of those accessions located in the Andean region.

As an important extension of this work, uncertainty estimates were used to define a spatial grain at which habitat suitability and niche modelling exercises should be conducted given the remaining uncertainties in the biological and environmental data. Results in the first revision period in 2007 suggested the use of a minimum grain of 2 km, whilst results during the second period in 2008 suggested a minimum grain size of 3 km. Graham *et al.* (2008) recently found evidence suggesting that error in georeferencing may have an effect in species range model performance. These authors

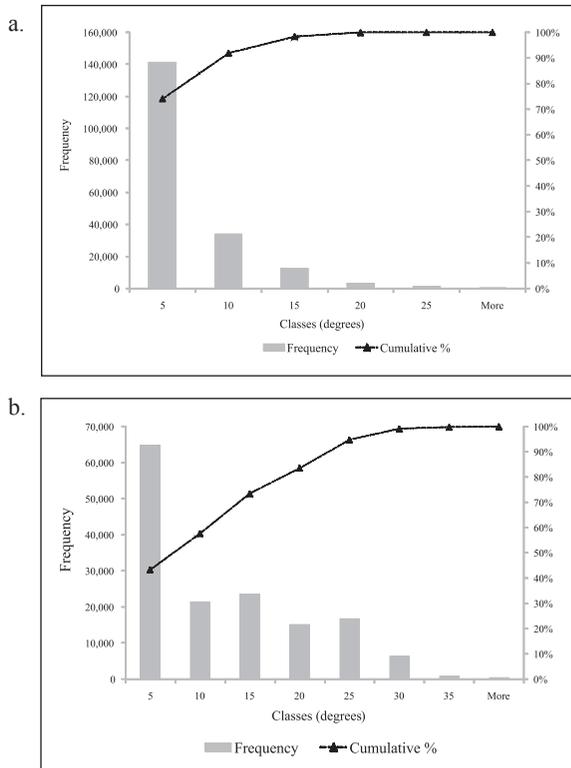


Figure 4.4.2. Frequency distribution of error estimations associated slope for localities in the Darwin-Hernandez Database. Although in both periods distributions were skewed to the left, during the first period of revision 2007 (a.) values are mostly in the first two classes, while in the second period in 2008 (b.) values are more spread in higher classes. Differences result from the use of different estimators in each period (see text for details), which have important effects in the filtering process and accessions retained.

modelled the geographical range of 40 different species in four different regions at a very high resolution (100 m) from occurrence data georeferenced using GPS in the field, which is highly accurate (<30 m). To test the effect of error they degraded the data adding error to coordinates generated at random from a normal distribution with mean 0 and standard deviation of 5 km, which they assume may be similar to the type of error contained in museum specimens' georeferencing. Their results showed that some modelling techniques are affected more than others, although models produced using degraded data still gave reasonable results, especially when using Boosted Regression Trees and MAXENT modelling techniques; exhibiting values for the Area Under the Curve (AUC) statistic higher than 0.75. These results are very promising since they suggest that even not accounting for all sources of uncertainty, presence-only data from secondary sources of information such as museums and

herbaria, in this case the Darwin–Hernandez Database, may be used successfully in habitat suitability and niche models obtaining reasonably accurate results. However, a limitation of this study is that the error inherent in museum specimens' georeferencing might not be normally distributed in the way that Graham's errors are. Moreover, error may be structured spatially and its effects may depend on the type of species being modelled (*e.g.* mountain *vs.* lowland species, sedentary *vs.* mobile species, *etc.*) and the nature of local environmental heterogeneity, which may differ between Graham's study and the current study. In fact, Graham *et al.* (2008) found differences in the effect of error between the different regions modelled and explain those as the result of differences in the spatial heterogeneity in environmental layers and the type of species modelled in each area; although they believe the latter is more important in explaining those differences.

In summary, secondary sources of information such as natural history museum and herbaria data are becoming increasingly freely available and constitute a unique resource to explore biodiversity at national scale, regionally and globally. Nevertheless, georeferencing and georeferencing practices represent a major limitation to fully use this information in GIS applications such as for example habitat suitability and niche modelling. To tackle error in databases containing this type of information it is desirable: 1) to revise thoroughly the data and georeferencing using GIS tools, 2) to produce georeferencing uncertainty estimations as completely as possible, and 3) to eliminate highly inaccurate accessions from the database.

The implementation of such an approach in the Darwin–Hernandez Database produced by Project BioMap was of great value in improving data quality aiming to make a better use of information in biodiversity science for Colombia. However, georeferencing uncertainty estimation is limited by error inherent in the use of ornithological gazetteers for post-collection georeferencing based on specimen tag placenames. First, because of the approximation, in ornithological gazetteers, of nearby localities of collection in one point, not defining explicitly the extent from the point to each locality and second because the approximation of not georeferenced localities in gazetteers to nearby localities when interpreting their descriptions in a retrospective georeferencing process. A possible solution to this problem is to go back to the original field diaries of collectors, when available, to clarify the interpretation of the described localities in the retrospective georeferencing process, though this would be extremely costly in resources and effort. Even more importantly, these difficulties highlight the relevance to adhere to clear georeferencing practices such as those described by Wieczorek *et al.* (2006) for future collections, trying as much as possible to produce georeferences of high accuracy taken in the field using GPS receivers.

CHAPTER 5
PATTERNS OF BIRD DIVERSITY AND RARITY

Summary –After assessing the quality of the species information in order to improve the utility of the database (Chapter 4), in this new chapter several purged versions of the database were used to map bird diversity in Colombia using different approaches.

First, BioMap–Fil500 dataset (generated in 2007) was used in DIVA–GIS to explore species richness at different grain sizes combining different techniques and richness estimators. Second, habitat suitability models and potential geographical ranges were generated at family and genus hierarchies using the dataset BioMap–BasicFilHP (generated in 2007) and MAXENT, and richness estimated by overlaying produced maps. Third, after completing a second round of revisions and corrections to the database in 2008, a second generation of mapping exercises conducted began testing the influence of sample size, number of replicates and grain size in model performance using newly improved datasets (BioMap–BasicFilHP_v2 and BioMap–BasicFilHP_v2_1950). Results were used to produce later habitat suitability models and consensus potential range maps for each modelled taxon according to the best performing criteria. Once appropriate methodologies were finely tuned, by reducing sampling bias, eliminating the richness–effort relationship and increasing mapping accuracy, there were integrated other measures of diversity such as the “weighted endemism score” and two new indices of ecomorphological diversity proposed and tested for hummingbirds and tyrant flycatchers, families Trochilidae and Tyrannidae respectively. Otherwise, final richness maps were cross–validated comparing them to richness maps elaborated using the geographical range maps from the “Western Hemisphere Digital Bird Distribution Database” and data obtained from field surveys conducted by ProAves in 76 sites distributed across West Colombia.

Results evidenced differences between the several biodiversity–mapping approaches used. It is hypothesised here that these are caused mainly due to: 1) the lack of appropriate sampling of particular zones in the country, 2) omission error increasing in taxa with a low number of sample localities, and 3) the failure to model some taxa due to lack of data. However, the thorough assessment of differences between mapping techniques as conducted in this study is helpful to better understand how sampling and effort bias affects diversity estimation in particular zones of the country.

Despite these inaccuracies, the use of “explicitly–modelled” maps to study diversity patterns in Colombia using most Colombian bird taxa represents a major advance in biodiversity science in the country. Moreover, the comparative study of different types of maps as conducted here, as well as the continuation of studies refining functional measures of diversity represents a unique opportunity to advance further biodiversity knowledge in the country and bring closer the concepts of biodiversity and ecosystems services. Additionally, other possible directions to continue research in this field may include the generation of hybrid maps based on both “explicitly–modelled” and “expert–drawn” maps.

5.1. Introduction

The rapid rate at which processes such as deforestation and habitat fragmentation are advancing worldwide demands careful planning and well thought through conservation strategies based on cutting edge scientific developments; aiming to secure the protection of biologically important natural ecosystems.

The paucity of primary data on biodiversity collected in the field in the megadiverse tropics has encouraged the development of a wide array of habitat suitability and niche modelling techniques with the aim of predicting as accurately as possible species geographical ranges. These modelling techniques combine species and environmental data and use different statistical methodologies in a GIS to produce probabilistic surfaces, which reflect how suitable a specific set of environmental conditions is for a particular species (Graham *et al.*, 2008). In this context, in the last two decades several modelling approaches have been developed that use either only–presence or presence–absence data to predict species geographical ranges. Some examples of the most used approaches in the literature are: BIOCLIM (Nix, 1986), DOMAIN (Carpenter *et al.*, 1993), GARP (Stockwell & Noble, 1992; Anderson *et al.*, 2002a; Anderson *et al.*, 2002b; Stockwell & Peterson, 2002; Anderson *et al.*, 2003), MAXENT (Dudik *et al.*, 2004; Phillips *et al.*, 2004; Phillips *et al.*, 2006), and Logistic Generalised Linear Models (GLM) and General Additive Models (GAMs) implemented in GRASP (Pearce & Ferrier, 2000; Guisan *et al.*, 2002; Lehmann *et al.*, 2002, 2003), *etc.* The same modelling techniques have also been used, increasingly, in ecological and biogeographical research to study a wide spectrum of topics. Such as for instance the attributes of species niches, niche conservatism in time, potential effects of climate change, species competitive interactions, biological invasions dynamics and to generate baseline maps for conservation planning and threatened species management (Peterson *et al.*, 1999; Anderson *et al.*, 2002b; Peterson *et al.*, 2002; Loiselle *et al.*, 2003; Peterson *et al.*, 2003; Graham *et al.*, 2008).

In many instances of ecological and biogeographical research, richness maps in grid format constitute the baseline data for analysis (Graham & Hijmans, 2006), such as

for example in studies defining biodiversity patterns, endemism hotspots, correlation of biodiversity patterns with the environment and for conservation planning (Pressey *et al.*, 2003; Barthlott *et al.*, 2005; Field *et al.*, 2005; Küper *et al.*, 2005; Davies *et al.*, 2007a; Kreft & Jetz, 2007). However, richness maps can be created using different approaches. The two most common methods include: 1) counting individual point occurrences for all species present within grids for a specific area, country, region or continent, and 2) overlaying individual maps of the geographical ranges of all species that inhabit a specific area, country, region or continent (Graham & Hijmans, 2006). The first method has the advantage that it uses raw data from primary or secondary sources of information, such as field surveys or museum holdings, respectively. Nonetheless, estimations of richness obtained by this method are strongly influenced by effort; and consequently, they may be spatially skewed due to bias in sampling effort and/or may be underestimated in areas that have been not sufficiently sampled (Hijmans *et al.*, 2000). Moreover, the accuracy of this method varies with grain size, with increasing accuracy at lower resolution (*i.e.* larger grain) (Graham & Hijmans, 2006), possibly because of a stabilisation of the relationship species–area–effort relationship. On the other hand, the second approach may use maps of the “potential” geographical ranges either drawn by experts or explicitly modelled using habitat suitability and niche modelling techniques (Graham & Hijmans, 2006). Overall, both types of maps represent abstractions from reality and, therefore, they constitute two different types of models. Although, to different degrees, they are both predominantly representations of the “extent of occurrence” (*sensu* Gaston, 1994) of species geographical ranges, since they represent the “potential” geographical range. The areas where mapped species actually occur, or “area of occupancy” (*sensu* Gaston, 1994), may be much smaller. However, it is interesting to note, as Graham & Hijmans (2006) do, that “expert–drawn” range maps may integrate different degrees of information and knowledge about the ecology of mapped species. Thus, they may be as simple as a polygon joining the extremes of known points of occurrence of a species to more sophisticated maps using elevational distribution limits, habitats occupied by the species, natural barriers, *etc.* to refine the “potential” geographical range map. In that sense, “expert–drawn” range maps are the result of a non–explicit modelling process. However, “explicitly–modelled” range maps have the advantage that rely on a systematic and repeatable process and are thus more transparent regarding the assumptions made in generating the range maps. In addition, the process in itself helps in better understanding the factors limiting and controlling geographical ranges. Otherwise, “explicitly–modelled” approaches have the disadvantage that sometimes they do not capture the complexity of phenomena involved in defining geographical ranges that “expert–drawn” range maps sometimes do.

Despite the importance of richness maps in ecological and biogeographical research, patterns and inferences made from maps resulting from different methodologies have

been compared very few times. Agreeing with Graham & Hijmans (2006), it is expected that richness maps obtained from counting individual point occurrences for species within grids may exhibit higher false negative (omission) errors (*sensu* Fielding & Bell, 1997; Anderson *et al.*, 2003) than other techniques, because of sampling effort bias and insufficient sampling. Conversely, maps generated by overlaying “expert-drawn” geographical ranges would tend to show higher false positive (commission) errors (*sensu* Fielding & Bell, 1997; Anderson *et al.*, 2003), since maps are usually created drawing coarsely range limits; and therefore, to overestimate richness. Otherwise, maps elaborated by superimposing “explicitly-modelled” geographical ranges using habitat suitability and niche modelling techniques are expected, if highly accurate, to present a lower rate of omission errors than counts and a lower rate of commission errors than maps obtained overlaying “expert-drawn” geographical ranges. However, this may not necessarily be true if for instance occurrences used for modelling are spatially biased or if the sample fails to capture the whole range of conditions under which the species occur, which may then lead to a greater rate of omission error (Graham & Hijmans, 2006).

Graham & Hijmans (2006), comparing maps resulting from different methodologies when mapping the richness of terrestrial amphibians and reptiles in California, found that different approaches may lead to different modelled patterns of richness. In general, their results showed, as expected, that maps derived from counts within grids had the lowest values of richness, apparently underestimating it. On the other hand, overlaying of “explicitly-modelled” ranges resulted in the highest estimations of richness, whilst superimposing of “expert-drawn” ranges exhibited intermediate values. It is interesting to highlight also, that correlations between maps derived from different approaches showed low coefficients (< 0.5) at high resolutions (1 km), although those increased to medium-high values (≈ 0.7) at low resolutions (50 km).

Since the Convention on Biological Diversity (CBD, 1992) it has become evident that if we intend to conserve biodiversity, we do need to address more than the number of species in a site. Thus, it is required to understand how different elements and hierarchies of biodiversity work and interact. In this context, the relatively new concept of “functional diversity” has emerged in ecology. According to Tilman (2001) functional diversity is defined as “those components of biodiversity that influence how an ecosystem operates or functions”.

Ecological indices focus mainly on species and their abundances, and therefore, are probably not appropriate to measure functional diversity and the potential services offered by the specific species assemblage of a community; at least if used in their conventional forms. Consequently, in recent years other ways of using existing indices and/or new indices have been proposed for the measurement of different features of communities and/or ecosystems in more appropriate ways (see Chapter 2, section 2.1.3).

Regardless of the importance of the concept of community diversity in ecology, there is still no complete consensus on how to measure it (Ricotta, 2005b). In this sense, as just mentioned, many different indices have been proposed in the literature (Magurran, 2004; Ricotta, 2005a). However, there is still decoupling between the properties measured by those indices and the way the possible implications that diversity may have on ecosystems are addressed, which make it difficult to test its role (Ricotta, 2007). To avoid this, first, it is necessary to identify constituent elements within diversity by generating a framework in which it is possible later to explore their connection to ecosystem functioning (Ricotta, 2007). This requires, in agreement with Ricotta (2007), a rigorous conceptualisation of the meaning of diversity. Thus, although the field has achieved great progress, most of it has been based on experimental and observational studies conducted in plant physiology at relatively small spatial scales (Schulze & Mooney, 1994; Chapin III *et al.*, 2000). Consequently, still there is great need to advance in indices, conceptualisation, definition and mapping, especially for Animalia groups.

On the other hand, to date, large-scale mapping of functional diversity has been very limited and has been mainly connected to global climate change studies. In this context, the so-called Dynamic Global Vegetation Models (DGVMs) have been developed. In general terms, DGVMs connect vegetation dynamics and major biogeochemical cycles, such as water and carbon cycles (Bachelet *et al.*, 2003). DGVMs model both individual and population processes such as photosynthesis, transpiration, competition, growth and disturbance regimes (Sitch *et al.*, 2003). The models use plant functional types (PFT) rather than species due to the obvious difficulty in gathering and processing data at species level for continental or global scales (Thuiller *et al.*, 2006); defining the functional types according to morphological and physiological attributes of the vegetation (Bonan *et al.*, 2003). Furthermore, DGVMs have proved successful in reproducing vegetation patterns in accordance with empirical data, and have been used to generate projections under past and future climatic conditions (Sitch *et al.*, 2003). However, both the biological (*i.e.* PFT) and geographical ($\approx 0.5^\circ \times 0.5^\circ$) resolution of these models is very coarse, limiting their usefulness for sub-global studies.

In this sense, in agreement with Thuiller *et al.* (2006), there is still a lack of studies connecting DGVMs with more detailed models of geographical range shifts at finer levels in the biological hierarchy, and in turn linking those to ecosystems and functional diversity. The same authors, in one of the few studies of this type, used habitat suitability and niche modelling to explore the effects of climate change on tree species distributions and its effects on functional diversity in Europe. They used current climatic conditions to model the geographical ranges of 122 tree species projecting generated models in climate change conditions for the year 2080. Moreover,

they estimated functional diversity using four PFTs and calculated it as the evenness in the number of species through all functional types; as the Simpson Diversity Index (D), $D = 1 - \sum_{i=1} p_i$, where p_i is the proportion of the total of the number of species (s) of a particular PFT in a pixel. The separate analysis of species geographical range prediction and diversity proved valuable to achieve a better understanding of probable future biogeographical scenarios (Thuiller *et al.*, 2006). Although, this research used greater detail than DGVMs, still projections of this study were generated at a coarse scale (50×50 km), which still restricts its use for regional and local analyses.

Hereafter we, first, present bird richness maps produced for Colombia using the Darwin–Hernandez Database and DIVA–GIS and MAXENT at different taxonomic levels, evaluating any correlations between bird richness and sampling effort. Second, we present two new indices of functional diversity mapped for hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae), based on equivalent species and modified by a morphological index. Finally, third, we evaluate map results against two independent sources; ProAves Foundation field data (Proaves, 2008) and expert–drawn maps from the Western Hemisphere Digital Bird Distribution Database – WHDBD Database (Ridgely *et al.*, 2007).

5.2. Methodology

Bird diversity mapping was conducted using different methodologies and filtered datasets aimed to conserve as much as possible information in the dataset whilst in successive steps eliminating spatial sampling effort and area size bias. Initial tests focused on richness (number of taxa in a specific taxonomic level) to measure diversity. First, BioMap–Fil500 dataset⁷ was used in DIVA–GIS to explore species richness mapping at different grain sizes combining different techniques and richness estimators. Second, after results showed the inadequacy of this method, because of the strong correlation between richness and effort (section 5.3.2), it was decided to generate habitat suitability models and potential geographical ranges at family and genus taxonomic levels using BioMap–BasicFilHP⁸ and MAXENT, and estimate richness by overlapping the produced maps.

Family and genus taxonomic levels are not the usual taxonomic levels employed when modelling niche and habitat suitability, possibly because of the tacit connection between the classical niche concept (Chapter 2, section 2.2.1) and the classical

⁷ BioMap–Fil500 dataset: 174,330 accessions retained. Deleted records with uncertain and non–continental localities, incomplete taxonomy, and attached species out of 500 m buffered altitudinal distribution known range.

⁸ BioMap–BasicFilHP dataset: 169,221 accessions retained. Deleted records with uncertain and non–continental localities, and incomplete taxonomy, plus deleted records with localities in areas with average slope > 5% and slope–weighted horizontal error > 1 km.

biological concept of species (*sensu* Mayr, 1963), both of them deeply rooted in long-held ecological thinking and still having a remarkable influence today. This renders the niche as a unique property of the species. Nonetheless, both genus and family taxonomic levels are suggested here as appropriate for spatial distribution modelling for at least five different reasons. First, as conducted here, distribution models link climate variables to a probability of occurrence, and therefore they represent habitat suitability models for a taxon rather than niche models *per se*, which would relate the environment to the fitness of the species (Hirzel & Le Lay, 2008). In this sense, as long as relationships exist between climate and the spatial distribution of the modelled taxon, the taxonomic level at which models are developed should not matter, since spatial distributions would be modelled according to the climate–distribution relationships for that particular taxon. Second, considering that in this study models are developed under a framework closer to the Grinnellian and/or the Hutchinsonian fundamental niche, they have the advantage that relax assumptions regarding processes and mechanisms, such as biological interactions, involved in the definition of the Eltonian and/or the Hutchinsonian realised niche (Chapter 2, section 2.2.3). Such processes have an important role in the definition of the Eltonian and/or the Hutchinsonian realised niche, and have a strong influence at local scales at species level. Thus, the models generated here represent more transparently habitat suitability at the scales studied, both spatially and taxonomically. Third, the use of higher taxonomical levels is convenient in order to aggregate more data within each taxon, thus generating models that are more accurate and represent a greater proportion of the avian taxa from the country. Fourth, given the proven correlation between diversity through taxonomic levels within the same group (Gaston, 1996a and contributions therein), we believe that modelling at higher taxonomic levels, although possibly reducing biological detail, still should reflect general diversity patterns in the country at infrageneric levels. Finally, fifth, species richness *per se* is not necessarily the best diversity index, since it does not integrate wider biological hierarchies *sensu* Noss (1990) or add in understanding diversity from other perspectives and metrics (*e.g.* ecological, taxonomic, phylogenetic, *etc.*) (Chapter 2, section 2.1.3). In this sense, a multi taxonomical level modelling, as conducted in this study permits a deeper insight into diversity patterns within different taxonomic levels, which may contribute to understand better mechanisms and processes operating at those levels.

Finally, as part of a second generation of analyses conducted after completing the second phase of georeference revision and correction, error estimation, and once having prepared all necessary bird and environmental datasets, an experiment to test the influence of sample size, number of replicates and grain size on model performance was performed. Results were used to produce habitat suitability models at different taxonomic levels according to the best performing criteria and produce consensus potential range maps for each modelled taxon. Additionally, once

appropriate methodologies were finely tuned, different measures of diversity were integrated, such as the “weighted endemism score” (Crisp *et al.*, 2001) and two new ecomorphological measures of diversity proposed for the first time in this work and tested for hummingbirds and tyrant flycatchers, families Trochilidae and Tyrannidae respectively. Finally, richness maps were cross-validated comparing them to richness maps elaborated using the geographical range maps from the “Western Hemisphere Digital Bird Distribution Database” (Ridgely *et al.*, 2007) and data obtained from field surveys conducted by the ProAves Foundation in 76 sites distributed across the Colombian Andes and north and west of them (Proaves, 2008).

5.2.1. DIVA–GIS mapping exercises

The BioMap–Fil500 dataset was used in DIVA–GIS to produce effort and species richness maps at different grain sizes combining two point–to–grid conversion procedures and several richness estimators. To start, effort (number of collected specimens) and species richness maps were produced using the simple point–to–grid conversion procedure (Hijmans *et al.*, 2005b), at grain sizes from 0.03125° to 1° (≈ 3.75 – 120 km). Additionally, maps were built using the circular neighbourhood point–to–grid conversion procedure (Hijmans *et al.*, 2005b), at grain sizes from 0.06251° to 1° (≈ 7.5 – 120 km); and a neighbourhood of 1 and 2 map units. Effort and species richness were mapped as well at municipal and departmental level using the point–to–polygon conversion procedure (Hijmans *et al.*, 2005b).

After those initial maps were completed, and considering the first generation of results obtained regarding the minimum horizontal error (Chapter 4, section 4.3.2), it was decided to generate species richness estimators’ maps at 0.125° (≈ 15 km) grain size. For this purpose, the simple and the circular neighbourhood (neighbourhood of 1 map unit) point–to–grid conversion procedures in DIVA–GIS was used. The estimators used were: Chao1, Chao1 Corrected, Chao2, Chao–Lee, Jackknife1, Jackknife 2, Raaijmakers and Rarefaction Analysis (Hijmans *et al.*, 2005b). Additionally, the species turnover rate was estimated using the Whittaker Index (Hijmans *et al.*, 2005b).

Finally, any possible correlation between effort and species richness was evaluated. Thus, maps produced using the simple point–to–grid conversion procedures at ≈ 15 , ≈ 30 , ≈ 60 and ≈ 120 km were exported as *.txt files from DIVA–GIS and imported in Excel where both variables were plotted at different grain sizes. Furthermore, DIVA–GIS was used to produce frequency distribution plots of grid cells mapped into effort intervals, which were exported also to Excel.

5.2.2. Habitat suitability modelling: first generation

Due to the inadequacy of the first methodology proposed to map bird richness, because of significant spatial concentration of effort in the database and the strong

correlation found between richness and effort (section 5.3.2), it was decided to use habitat suitability modelling in a taxon-based approach as an alternative. In this way diversity is mapped using the geographical range of each individual taxon as the primary source of information, and all geographical ranges are then superimposed using different algorithms to obtain a specific estimate (Mutke *et al.*, 2001). For this first generation in particular, the potential geographical range of each bird taxa at family and genus taxonomic levels was modelled using MAXENT (Dudik *et al.*, 2004; Phillips *et al.*, 2006), and diversity estimated adding all modelled potential geographical ranges at each specific taxonomic level.

Prior to modelling, a Principal Components Analysis (PCA) of the 19 BioClim variables for current climate conditions, clipped to Colombia at ≈ 1 km, was performed using ENVI 4.3 to decide which variables explained better the total variability observed among them. ENVI 4.3 PCA calculated the eigenvalue for each variable and the correlation matrix. Results showed a strong correlation within two main groups of variables, those related to temperature and those related to rainfall. However, the highest eigenvalues were exhibited by those variables related to temperature (Appendix 2). Despite this, it was decided to use those variables explaining most of the variation (*i.e.* with highest eigenvalues) and those that were not highly correlated within each group, aiming to include variables from both groups thought to be important in controlling the ranges of bird species (Table 5.2.2.1).

Table 5.2.2.1. Bioclimatic variables selected for habitat suitability modelling in MAXENT; first generation of analyses.

BioClim code	BioClim variable name	Eigenvalue
BIO1	Annual Mean Temperature	8.016
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	6.614
BIO3	Isothermality (BIO2/BIO7) (* 100)	1.778
BIO4	Temperature Seasonality (standard deviation *100)	1.398
BIO7	Temperature Annual Range (BIO5 - BIO6)	0.098
BIO12	Annual Precipitation	0.005
BIO15	Precipitation Seasonality (Coefficient of Variation)	0.001

Selected geovariables, at ≈ 1 km in ASCII format, were moved to the respective folder in preparation to run habitat suitability models in MAXENT. In addition, BioMap-BasicFilHP (Table 4.3.3.1) dataset was exported separately at family and genus hierarchies in CSV format using just three columns: taxa, longitude and latitude. Models were run for all taxa with at least 15 site localities, using 30% of the

observations to evaluate model performance and 70% for parameterisation. Models were assessed using the Receiver Operating Characteristic Curve (ROC) and the associated Area Under the Curve statistic (AUC) calculated by the software for the test sample in each case. According to Phillips *et al.* (2006) this statistic is useful since it permits the evaluation of models produced from presence-only data points in a single number. Finally, models were run by removing duplicate presence records and setting all other parameters to their MAXENT default values. All resulting maps were produced at ≈ 1 km grain.

For the family level runs, raw cumulative probability results from MAXENT (71 maps) were imported into DIVA-GIS and manually reclassified to produce potential geographical range maps. The equal test sensitivity and specificity (ETSS) threshold⁹ of cumulative probability was used to define areas of presence and absence for each model (Figure 5.2.2.1). Values above the threshold were reclassified as presences (1), meanwhile those below it were reclassified as absences (0). Since this procedure took a long time a batch file was written to import the ASCII files into PCRaster, apply a fixed cumulative probability threshold value, add all potential range maps and finally export the result as an ASCII file. For the batch script, the cumulative probability threshold was always fixed at 30% – the value usually taken by the ETSS threshold.

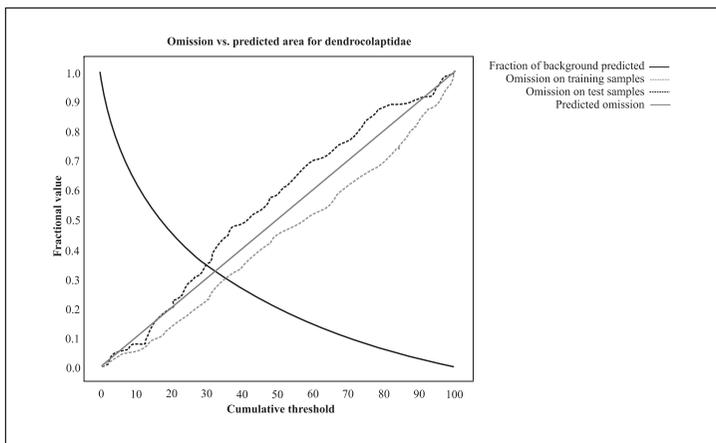


Figure 5.2.2.1. Omission rate (sensitivity) and predicted area (specificity) as a function of the cumulative threshold for Woodcreepers (Family Dendrocolaptidae). Map modelled in MAXENT using BioMap-BasicFilHP. Values above threshold value of equal test sensitivity and specificity (ETSS) were reclassified as presence (1), meanwhile below were reclassified as absence (0).

⁹ Although the threshold used to select areas of presence and absence is subjective, the ETSS threshold is by definition an intuitive approximation to the region where potentially omission and commission errors are more homogeneous.

This permitted a quick processing of files to obtain richness without significant differences from the manual method (Figure 5.2.2.2). This script was especially important at genus level where it was necessary to process 491 potential range maps. Nonetheless, it is important to remember that, although this value was based on the experience developed through the modelling exercises, it was a subjective choice.

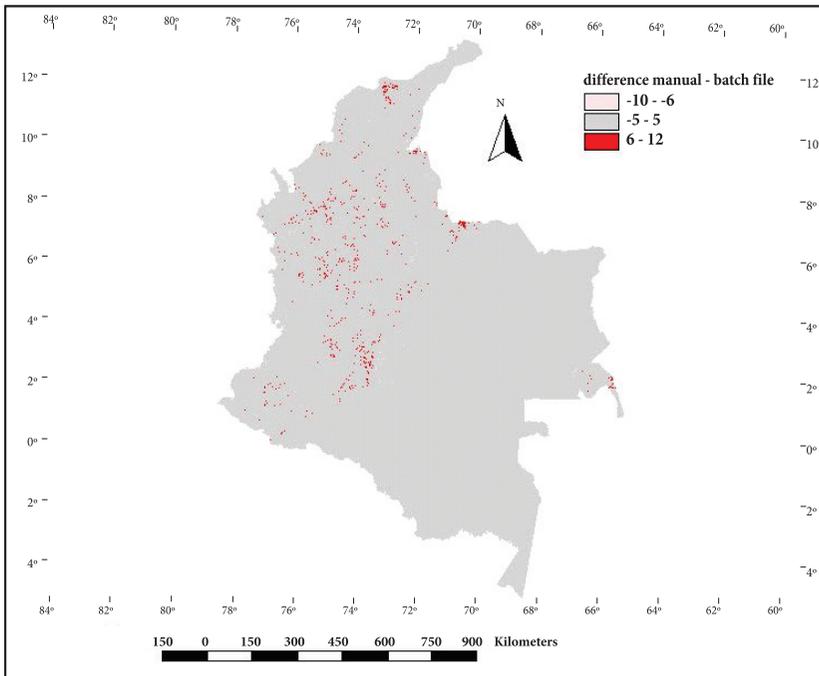


Figure 5.2.2.2. Difference between family richness maps generated using different cumulative probability thresholds. In one case, potential geographical range maps were produced reclassifying manually each raw result map based on the ETSS cumulative probability threshold value and in a second case using a fixed value of 30% (see text for details).

5.2.3. Elimination of richness–effort relationships

Although, this alternative richness mapping methodology using habitat suitability models resulted in improved richness maps, it was soon realised that the richness–effort relationship had not been eliminated completely. To test again the existence of this relationship richness maps were aggregated as a spatial average from original maps at ≈ 1 km to maps at ≈ 120 km in Arc View, meanwhile effort maps were produced in DIVA–GIS at ≈ 120 km grain using the simple point–to–grid conversion procedure. Effort maps were imported into Arc View, and all maps were clipped to the same display extension. Finally, maps were exported as *.txt files and imported

into Excel where richness was plotted against effort for the whole country. In this case, effort was estimated as the total number of site localities per grid and not the number of collected specimens, as was calculated previously. Since MAXENT in this study was set to remove duplicates when generating habitat suitability models, this change was appropriate to assess the density of single sites of collection and therefore to understand better the relationship between richness and effort in the context of MAXENT.

Afterwards, based on results (see results, section 5.3.3), the original bird datasets used for habitat suitability modelling were resampled trying to eliminate the excess of site localities from heavily collected areas (Figure 5.2.3.1) and thereby even out the effort. This approach permitted us to use as much information as possible, while reducing model overfitting to areas with high effort. Resampling was performed manually in Excel from the list of site localities used for habitat modelling. Excel filters were used to obtain the complete sublist of site localities into each area (grid) selected for resampling. Each sublist was copied and each locality given a unique random number. Sublists were sorted in ascending order according to the assigned random number, and the excess of localities, after the 70th locality, were copied to new sublists as localities “to be deleted”. Finally, using the function “vlookup” and

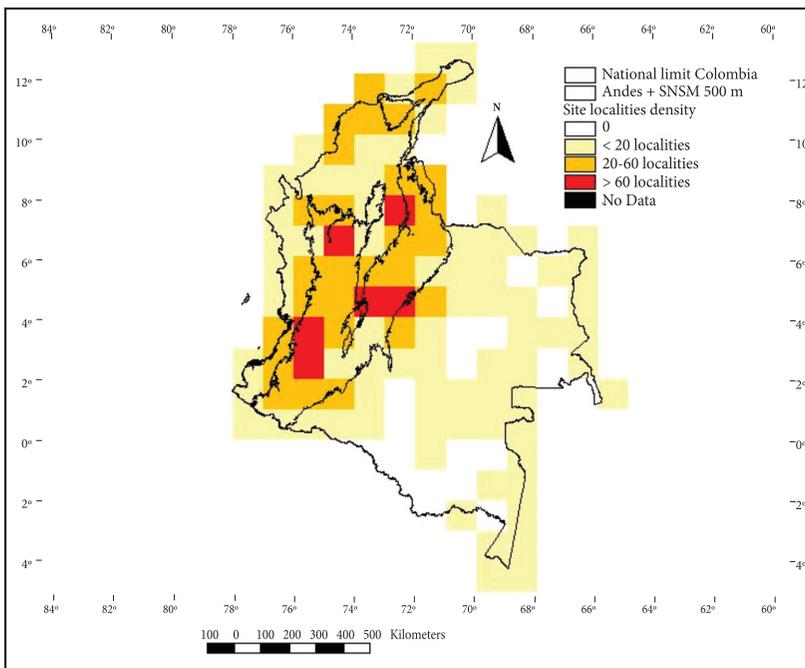


Figure 5.2.3.1. Density of site localities at ≈ 120 km prepared from dataset used to model richness using niche modelling techniques.

the sublists of localities “to be deleted” excess localities were marked for deletion and later eliminated in the original files used for habitat suitability modelling. In this way the excess of sites of collection above the 70th locality for each grid were deleted at random.

Then new resampled files were used to repeat the habitat suitability modelling exercises in MAXENT using the same settings as before (described in section 5.2.2). Finally, the new richness maps were aggregated again at ≈ 120 km and richness plotted against effort for the whole country and West-Colombia separately. West-Colombia was defined as the area of the country west and north of the eastern slope of the Eastern Andes Cordillera; initially above 300 m of elevation and in several later analyses above 500 m of elevation, which is considered more often the limit for the Andean zone in Colombia.

5.2.4. Habitat suitability modelling: second generation

After having improved bird dataset quality and based on results from the second generation of error estimation (Chapter 4, section 4.3), a series of new habitat suitability exercises were conducted using a newer MAXENT version (version 3.2¹⁰) and improved bird datasets (BioMap-BasicFilHP_v2¹¹, BioMap-BasicFilHP_v2_1950¹²). These aimed to produce more robust habitat suitability models and potential geographical range maps, including range maps under future climate-change scenarios as well as integrating new ecomorphological measures of bird diversity.

5.2.4.1. Sample size, replicates and grain size effects on model performance

Usually the evaluation of a model is performed by splitting the dataset in two parts: training data and validation data. Since this partition may be conducted in different ways and using different proportions of the data available, different resampling techniques have been proposed to produce model replicas, and thus evaluate the uncertainty associated with models and thereby select the best performing models (Fielding & Bell, 1997; Anderson, 2003; Anderson *et al.*, 2003). One of these techniques is bootstrapping, resampling with replacement, in which the dataset is divided at random many times and the modelling iteratively repeated. This tests

¹⁰ A complete list of the new features and bugs fixed in relation to past versions can be found at <http://www.cs.princeton.edu/~schapire/maxent/>

¹¹ BioMap-BasicFilHP_v2: 141,140 accessions retained. Deleted records with uncertain and non-continental localities, and incomplete taxonomy plus deleted records with localities in areas with average slope > 5% and collection-event horizontal error > 2 km.

¹² BioMap-BasicFilHP_v2_1950: 69,059 accessions retained. Same as BioMap-BasicFilHP_v2 plus deleted accessions with incomplete recorded date of collection or collected before 1950.

sensitivity to the volume of data used. Uncertainty may be estimated as the confidence interval for the mean of the statistic used to evaluate model performance over all iterations (Fielding & Bell, 1997).

In this sense, the lack of model replication in the first generation of mapping exercises of this study represented a caveat on the prediction certainty of total richness presented. To produce more robust model predictions and evaluate model uncertainty when bootstrapping, we conducted an experiment to assess the effect of training sample size, number of replicates and grain size on the overall performance of the habitat suitability models. The experiment was designed as a three factor ANOVA. This permitted, first, the generation of criteria to improve the quality of habitat suitability models and thus bird diversity projections, and second, increase computational efficiency using a slightly coarser grain than the first generation during the final modelling process. For this purpose one family, one genus and one species with a relatively good amount of data were selected, and habitat suitability models produced using an increasing number of training points, building 25, 50 and 100 replicates at 1.5 and 3 km grain sizes each time (Table 5.2.4.1.1). Results files from MAXENT for each taxon used were imported into SPSS version 16.0 (SPSS, 2007) to produce plots for the confidence interval of the mean AUC statistic at the 95% probability and data were analysed using a three factor ANOVA each time. Afterwards, based on the results, the optimum configuration was defined as producing habitat suitability models using 25 replicates at 3 km grain size; thus, minimising the computational requirement for modelling all taxa, while not affecting adversely model performance (section 5.3.4.1).

Bird datasets were prepared as before and original BioClim variables for current climate conditions at 1 km aggregated at 3 km; through spatial averaging. Except for precipitation related variables, which were summed instead of averaged. Also similarly to that described before, prior to running models a PCA in ENVI 4.3 was performed (see section 5.2.2), but in this case conducted for the 19 BioClim variables clipped to north South America and Panama to decide which variables explained better the total variability observed among them. Results from the PCA were very similar to those described before with some slight variations (Appendix 2). Accordingly, those variables explaining most of the variation and exhibiting the lowest correlation within the temperature and rainfall related subgroups of variables were selected for use (Table 5.2.4.1.2).

Models were run for all taxa with at least 5 site localities, using 30% of the observations to evaluate model performance when taxa had at least 12 site localities, and not performing any evaluation for taxa with a number of localities below that threshold. Thus, when used all data 148 families and 569 genera were modelled, five and 83 of them were not evaluated respectively. Otherwise, when using data collected

post 1950 (inclusive) 142 families and 513 genera were modelled, six and 115 of them were not evaluated respectively. Finally, similarly to that described in section 5.2.2, duplicate presence records were removed in each run and all other parameters were set to MAXENT default values. Models were produced using a mask of Colombia and projected to northern South America and Panama for current climatic conditions and under expected climate conditions generated by the HadCM3 model, scenarios A2A and B2A for the years 2020, 2050 and 2080 (Nakicenovic *et al.*, 2001). All resulting maps were produced at 3 km grain size.

Table 5.2.4.1.1. Selected taxa and number of training and test samples used to evaluate the combined effect of training sample size, number of replicas and the grain size in overall habitat suitability models performance generated with MAXENT. The experiment was conducted building 25, 50 and 100 replicas and using 1.5 and 3 km as grain sizes each time.

Taxon	Total localities	Train samples	%Train samples	% Test samples
THROCHILIDAE	958	19	2	98
THROCHILIDAE	958	29	3	97
THROCHILIDAE	958	57	6	94
THROCHILIDAE	958	77	8	92
THROCHILIDAE	958	105	11	89
THROCHILIDAE	958	153	16	84
THROCHILIDAE	958	479	50	50
THROCHILIDAE	958	671	70	30
<i>Chlorostilbon</i>	194	14	7	93
<i>Chlorostilbon</i>	194	25	13	87
<i>Chlorostilbon</i>	194	50	26	74
<i>Chlorostilbon</i>	194	76	39	61
<i>Chlorostilbon</i>	194	101	52	48
<i>Chlorostilbon</i>	194	136	70	30
<i>Chlorostilbon</i>	194	150	77	23
<i>Chlorostilbon melanorhynchus</i>	164	13	8	92
<i>Chlorostilbon melanorhynchus</i>	164	26	16	84
<i>Chlorostilbon melanorhynchus</i>	164	51	31	69
<i>Chlorostilbon melanorhynchus</i>	164	75	46	54
<i>Chlorostilbon melanorhynchus</i>	164	100	61	39
<i>Chlorostilbon melanorhynchus</i>	164	115	70	30
<i>Chlorostilbon melanorhynchus</i>	164	126	77	23
<i>Chlorostilbon melanorhynchus</i>	164	151	92	8

Table 5.2.4.1.2. Bioclimatic variables selected for habitat suitability modelling in MAXENT; second generation of analyses.

BioClim code	BioClim variable name	Eigenvalue*	Eigenvalue**
BIO1	Annual Mean Temperature	7.093	8.176
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	2.456	2.332
BIO3	Isothermality (P2/P7) (* 100)	1.065	0.340
BIO12	Annual Precipitation	5.278	5.994
BIO13	Precipitation of Wettest Month	1.634	0.942
BIO14	Precipitation of Driest Month	0.640	0.575

* Column of eigenvalues obtained at 1 km grain size

** Column of eigenvalues obtained at 3 km grain size

5.2.4.2. Model selection and consensus potential range maps

Once the replicates of habitat suitability models were produced, the best models were selected to generate consensus potential range maps for each taxon. Some authors such as Anderson *et al.* (2003) propose selection of models exhibiting the highest accuracy (“best models subset”) as a means of producing more robust final range maps predictions. Building their models using 50% of the data for validation each time, they start with a minimum of 100 replicas, from where they select a set of 20 models of optimum performance. Otherwise, in cases where the subset is not completed within the 100 replicates, the authors recommend to increase the number of replicates until the subset is completed. Because of the high number of taxa used in this research, especially at the genus taxonomic level and pondering results from the previous experiment (section 5.3.4.1), we decided to follow a variation of the “best models subset” methodology. In this sense, we selected a “best models subset” of 10 models from the 25 replicates produced for each taxon at each one of the different taxonomic levels used. The subset included models with the highest AUC values, lower intrinsic omission error and with significant probabilities for the Binomial Test of Omission ($p \leq 0.05$). It is important to highlight that it was not always possible to use a subset of 10 models, and in such cases we selected the best performing models even where only one was available. Thus, when using all data this happened for 10 families ($\approx 7\%$) and 90 genera ($\approx 16\%$), whilst when using data collected post 1950 (inclusive) the same occurred for 41 families ($\approx 29\%$) and 177 genera ($\approx 35\%$).

Finally, to generate presence/absence maps (potential range maps) and the final richness maps, selected raw MAXENT results maps were imported into PCRaster and processed using batch files to run different PCRaster operators as described in section 5.2.2. However, it is important to note that differently to the first generation

of analyses, in this case MAXENT raw results were obtained as logistic probability instead of cumulative probability, in accordance with some new features in the new version of MAXENT used this time. Moreover, this time areas of presence and absence were defined using each time the equal test sensitivity and specificity (ETSS) threshold instead of using a fixed threshold value as previously. During the first generation the results file from MAXENT (results.xls) to which are exported all results from modelling exercises was ignored. Not knowing that the ETSS values were written to this file, when writing the batch files for simplicity it was decided to use a fixed threshold value. In the second generation, although threshold selection is still subjective in general, the use of the exact ETSS threshold permitted a major improvement, since by definition it is the point where the rate of omission/commission error (*i.e.* specificity/sensitivity) is near one (1), and thus errors more similar (see Figure 5.2.2.1).

Consensus potential range maps for each taxon were produced using batch files to run PCRaster operators in two different ways. First, all potential range maps (presence/absence maps) from the best model subset were added; thus resulting in a unique map having a value of zero (0) where a taxon is absent and values between 1 and 10 where a taxon is present. In a second step these were reclassified to produce presence/absence maps using a simple algorithm in PCRaster to reclassify all areas with cell values higher than 1 to presence (operator “if then else”). Therefore, a taxon was predicted as present (1) in a cell if it had been predicted as present at least in one of the models from the “best models subset”. Since, these were the most accurate models produced, it was considered that the taxon should be regarded as present if it had been predicted in that way by at least one of these models, hopefully reducing omission error overall. Final predictions of richness were generated as before in PCRaster by adding all potential range maps.

5.2.4.3. *Weighted endemism score*

Consensus potential range maps were used as the basis to estimate the “weighted endemism score” (Crisp *et al.*, 2001). This index is calculated adding all range maps as was done for the simple richness score, but first weighting the value of each cell where each taxon is present by the inverse of the predicted geographical range (*i.e.* $1 / \text{range size}$) (Crisp *et al.*, 2001). This index is correlated to richness since all taxa are summed, though it has a strong emphasis on the rarity of taxa present in a cell. Thus, potential range maps were processed in PCRaster, and several batch files and one dynamic model were written to produce a map stack for all taxa and report the total number of pixels occupied by each taxon to a text file, *.tss (operators “maptotal”, “report”). This information was later used to weight the value of each cell where each taxon was present, dividing in each case its corresponding potential range map

by the total number of pixels predicted as having this taxon present in northern South America; the total extent at which MAXENT modelling was performed. Finally, the “weighted endemism score” map was calculated by adding all potential range maps weighted by their range size at both family and genus hierarchies.

5.2.4.4. *Ecomorphological measures of diversity*

Aiming to improve understanding of alternative measures of bird diversity a new methodology to generate at least two new indices focusing on functional diversity was proposed in this research. The first of these is called the “equivalent–species ecomorphological diversity index” (ESE index) and the second the “ecomorphological groups equitability index” (E’ index). It is important to note that both indices were tested for the families Trochilidae and Tyrannidae, which are two of largest families of Neotropical birds present in Colombia. Moreover, those families are of particular interest because they occupy a wide array of conditions and habitats, have a wide diversity of forms and exhibit a wide amplitude of functional relations to their environment, and therefore may be used as proxies to measure the level of some ecosystem services such as for instance pollination, insect population control and seed dispersal.

To calculate the ESE index, first, we defined a set of different functional groups *a priori* and determined their traits describing roughly habitat, diet, foraging strategies and occupied strata in the vertical dimension. For this research, for simplicity, functional groups are treated as equivalent to the more traditional ecological guilds. Although they are not exactly the same, ecological guilds represent a rough approximation of functional groups. Thus, functional groups are defined based on Stiles & Rosselli (1998) ecological guilds for birds in a montane forest of the Eastern Andes Cordillera of Colombia. These authors defined a series of seven coarse diet groups based on main items included in the diet and a series 16 detailed foraging groups based additionally on foraging strategies and the level in the forest where usually the species forages. Their treatment was used as basis and expanded to the whole set of modelled birds from the Trochilidae and Tyrannidae families. Thus, 20 functional groups are proposed here (Table 5.2.4.4.1).

Afterwards, similarly as with other simple methodologies for functional diversity that have been proposed, different species were assigned to different functional groups. However, here as proposed by Stiles & Rosselli (1998) for ecological guilds, species were not forced into one functional group but allocated into one or several depending on their occupancy of each as a fraction of the species unit. Fractions in each of the functional groups to which a species belongs were assigned proportionally to the importance each particular group plays in the ecology of the species. For example

Table 5.2.4.4.1. Functional groups predefined for families Trochilidae and Tyrannidae (for details see text).

Functional group	Description
UMHII	Undergrowth and Medium Level Hawking Insectivore and Invertebratvore
CBHII	Canopy and Borders Hawking Insectivore and Invertebratvore
GLUHII	Ground and Lower Undergrowth Hawking Insectivore and Invertebratvore
GLUFII	Ground and Lower Undergrowth Foliage Gleaner Insectivore and Invertebratvore
UMFTNBII	Upper Undergrowth and Medium Level Foliage and Thin Branches Gleaner Insectivore and Invertebratvore
CBFII	Canopy and Borders Foliage Gleaner Insectivore and Invertebratvore
ASBII	Aquatic and Stream Border Insectivore and Invertebratvore
UFTNBVII	Undergrowth Foliage and Thin Branches Gleaner Vertebratvore and Invertebratvore
MCFTNBVII	Medium Level and Canopy Foliage and Thin Branches Gleaner Vertebratvore and Invertebratvore
TKKBII	Trunk and Thick Branches Gleaner Insectivore and Invertebratvore
VBH	Vertebrate Besiegers and Hunters
SCAR	Scavenger and Carrion Eater
GLUFF	Ground and Lower Undergrowth Foliage Frugivore
UMFF	Upper Undergrowth and Medium level Foliage Frugivore
CBF	Canopy and Borders Frugivore
GCG	Graminae and Compositae Granivore
UMNECPCL	Undergrowth and Medium Level Nectarivores – Corolla Piercing and Licking
UMNECOCL	Undergrowth and Medium Level Nectarivores – Open Corolla Licking
CBNECPCL	Canopy and Borders Nectarivores – Corolla Piercing and Licking
CBNECOCL	Canopy and Borders Nectarivores – Open Corolla Licking

for a species of hummingbird known to feed most of the time in the undergrowth of a forest both on nectar and small insects and invertebrates two or three functional groups may be assigned depending on the strata in the forest it occupies (UMHII, UMFTNBII, UMNECOCL). As described by Stiles & Rosselli (1998) the addition of all fractions within an ecological group, or in this case functional group, results in the total of equivalent-species in that particular group. The fractions into each functional group for each species were allocated with the aid of information contained in several key publications (Ridgely & Tudor, 1989; Stiles & Skutch, 1989; Ridgely & Tudor,

1994; Hilty & Brown, 2001), internet searches, articles and the researchers' own field experience.

In parallel, for each one the species of the families Trochilidae and Tyrannidae two different morphological indices relating the interaction between different relative body and weight measures were calculated. The indices were calculated as a means of modifying the contribution a particular species has in a functional group according to its morphology, which is assumed here to influence resources accessed and exploited in the environment. In this way, for the family Trochilidae an interaction term between the relative bill length and the relative weight (Equation 5.2.4.4.1) was estimated, whilst for the family Tyrannidae an interaction term between the relative total body length and the relative weight (Equation 5.2.4.4.2) was calculated. In each case relative values for the examined species measure were found by dividing by the maximum value for that particular measure in the whole set of species belonging to the family under scrutiny. This permitted to obtain standardised rates with values between 0–1, more intuitive and appropriate to modify the functional groups assigned fractions. Differences in proposed interaction terms between the two families obeyed purely to the morphological data available for each family to estimate each one of them. Data for Trochilidae bill length was obtained from “A Guide to the Birds of Colombia” (Hilty & Brown, 2001) and ProAves Migratory Monitoring Program Database, PMAMN Database by its acronym in Castellano (Proaves, 2008). Data for Tyrannidae total length was obtained from “A Guide to the Birds of Colombia”. Weight measurements were taken from the “Handbook of Avian Body Masses” (Dunning, 2008) and PMAMN Database. For each species, measurements were averaged when they were available from more than one source.

$$MI_{Trochilidae} = rBiL_i \times rWe_i \quad (\text{Equation 5.2.4.4.1})$$

$$MI_{Tyrannidae} = rBoL_i \times rWe_i \quad (\text{Equation 5.2.4.4.2})$$

Where:

$MI_{Trochilidae}$ = morphological index for the i^{th} Trochilidae species

$rBiL_i$ = bill length of the i^{th} Trochilidae species relative to maximum in sample for the family

rWe_i = weight of the i^{th} Trochilidae species relative to maximum in sample for the family

$MI_{Tyrannidae}$ = morphological index for the i^{th} Tyrannidae species

$rBoL_i$ = body length of the i^{th} Tyrannidae species relative to maximum in sample for the family

rWe_i = relative weight of the i^{th} Tyrannidae species relative to maximum in sample for the family

Batch files to run a series of operations in PCRaster to complete the ESE index calculations were prepared. Thus, using spreadsheets in Excel the morphological ratio for each species was multiplied by the equivalent–species fractions within each functional group obtaining modified equivalent–species values (Equation 5.2.4.4.3). Using batch files in PCRaster, modified equivalent–species for each species within each functional group were multiplied by the potential range map of each species. We thus obtained for each species one map per each functional group showing the potential geographical range, and in each one of them all cells having a unique value in the whole range expressing the morphologically weighted contribution of equivalent–species of each particular functional group to which the species belongs. Thus, the “equivalent–species ecomorphological diversity” for each functional group (ESE_f , index) was calculated by adding maps for all species (n) in each family (Equation 5.2.4.4.4) for each particular group and the total ESE index adding all ESE_f indices through all functional groups (m) (Equation 5.2.4.4.5). Finally, E' was calculated by applying information entropy theory as proposed for other diversity indices such as Shannon–Wiener (Magurran, 2004). However, differently in this case the index measures the equitability with which equivalent–species morphologically weighted richness is distributed between all functional groups present (Equations 5.2.4.4.6 and 5.2.4.4.7).

$$MES_i = MI_i \times ES_i \quad (\text{Equation 5.2.4.4.3})$$

$$ESE_f = \sum_{i=1}^n MI_i \times ES_i \quad (\text{Equation 5.2.4.4.4})$$

$$ESE = \sum_{i,f=1}^{n,m} MI_{if} \times ES_{if} \quad (\text{Equation 5.2.4.4.5})$$

$$p_f = \frac{ESE_f}{ESE} \quad (\text{Equation 5.2.4.4.6})$$

$$E' = \sum_{f=1}^m p_f \times \ln p_f \quad (\text{Equation 5.2.4.4.7})$$

Where:

MES_i = modified equivalent–species for the i^{th} species

MI_i = morphological index of the i^{th} species

ES_i = equivalent–species for the i^{th} species

ESE_f = equivalent–species ecomorphological diversity in the f^{th} functional group

ESE = total equivalent–species ecomorphological diversity through all functional groups

p_f = proportion of equivalent–species for the f^{th} functional group in relation to the total ecomorphological diversity (ESE)

E' = equivalent–species ecomorphological equitability between functional groups

5.2.4.5. Richness and rarity maps evaluation

All final richness and weighted endemism score maps were cross-validated comparing them to maps elaborated using range maps from the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (Ridgely *et al.*, 2007) and data obtained from field surveys conducted by ProAves in 76 sites distributed across the Colombian Andes including areas north and west of them (Proaves, 2008). Geographical range maps from WHDBD Database were processed in PCRaster. Original data from the WHDBD Database was obtained as shape files (*.shp) and converted to PCRaster grids at ≈ 1 km by M. Mulligan. Several batch files were written to resample these files to north South America at ≈ 3 km cell size (*i.e.* 0.08333° to 0.25°). Maps were processed unprojected in geographical coordinates in decimal degrees (GCS), and whenever necessary masks produced for previous mapping exercises reprojected to GCS from Lambert Equal Area Azimuthal Equatorial (LEAAE) in Arc View. It is important to highlight that from the original polygon and point maps for each species present in the WHDBD Database almost exclusively the polygon maps were used. However, point maps were used in cases where a polygon did not exist for the same species in the database. This has the disadvantage that in some cases it misses a minor part of the geographical range of some species, although, on the other hand, it does permit to make emphasis in the most cohesive sections of the geographical ranges, which may be more convenient for conservation purposes. Geographical range maps at family and genus taxonomic levels were generated by adding species maps within each taxon (*i.e.* estimating species richness within each taxon) and reclassifying them to presence/absence (1/0) Boolean maps (operator “if then else”) and converting those later to Scalar format to be used in later operations.

Richness and weighted endemism score maps were also cross-validated against data from ProAves’ Migratory Monitoring Program Database – PMAMN Database (Proaves, 2008). The database compiles information from surveys conducted by ProAves in 76 site localities in West Colombia (WC). The analysis was conducted using fixed-radius point counts, transects and mist-nets during the period 2003–2008. This database represents a total of 113,214 observation records and 42,814 registered captures in 6,758 hours of observations and 167,471 standard mist-nets \times hours (1 mist-net \times hour is equivalent to 1 mist-net of 12 m operated during 1 hour). Information was processed in Excel to generate bird lists of the different localities in the database, and to assign and revise georeferencing manually (projected to LEAAE). Information was exported as *.txt files and imported in DIVA-GIS to produce richness maps at family and genus taxonomic levels using the simple point-to-grid conversion procedure (Hijmans *et al.*, 2005b) at 3 km grain size.

Additionally, a cartographic model was written in PCRaster to select 496 points at random from Western Colombia and extract values from both MAXENT generated maps and Western Hemisphere generated maps and write values to a text file (*.txt). Additionally, the same procedure was used to extract separately values for the 76 sites surveyed by ProAves. Text files were imported into Excel and prepared for analysis in the statistical package SPSS (SPSS, 2007). Differences in richness and weighted endemism score maps were investigated using Spearman's ρ correlation coefficients and multifactor ANOVAS. Furthermore, as part of these analyses we included the estimation of descriptive statistics, confidence intervals for the means, Homogeneity Tests for the variance and *Post Hoc* multiple comparisons. These are general and widely used parametric tests easy to apply and interpret to explore and understand better the observed differences in diversity. Moreover, confidence intervals for the means were plotted to explore graphically differences between treatments. In all cases, statistical treatments used a minimum level of probability for type I error of 5% (α).

Finally, cross-validation was conducted also using "approximately equal surface interval bands" (AEQSIB) to evaluate richness and rarity patterns along the elevational gradient of the country. To produce the bands first the SRTM 1km DEM was reclassified into 1 m bands of elevation and masked for West Colombia. Using PCRaster and the new reclassified DEM the total surface area for the 1 m bands for each zone was estimated. New files were exported as ASCII files and imported into Arc View where band values for surface were summarised and exported as *.txt files that were imported into Excel. The 1 m bands and their surface area were examined and they were reclassified increasing the width of the bands. Thus, original 1 m bands were aggregated trying to generate new bands of approximately equal surface area, having a total surface area bigger than the minimum observed when aggregating intervals of 100 m, meanwhile using a manageable number of bands (Appendix 3). This led to decide using bands of approximately 10,000 km² of surface area with different altitudinal intervals. Thus, the DEM was reclassified and converted to ordinal type to be posteriorly used in PCRaster. Afterwards, using a series of batch files and models a simple algorithm was implemented in PCRaster to determine the total number of taxa in each band, based on the individual geographical range maps and to write obtained results to *.txt files. In addition, averages and totals for both richness and rarity in bands were produced (operators: areaaverage and areatotal). Text files were imported into Excel and prepared for analysis in the statistical package SPSS (SPSS, 2007). The altitudinal pattern for the different variables was plotted and differences in richness and weighted endemism score AEQSIB maps were investigated using Spearman's ρ correlation coefficients and the Wilcoxon Test. Statistical treatments used a minimum level of probability for type I error of 5% (α).

5.3. Results

5.3.1. *DIVA–GIS mapping exercises*

Through the visual inspection of all the different maps produced using the mentioned point-to-grid conversion procedures and estimators to calculate effort and richness several lessons were learnt. Regarding conversion procedures, results showed that simple vs. circular neighbourhood point-to-grid conversion procedures offer different results (Figure 5.3.1.1). In general, the circular neighbourhood procedure resulted in smoother and more continuous surfaces than the simple point to grid procedure. Although desirable under certain circumstances, especially to estimate effort and richness at national level in a quick and raw way, the circular neighbourhood procedure demanded a high computational power to calculate richness estimators. This was especially the case when performing mapping exercises at grain sizes smaller than ≈ 15 km, both with 1- and 2-map units neighbourhoods.

In relation to estimators of species richness, results showed a significant variation in the difference between the average value of the estimators and the observed richness (Figure 5.3.1.2). In most cases, estimators exhibited higher values than observed species richness, for both the simple and the circular neighbourhood (1-map unit) point-to-grid procedures. However, contrary to what was observed for the rest of the estimators (Chao1, Chao1 Corrected, Chao2, Chao-Lee, Jackknife1, Jackknife 2, Raaijmakers), the Rarefaction (simple procedure) estimator exhibited a positive average difference (53.9 ± 53.2). Furthermore, average differences to observed species richness for maps produced through the circular neighbourhood procedure were higher than differences obtained through the simple procedure (Figure 5.3.1.2). They also tended to be less spread statistically and exhibited higher values in the west and north half of the country, especially in the Andes.

These first maps generated through DIVA–GIS showed avian richness concentrated west and north of the Andes (Figure 5.3.1.1). Although specific areas varied depending on the technique and grid size, pockets of high diversity were observed frequently in departments of Cesar, Norte de Santander, Santander, Cundinamarca, Meta, Huila, Caqueta, Putumayo, Nariño, Cauca, Valle del Cauca, Quindio, Risaralda, Choco, Caldas, Tolima, Antioquia, Cordoba, Bolivar and Magdalena. These maps reflect the sampling bias of the collections taken from Colombia, as will be shown in the next section.

5.3.2. *Richness–effort relationship*

Since estimators of species richness showed a great deal of variation between estimators and in relation to observed richness, it was decided to study the relationship

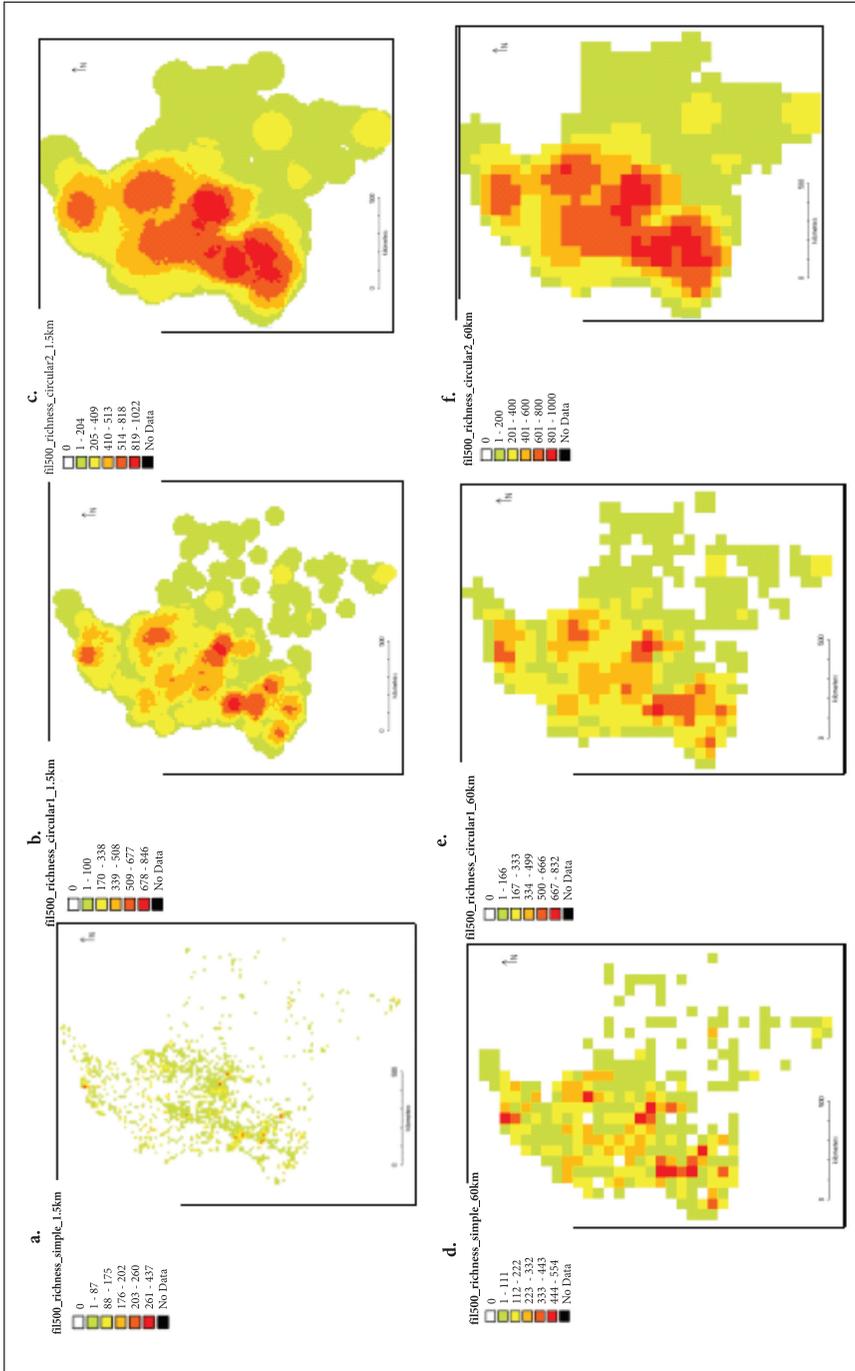


Figure 5.3.1.1. Example of species richness maps produced with DIVA-GIS at ≈ 15 and ≈ 60 km using the simple (a., d.) and the circular neighbourhood (1-map unit b., e. and 2-map units c., f.) point-to-grid conversion procedures.

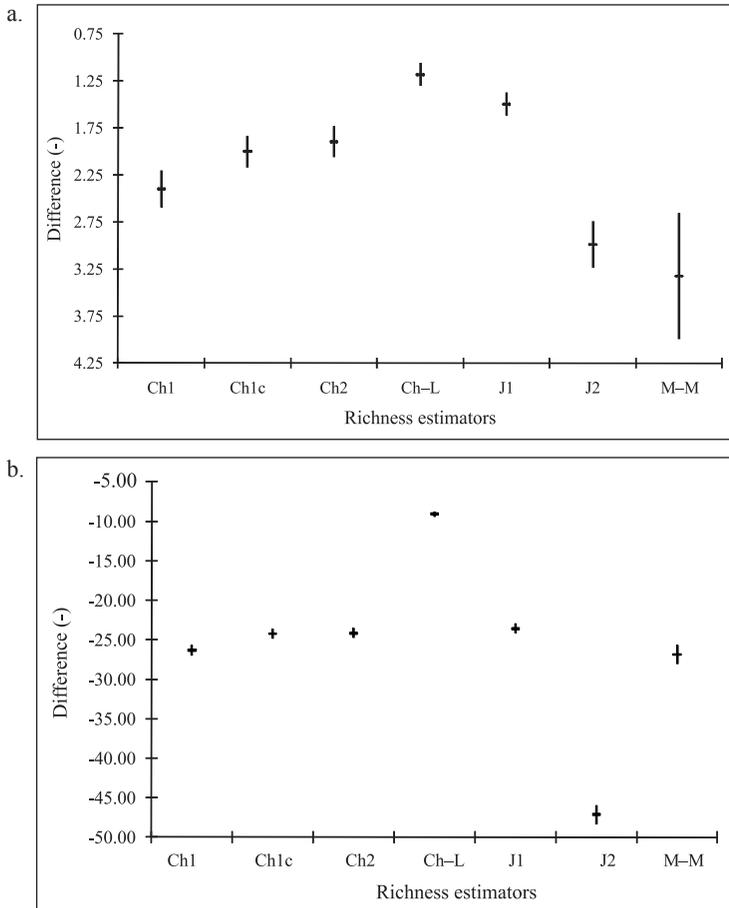


Figure 5.3.1.2. Average difference between observed richness and each species richness estimator (observed - estimated) for maps produced at ≈ 15 km in DIVA-GIS by the simple (a.) and the circular neighbourhood, 1-map unit (b.) point-to-grid conversion procedures. Most estimators exhibited values higher than observed richness and differences between some of them were significant (Confidence Intervals for the Mean, $p < 0.05$). Ch1, Chao1; Ch1c, Chao1 corrected; Ch2, Chao2; Ch-L, Chao-Lee; J1, Jackknife1; J2, Jackknife2; M-M, Michaelis-Menten.

between richness and effort, using the observed richness maps produced through the simple and circular neighbourhood (1-map unit) point-to-grid procedures as a means to understand and avoid effort bias in the analyses. Results showed unequivocally in each case that richness and effort were highly correlated (Spearman's $\rho > 0.98$, $p < 0.01$), exhibiting a clear logistic relationship (Figure 5.3.2.1). In maps produced using the simple point-to-grid method, the relationship showed the highest z values at ≈ 15 and ≈ 30 km grain, while values at ≈ 60 and ≈ 120 km grain were very similar

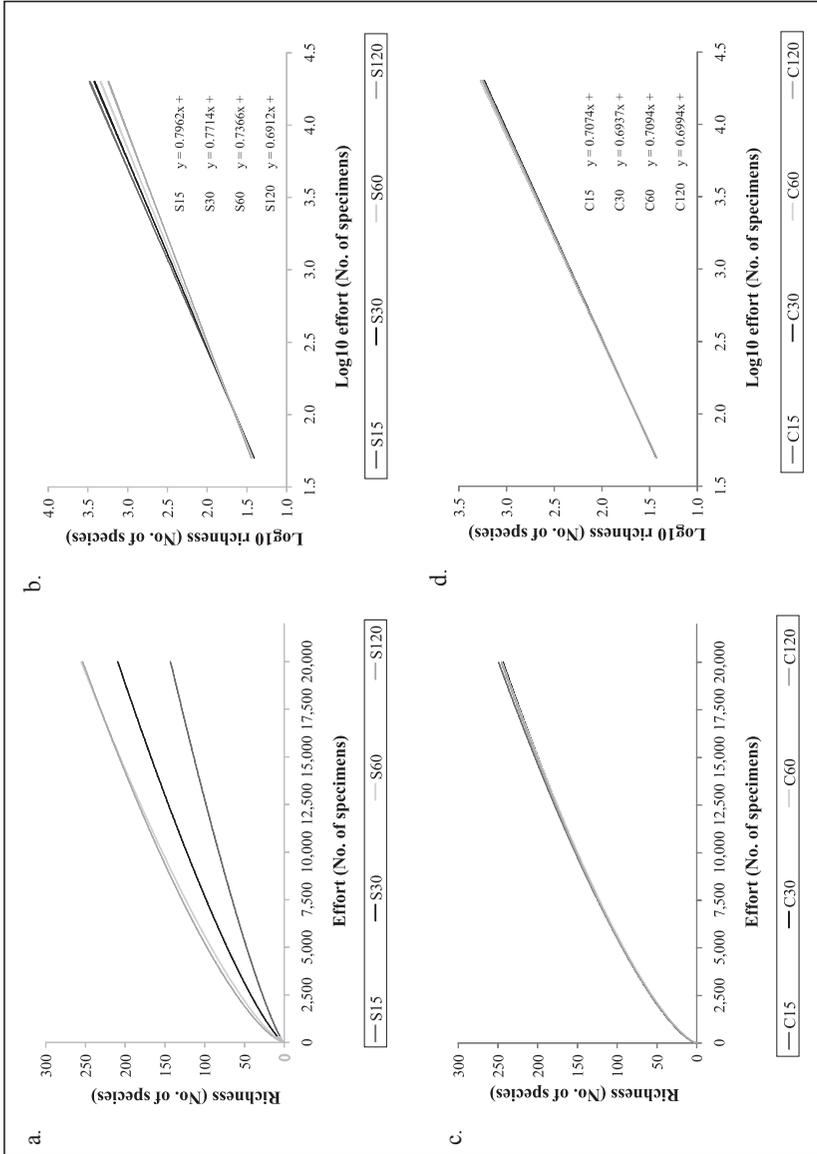


Figure 5.3.2.1. Observed richness versus effort (No. of collected specimens) at different grain sizes ($\approx 15\text{--}120$ km) modelled using the species-area relationship for maps produced through the simple and circular (1-map unit) point-to-grid conversion procedures. Simple conversion procedure: logarithmic model (a), linear model (b). Circular conversion procedure: logarithmic model (c), linear model (d). In all cases both variables showed a very strong relationship ($R^2 > 0.95$, $p < 0.05$ in all cases).

and exhibited lower values than the ≈ 30 km grain. The maximum accumulated number of species exhibited the highest values at ≈ 60 and ≈ 120 km as expected. For maps produced using the circular point-to-grid conversion method, the modelled relationships were very similar to the simple point-to-grid conversion method, and the maximum accumulated number of species very close to the values observed for maps produced by the simple method at 60 and 120 km. Moreover, when plotting the frequency distribution of grid cells into effort intervals (No. of specimens), in all cases the distribution was skewed to the left showing that most of the cells contain less than 500 specimens (Figure 5.3.2.2). This number is one order of magnitude lower than the value where the slope of the curve in the richness vs. effort plots begins to decrease ($\approx 5,000$ specimens). These results suggest strongly that the Darwin-Hernandez Database is not suitable to be used in DIVA-GIS to map bird richness at any scale since the country, in strictly spatial terms, has been under-sampled at all reasonable scales.

5.3.3. Habitat suitability modelling: first generation

In general, maps produced at family and genus taxonomic levels using MAXENT were relatively accurate and showed good discrimination (*i.e.* predictive accuracy). In most cases the Receiver Operating Characteristic (ROC) curves and the Area Under the Curve statistic (AUC) associated showed that model predictions performed significantly better than random for the test sample (AUC family models: $\mu = 0.771$, $SD = 0.067$, $N = 71$; AUC genus models: $\mu = 0.809$, $SD = 0.091$, $N = 491$). In few cases the ROC curves exhibited AUC values lower than 0.7, reaching values lower than 0.6 for 1 model at family level and for 10 models at genus level.

Once MAXENT range maps were added together, improved richness models at national level were obtained in comparison to those previously generated through DIVA-GIS analysis of the raw point data. For family and genus levels, richness maps exhibited smoother and more continuous surfaces than the maps produced previously, as is to be expected. Similarly, to the DIVA-GIS maps, MAXENT maps showed avian richness concentrated west and north of the Andes. However, in this case areas with the highest values of richness occupied a more continuous surface along the inter-Andean valleys and their associated slopes, the foothills of the Andean ranges and the foothills of the Sierra Nevada de Santa Marta (Figure 5.3.3.1).

Furthermore, in this case some pockets of high avian richness appeared in the high and mid Cauca valley, the high Magdalena valley and the eastern foothills of the mid Magdalena valley (*i.e.* western slopes of the Eastern Andes), the Patia valley, the north end of the Andes ranges including the areas around Serrania de Abibe, Serrania de San Jeronimo, Serrania de Ayapel, Serrania de Los Motilones y Serrania del Perija, the foothills of Sierra Nevada de Santa Marta and the lowlands west of it.

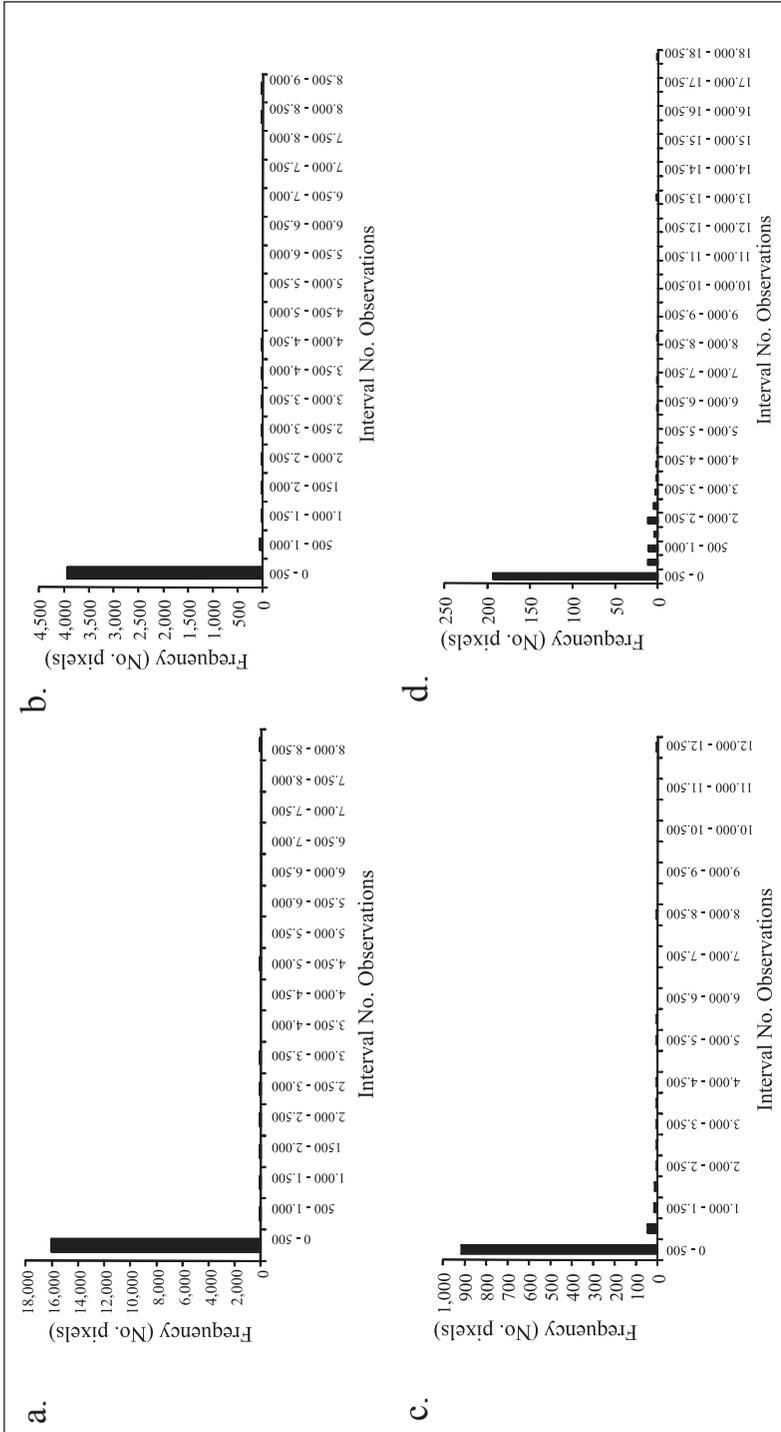


Figure 5.3.2.2. Frequency distribution of effort (No. of collected specimens) at ≈ 15 (a), ≈ 30 (b), ≈ 60 (c) and ≈ 120 km (d). In all cases the major part of the cells shows to be in the range 0–500 specimens, which suggest that, in strictly spatial terms, at any scale the country has been under-sampled.

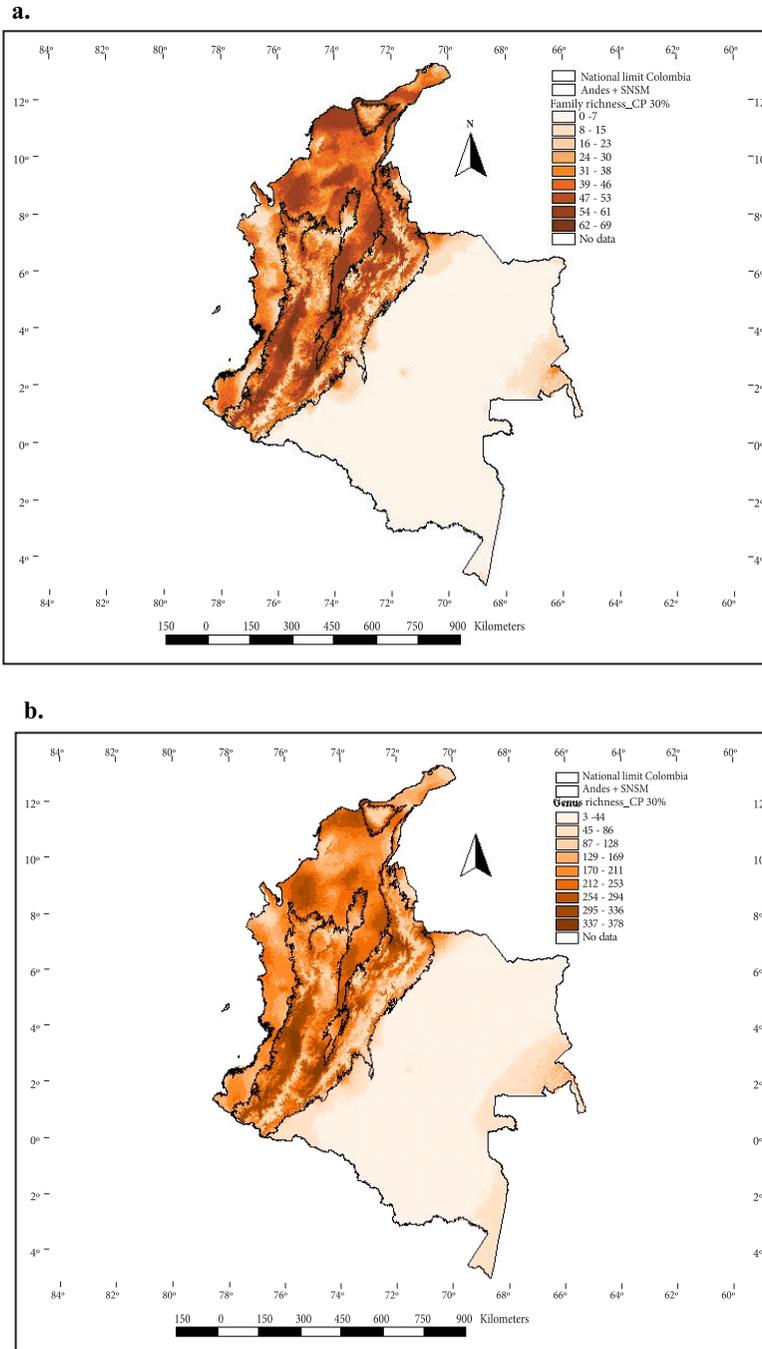


Figure 5.3.3.1. Family (a.) and genus (b.) richness maps produced using MAXENT software. Habitat suitability modelling: first generation.

Although new richness models used the information in a different way, producing maps that in general terms agreed with bird richness patterns expected for the country, when tested, still these exhibited some traces of the richness–effort relationship (see methodology, section 5.2.3). Thus, maps aggregated to ≈ 120 km showed a strong relationship between richness and effort that tended to be logistic at both family and genus hierarchies; Spearman’s $\rho = 0.714$ and 0.726 respectively, $p < 0.01$ (Figure 5.3.3.2). However, differently to what was observed previously, this time the curves did not fit that well to logistic models.

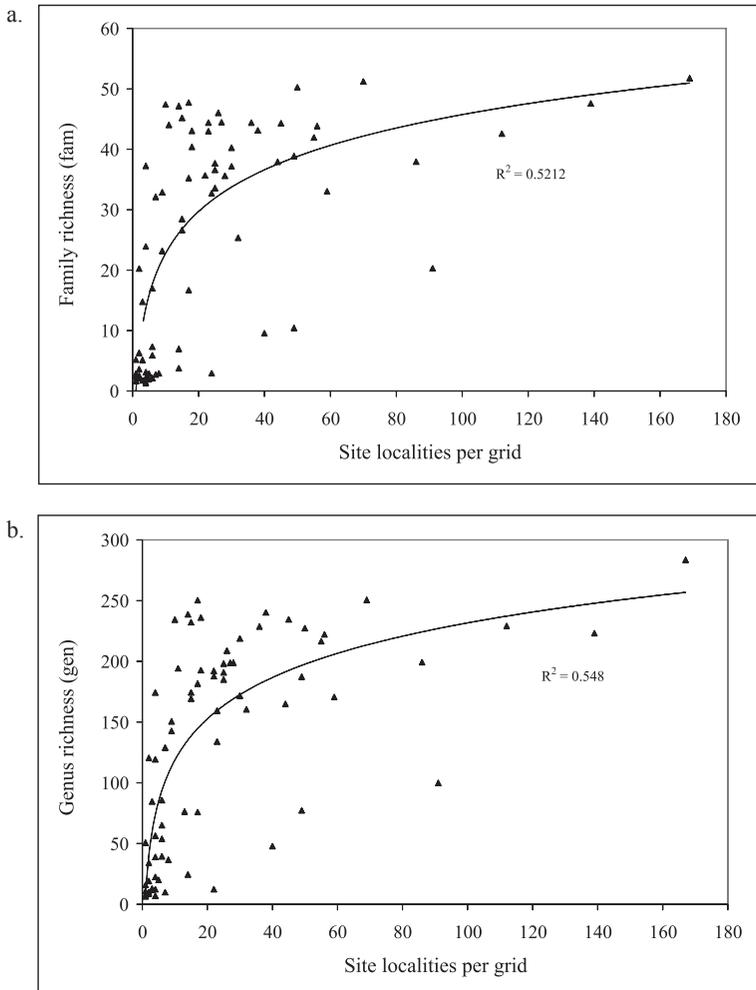


Figure 5.3.3.2. Richness *versus* effort (No. of localities) at ≈ 120 km using MAXENT richness models. Logistic regression showed lower determination coefficients ($R^2 < 0.55$) than those observed previously for richness maps produced in DIVA–GIS ($R^2 > 0.9$). Habitat suitability modelling: first generation.

Based on those results it was decided to resample at random the cells with a high density of localities (> 60 localities) to a maximum of 70 site localities, since apparently after this value the relationship between richness and effort was exacerbated. Thus, six cells from the ≈ 120 km grid of localities, located west of the Eastern Andes, were resampled for both the family and genus datasets (see methodology, section 5.2.3). New richness–effort plots showed data with a more sparse and a less evident relationship, although still a significant correlation was present; Spearman’s $\rho = 0.642$ and 0.652 , $p < 0.01$ (Figure 5.3.3.3). In a next step, when maps were masked to West Colombia, just using areas west and north of the Andes (see methodology, section 5.2.3), the relationship richness–effort was eliminated completely, since these areas are all relatively well sampled compared with the Orinoco and Amazon regions of Colombia; Spearman’s $\rho = -0.113$ and -0.029 respectively, $p > 0.49$ (Figure 5.3.3.4).

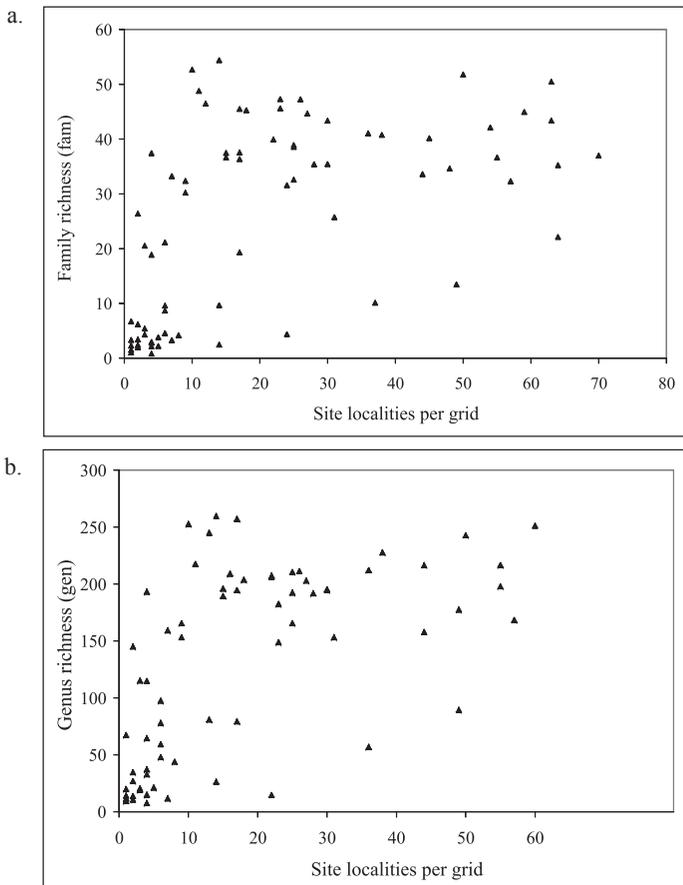


Figure 5.3.3.3. Richness *versus* effort (No. of localities) plot at ≈ 120 km using MAXENT richness models after resampling high effort areas. There is no evident logistic relationship present, but both variables still exhibit a significant correlation (Spearman’s $\rho \approx 0.6$, $p < 0.01$). Habitat suitability modelling: first generation.

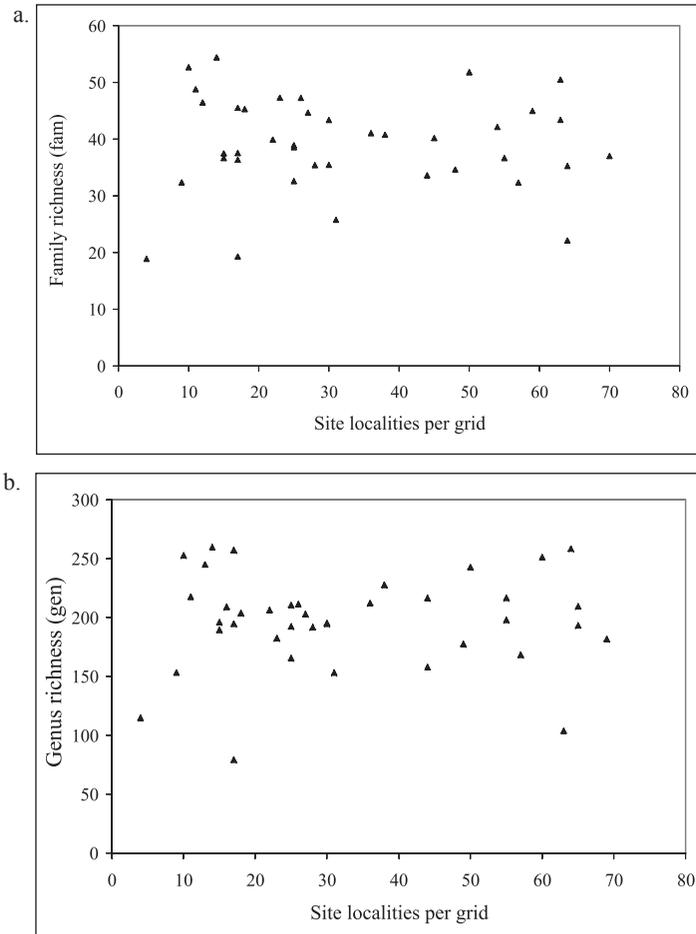


Figure 5.3.3.4. Richness *versus* effort (No. of localities) plot at ≈ 120 km using MAXENT richness models after resampling high effort areas and masking to West Colombia. There is no correlation present in the dataset (Spearman's $\rho \approx -0.1$, $p > 0.49$). Habitat suitability modelling: first generation.

5.3.4. Habitat suitability modelling: second generation

5.3.4.1. Sample size, bootstrapping and grain size effects on model performance

Results showed a significant improvement in overall model performance with increase in training sample size (Figures 5.3.4.1.1, 5.3.4.1.2 and 5.3.4.1.3). Additionally, no effect was found related either to grain size or the number of replicates built and there was no interaction between any of the three factors – grain, replicates and training sample size (Univariate–Three Factor ANOVA, $p \leq 0.05$). Although for all the three

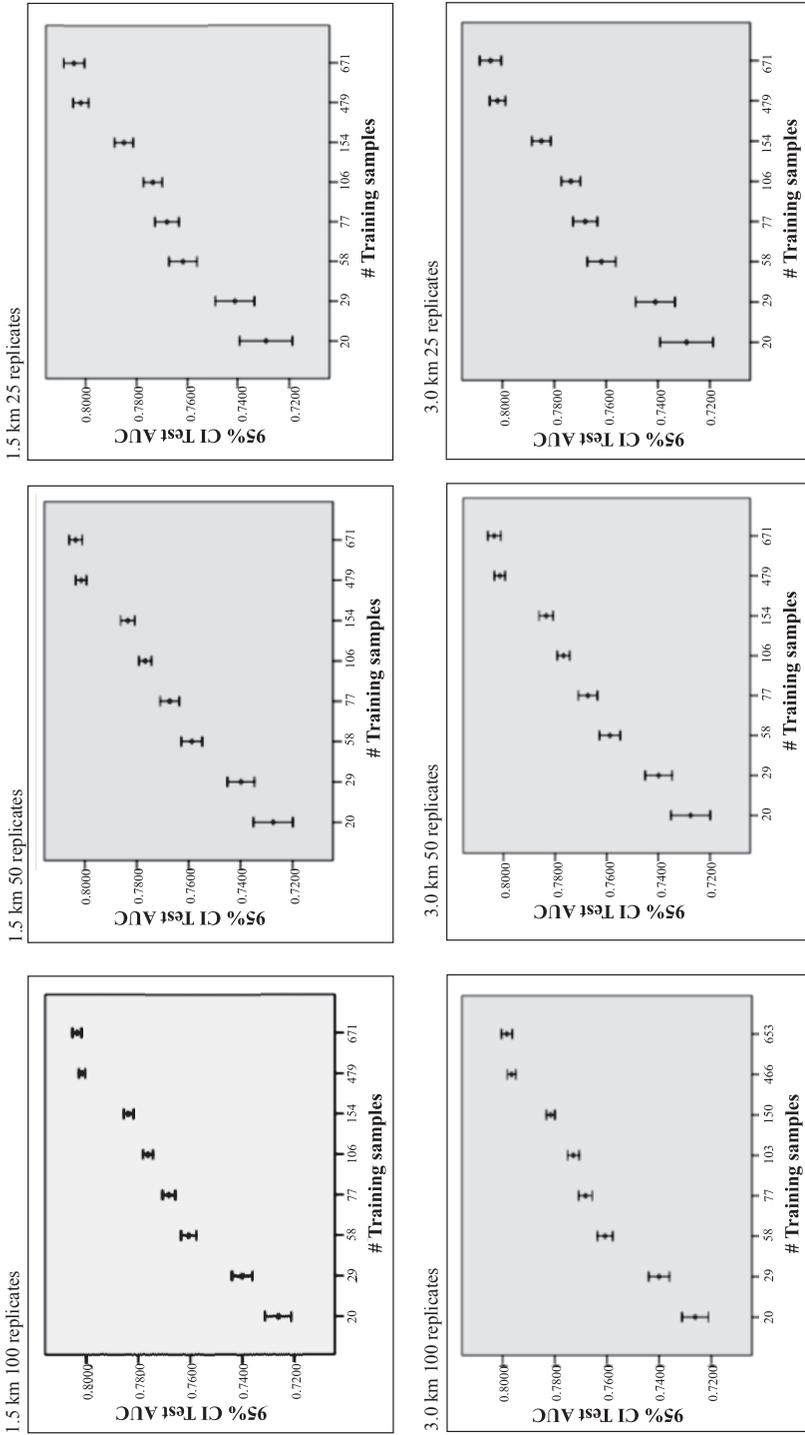


Figure 5.3.4.1.1. Confidence intervals at the 95% probability for the mean AUC statistic for the family Trochilidae when tested using multifactorial ANOVAS the effect of the number of replicates, samples used for training and the grain size in the overall performance of the models produced. Habitat suitability modelling: second generation.

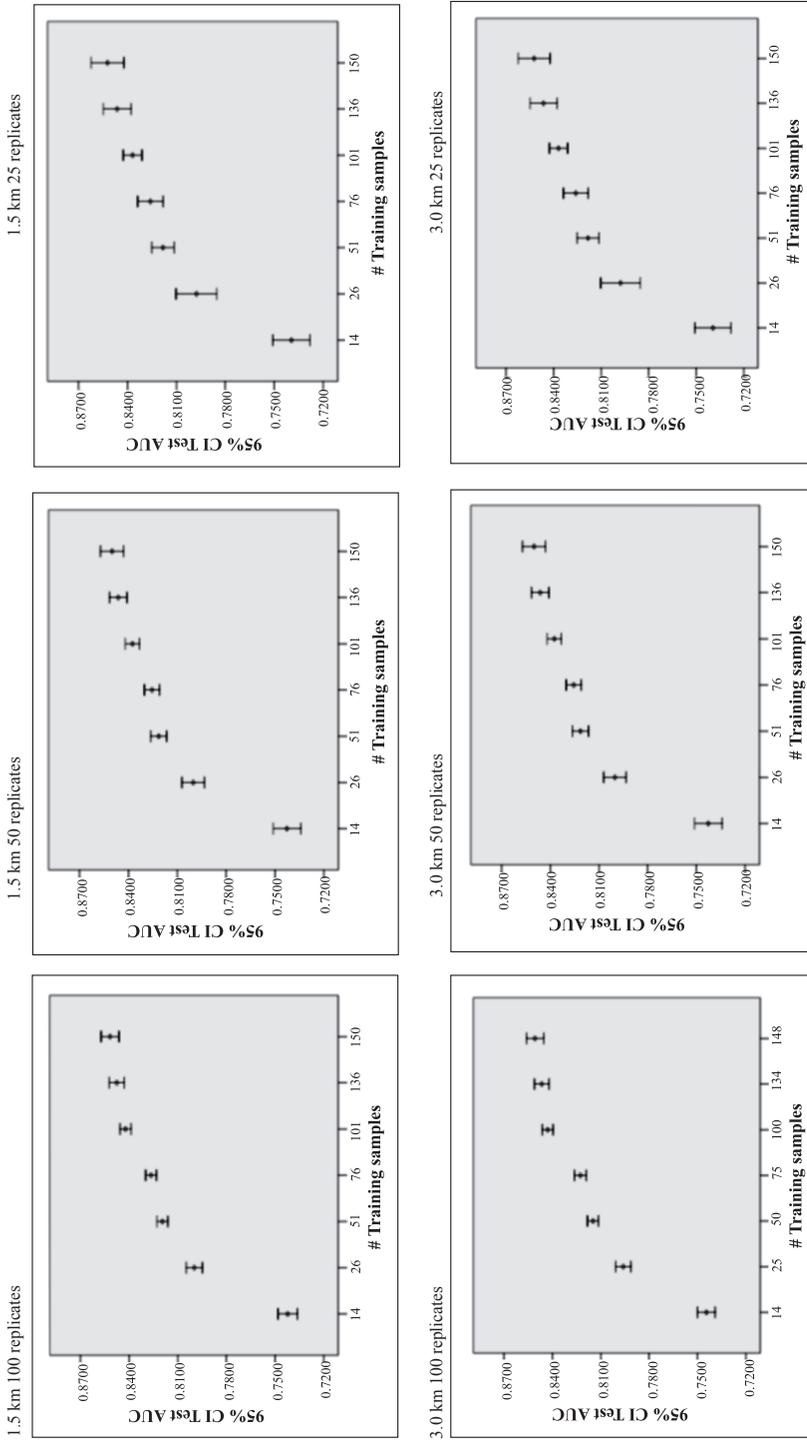


Figure 5.3.4.1.2. Confidence intervals at the 95% probability for the mean AUC statistic for the genus *Chlorostilbon* when tested using multifactorial ANOVAS the effect of the number of replicates, samples used for training and the grain size in the overall performance of the models produced. Habitat suitability modelling: second generation.

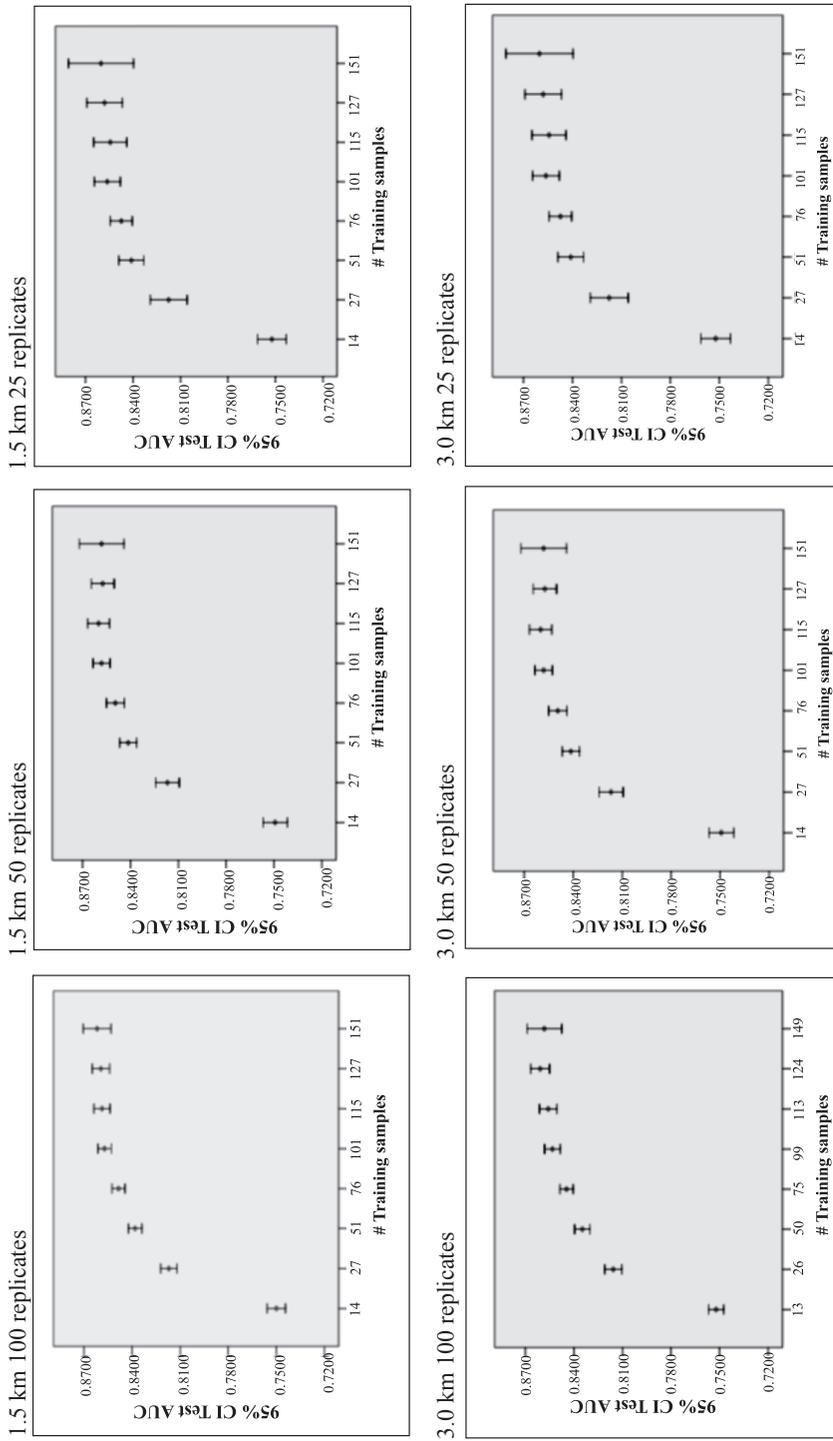


Figure 5.3.4.1.3. Confidence intervals at the 95% probability for the mean AUC statistic for the species *C. melanorhynchus* when tested using multifactorial ANOVAS the effect of the number of replicates, samples used for training and the grain size in the overall performance of the models produced. Habitat suitability modelling: second generation.

taxa selected the general trend in model performance *versus* training samples was logistic, it was noticeable that the curve shape changed with taxonomic level. Thus the relationship is more humpback shaped, suggesting a quicker stabilisation in model performance, at species level. This pattern is somehow logical since at higher taxonomic levels it would take more training samples to include all subtaxa at lower levels and the full set of climatic conditions in which they inhabit.

5.3.4.2. *General avian richness and rarity patterns in West Colombia*

Avian richness patterns

Results from this study indicate that potentially richest bird areas in West Colombia are located in the foothills above the Magdalena and Cauca rivers, including the highest parts of these valleys, several interior dry valleys and the slopes of the Andes below 2,000 m (Figure 5.3.4.2.1). In addition, some interior dry valleys such as the Sogamoso and Chicamocha, in the Eastern Cordillera, and the Patia and Dagua, in the Western Cordillera. The slopes of Serrania del Perija and Serrania de Los Motilones in the northern end of the Eastern Cordillera, and Sierra de La Macarena, its southeastern offshoot. Serrania de San Lucas in the northern end of the Central Cordillera, and Serrania de Abibe, Serrania de San Jeronimo (including Montes de Maria) and Serrania de Ayapel in the northern end of the Western Cordillera are also included. Additionally, the slopes of some isolated mountain systems such as Sierra Nevada de Santa Marta, Serrania del Baudo and Serrania del Darien constitute potential pockets of high bird richness in the country. Finally, several areas near the Caribbean coast along a system of low hills extending north from the Montes de Maria to areas north of the Sierra Nevada de Santa Marta, Serrania de Cosinas and Serrania de Macuira in the high Guajira, and the Pacific Lowlands are included.

Potential pockets of high richness seem coarser at family than at genus level, extending over more areas, especially, in the Central and Western cordilleras, and coastal and nearby lowland areas around the Sierra Nevada de Santa Marta and the Serrania del Baudo, in the Caribbean and the Pacific regions respectively (Figure 5.3.4.2.1).

Patterns were not identical between taxonomic levels or different subsets of the avifauna. The intersection of areas of highest potential richness at all taxonomic levels studied showed those to be confined sparsely within a broken belt in the Andean slopes and foothills between ≈ 500 –2,000 m and the highest areas of Serrania de La Macarena and Serrania del Baudo (Figure 5.3.4.2.2).

This belt includes the eastern slope of the Eastern Cordillera in Caqueta and from north of Serrania de La Macarena to the high Catatumbo valley, as well as some few sparse areas in Nariño, Putumayo and Cauca. Additionally, the western slope of the Eastern Cordillera is included less continuously in Santander (including Cordillera

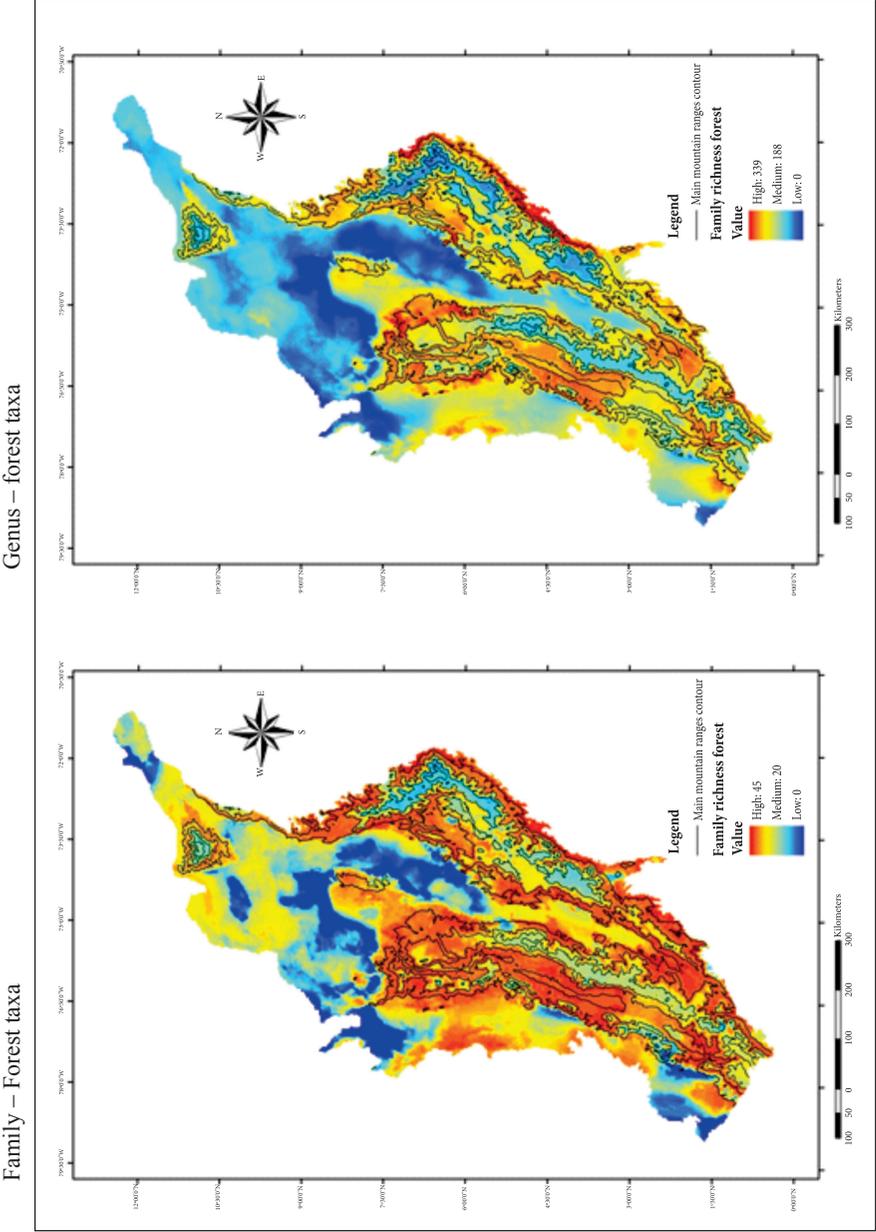


Figure 5.3.4.2.1. Potential avian families and genera richness in West Colombia modelled using the Darwin–Hernandez Database and MAXENT software. Habitat suitability modelling: second generation.

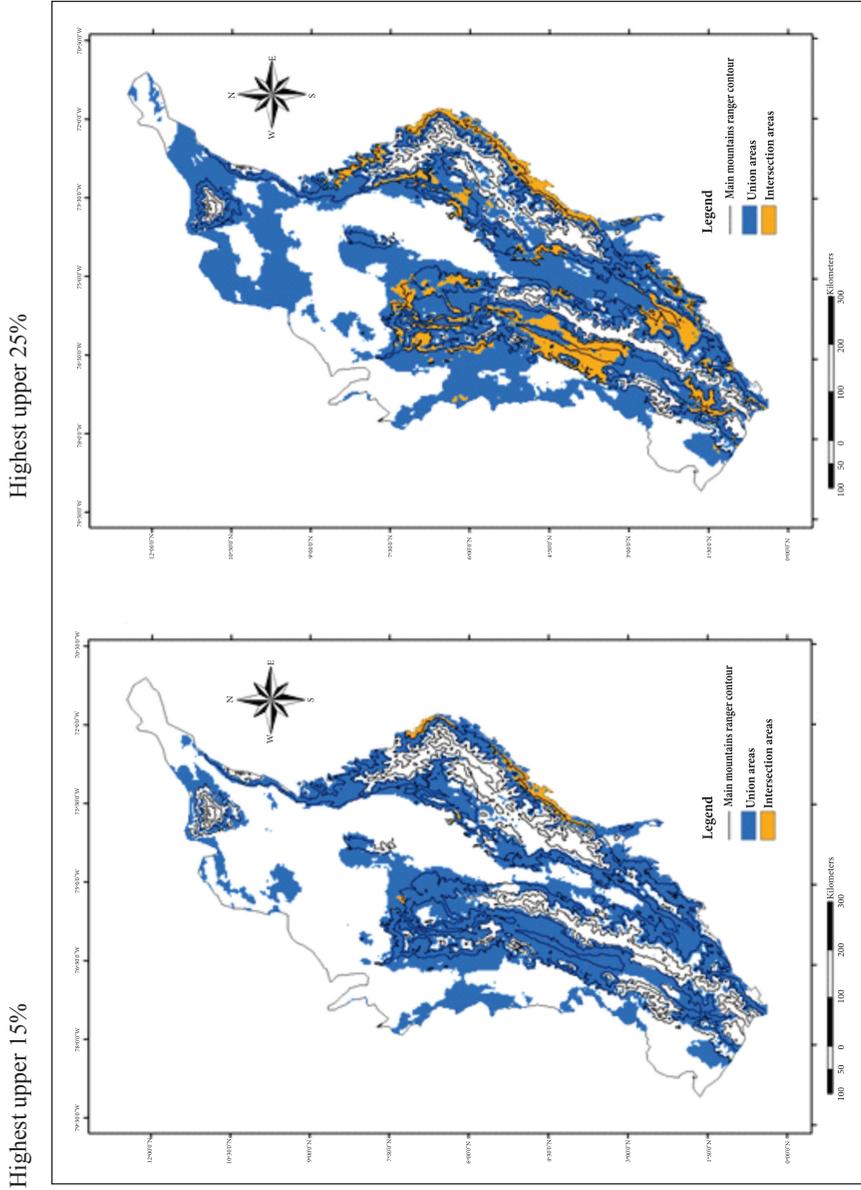


Figure 5.3.4.2.2. Potential areas of high avian richness in West Colombia using as threshold the upper 15 and 25 percent of the range of values observed in each richness map through all taxonomic levels (family and genus) and avian subsets (all taxa, non-marine, forest and strictly forest). Habitat suitability modelling: second generation.

de Los Cobardes), Boyaca and Cundinamarca, as are slopes above both sides of the high Magdalena valley in Huila and the eastern most part of Cauca, and the eastern slope of the Central Cordillera in Tolima and slopes and foothills of both the Central and the Western cordilleras in Antioquia. In addition, slopes above both sides of the Cauca valley in Caldas, Risaralda, Quindio and Valle del Cauca (from Farallones to Serrania de Los Paraguas) and finally, the western slope of the Central Cordillera in north and south Cauca and Nariño (including the high Patia and Dagua valleys), and the Pacific slope of the Western Andes in Choco and Valle del Cauca are included.

Avian rarity patterns

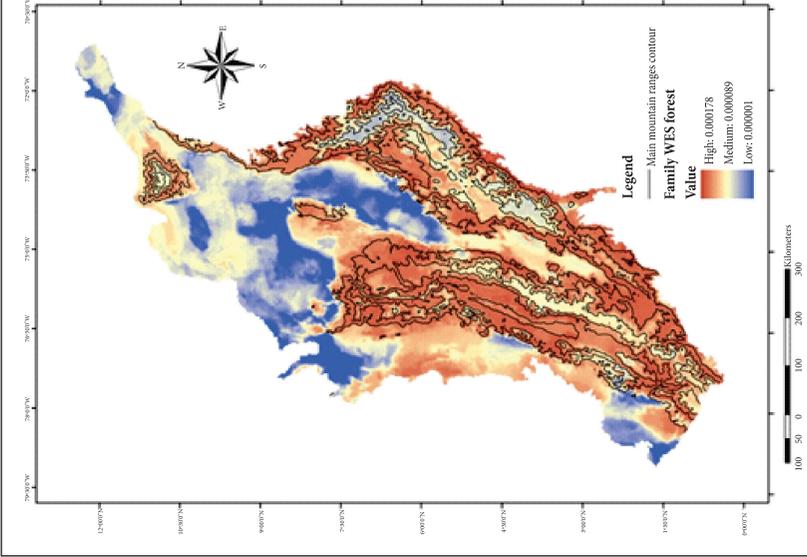
Avian rarity, measured as the weighted endemism score in this study, shows contrasting patterns between different taxonomic levels. At family level areas with the highest scores resemble the general richness patterns, although they are more elevationally constrained to the foothills and slopes of the Andean cordilleras and several of the mountainous systems mentioned in previous paragraphs, as well as to thinner stripes in the coastal areas in both the Caribbean and the Pacific regions (Figure 5.3.4.2.3). At genus level potential areas of high rarity lie mainly in the highest sections of the Eastern and Central Andes (including the Huaca Massif) and the Sierra Nevada de Santa Marta, between $\approx 2,000$ – $4,500$ m. Additionally, several areas below 2,000 m in the eastern slope of the Eastern Cordillera, north of Serrania de Macarena, and sparsely in the Central and Western cordilleras and the Serrania de Abibe exhibit high rarity scores (Figure 5.3.4.2.3).

Interestingly, due to these differences, when all areas of highest potential rarity at both taxonomic levels and all avian subsets are intersected a very restricted pattern of common areas emerges (Figure 5.3.4.2.4). The most recurrent high avian rarity pockets in all cases are a very narrow strip in the eastern slopes of the Eastern Cordillera, north of Serrania de La Macarena, and some few areas in the northeastern portion of Boyaca Department and north and south into North Santander and Arauca. In addition, a couple of areas in the western slope, in the municipalities Landazuri, Bolivar and Velez in Santander Department, the highest portions of the Serrania de Abibe and the Pacific slope in Nariño in municipalities Barbacoas and Ricaurte are included (Figure 5.3.4.2.4).

5.3.4.3. Ecomorphological avian diversity in West Colombia

In general, patterns observed in ecomorphological diversity (ecomdiversity) were consistent with observations made for simple richness distribution in the country. In this sense, again the Andean region, Sierra Nevada de Santa Marta and Serrania del Baudo had the highest scores in ecomdiversity. However, patterns between families Trochilidae (hummingbirds) and Tyrannidae (tyrant flycatchers) were slightly

Family – Forest taxa



Genus – forest taxa

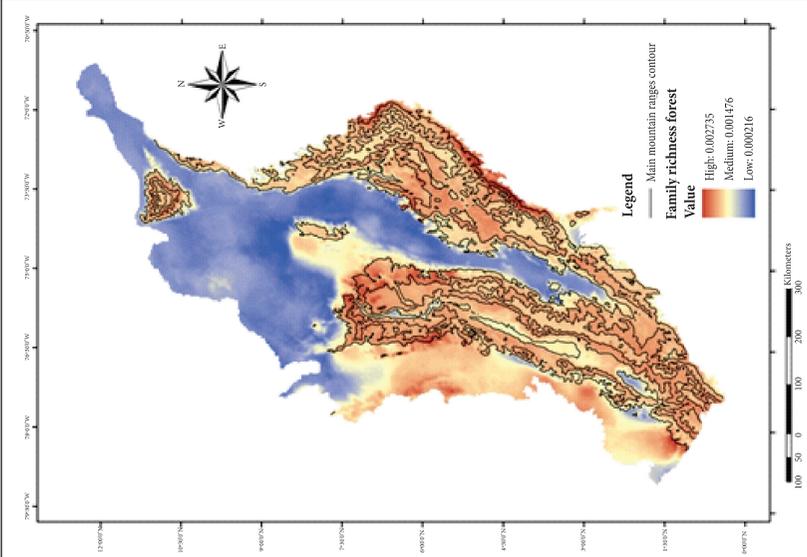


Figure 5.3.4.2.3. Potential avian families and genera rarity (Weighted Endemism Score) in West Colombia modelled using the Darwin–Hernandez Database and MAXENT software. Habitat suitability modelling: second generation.

different and there were evident dissimilarities between the two different indices used.

In the case of hummingbirds the first ecomdiversity index used, the “equivalent–species ecomorphological diversity index” (ESE index), showed the highest values to be located in areas roughly between $\approx 2,000$ – $4,000$ m in the three Andean cordilleras including Serrania de La Macarena, Serrania de los Motilones and Serrania del Perija. Further, several areas below this range in the Andean foothills and the Serrania del Baudo, and a few more above this range in the Sierra Nevada de Santa Marta (Figure 5.3.4.3.1) are included. Moreover, some areas with remarkably high values emerged in the Eastern Cordillera¹³, the northwestern end of the Central Cordillera¹⁴ and the southern Central Cordillera¹⁵. Otherwise, most of the Andean foothills and the Biogeographic–Choco (Pacific) Region exhibited medium values whilst most of the lowlands in the Caribbean Region exhibited low values. With the lowest values in the ESE index appearing in the low Atrato, low Sinu, San Jorge, low Cauca, low Nechi and the mid Magdalena valleys.

On the other hand, the second ecomdiversity index used in this study, the “ecomorphological groups equitability” (E' index), exhibited a similar general pattern where most high–score areas appeared in the Andean Region. Nevertheless, high–score areas extended relatively evenly in the Andes including also areas above $\approx 1,000$ m and the inter–Andean valleys (Figure 5.3.4.3.1). In addition, contrary to what was observed before for the ESE index, for the E' index emerged a series of areas with high scores in the lowlands in the Pacific Region in Nariño and in the Caribbean Region from Antioquia to La Guajira. Of especial interest is the fact that appeared some areas with very high E' index values west of the Sinu valley in the Antioquia's Uraba and the high Guajira. Otherwise, most lowlands areas ranked in medium values keeping the lowest values in fewer areas in the low Atrato, San Jorge, low Cauca, low Nechi and the mid Magdalena valleys. Finally, it is interesting to highlight that adjunct to the areas with the lowest values appeared several areas for which calculations were not possible and received as result “missing value”. This occurred in areas where there was a value of zero for the ESE_j of any particular

¹³ In the municipalities of Medina (Cundinamarca), El Calvario and Restrepo (Meta), and in the Altiplano Cundiboyacense in the municipalities La Calera, Guasca, Sopo, Guatavita, Gachancipa, Sesquile, Suesca, Nemocon and Cogua (Cundinamarca).

¹⁴ In the municipalities San Jose de La Montaña, Santa Rosa de Osos, Yarumal and San Andres (Antioquia).

¹⁵ In the municipalities of Caldone, Silvia, Belalcazar and Toribio (Cauca), and in the Huaca Massif in the vicinity of the Galeras, Cumbal and Azufral Volcanoes in the municipalities Cumbal, Cuaspud, Aldaña, Pupiales, Ipiales, Cordoba, Puerres, Contadero, Iles, Funes, Ospina, Imues, Yacuanquer, Guaitarilla, Pasto, Tuquerres and Santa Cruz (Nariño).

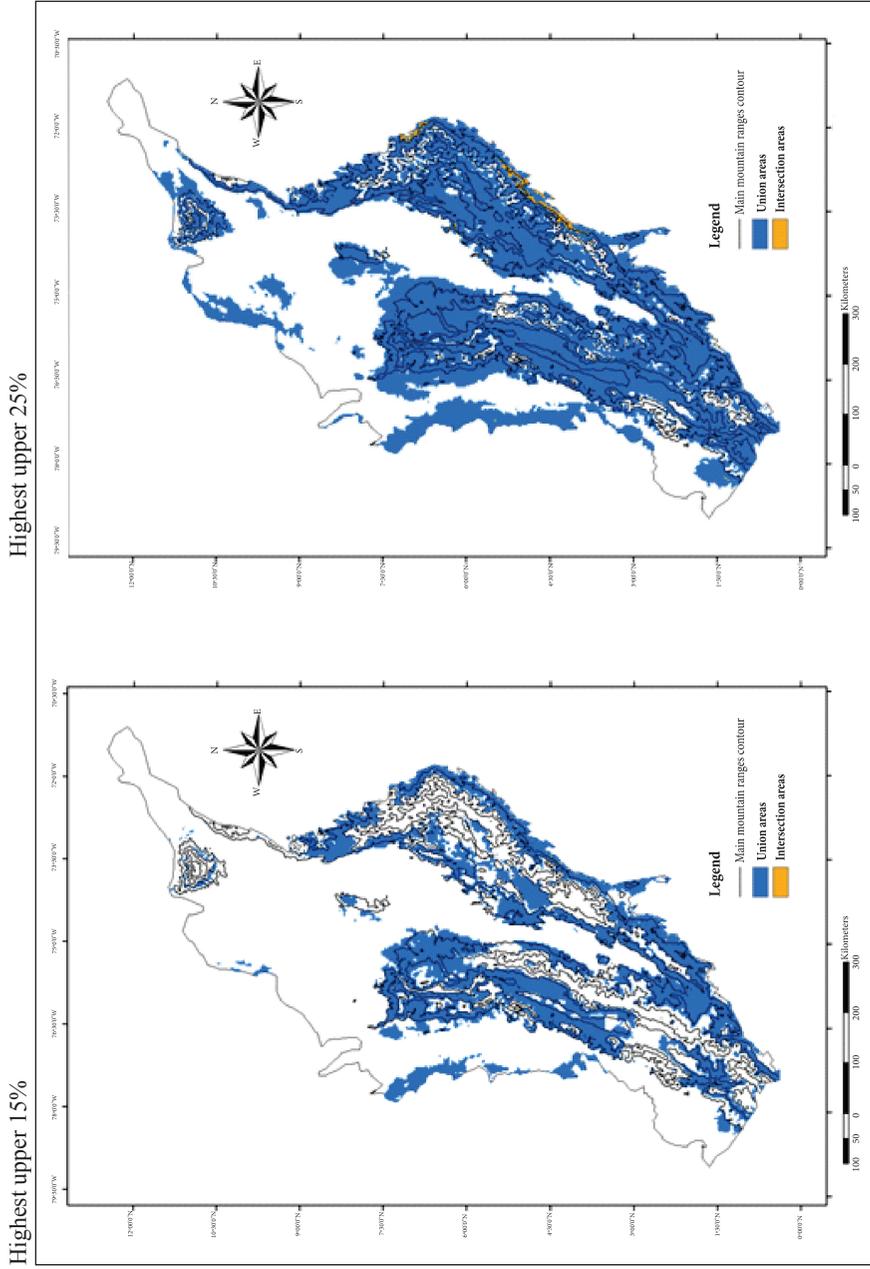
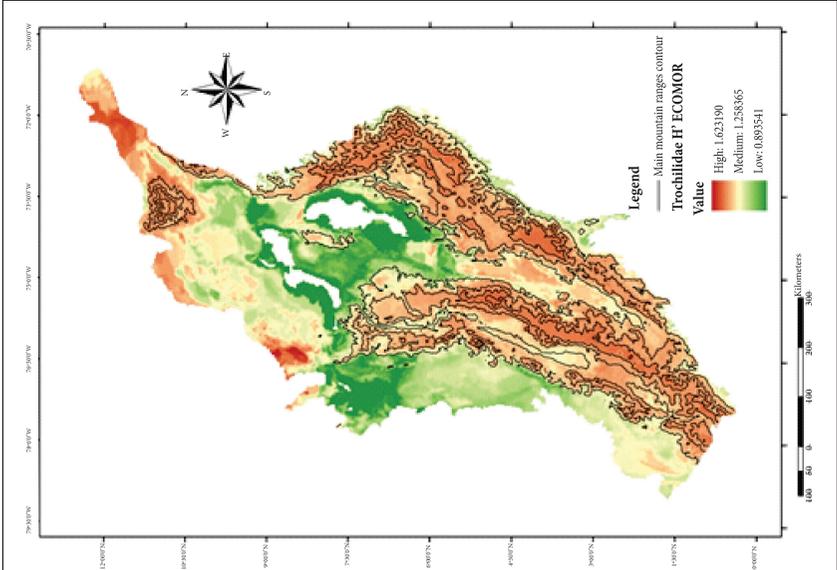


Figure 5.3.4.2.4. Potential areas of high avian rarity (weighted endemism score) in West Colombia using as threshold the upper 15 and 25 percent of the range of values observed in each richness map through all taxonomic levels (family and genus) and avian subsets (all taxa, non-marine, forest and strictly forest).

Hummingbirds (Trochilidae) – E' index



Hummingbirds (Trochilidae) – ESE index

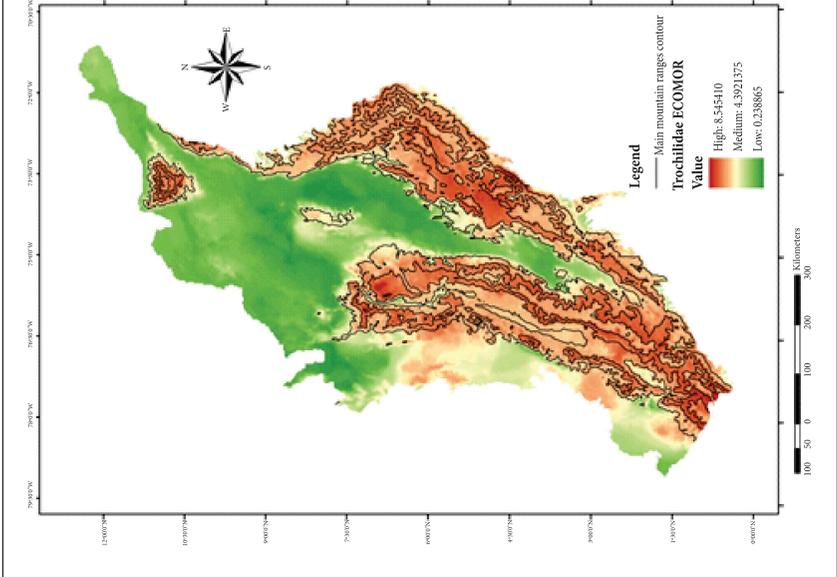


Figure 5.3.4.3.1. Equivalent–species ecomorphological diversity index (ESE index) and ecomorphological groups equitability (E' index) distribution in West Colombia for hummingbirds (Trochilidae). Habitat suitability modelling: second generation.

functional group; not present at all between taxa predicted to occur in a particular area. As result, in such cases the proportion between ESE_j and ESE became zero making not possible to calculate the natural logarithm function in the equation, which tends to infinity and cannot be calculated.

For tyrant flycatchers, again the Andean Region occupied a very important role in the distribution of the highest values for the ESE index. However, for this family the potentially highest ecomdiversity areas were located in the range between $\approx 1,000$ – $3,000$ m in the three Andean cordilleras, including Serrania de los Motilones, Serrania del Perija and some few areas in Serrania de San Lucas and Serrania de La Macarena. As well as several areas below this range in the Andean foothills and the Serrania del Baudo (Figure 5.3.4.3.2). Furthermore, some areas with outstandingly high values appeared in a semi-continuous belt on the slopes of the Eastern Cordillera¹⁶.

Also in the northern end of the Central Cordillera¹⁷ and in the Western Cordillera¹⁸. Otherwise, as previously noted for hummingbirds, the majority of the Andean foothills and the Biogeographic-Choco (Pacific) Region exhibited medium values, whilst in contrast most lowlands in the Caribbean Region also exhibited medium values. Finally, the lowest values in the ESE index appeared in the low Atrato, low Sinu, San Jorge, low Cauca, low Nechi and the mid Magdalena valleys, as observed for hummingbirds previously.

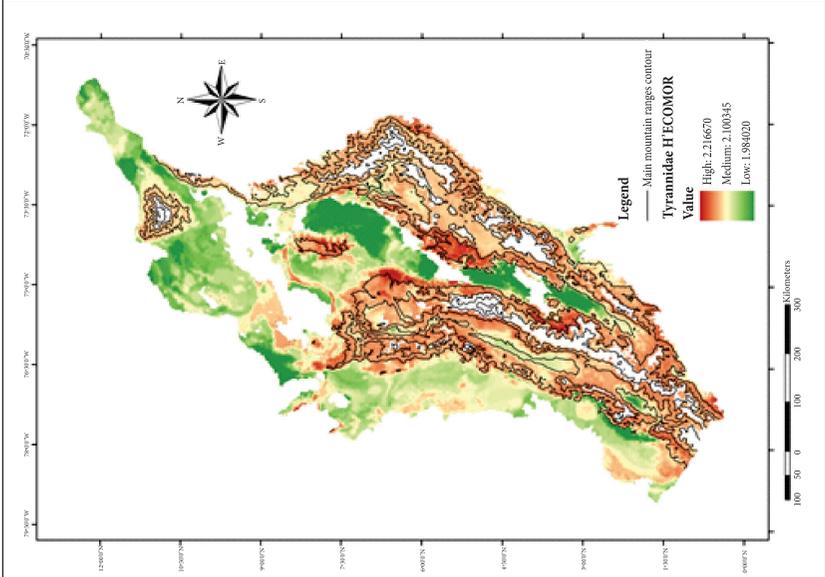
In tyrant flycatchers the “ecomorphological groups equitability” (E’ index) exhibited a general pattern similar to that for hummingbirds. Thus, high-score areas extended relatively evenly throughout the Andes, the Sierra Nevada de Santa Marta and their foothills. Nonetheless, including areas below $\approx 1,000$ m and excluding the inter-Andean valleys and areas in the Andes above $\approx 3,000$ m (Figure 5.3.4.3.2). Differently, in this case, inter-Andean valleys showed medium values, whilst the top

¹⁶ In the eastern slope including portions in the municipalities El Castillo, El Dorado, Cubarral, Guamal, Acacias, Villavicencio, El Calvario, Restrepo and Cumaral (Meta); Guayabetal, Medina, Gachala, Ubala and Paratebueno (Cundinamarca); Chivor, Santa Maria, San Luis de Gaceno, Campohermoso, Paez, Pajarito, Labranzagrande, Pisba, Paya and Cubara (Boyaca); Sabanalarga, Monterrey, Tauramena, Chameza, Recetor, Aguazul, Yopal and Tamara (Casanare); Tame, Fortul and Saravena (Arauca) and Toledo (Norte de Santander). Additionally, in the western slopes of the Eastern Cordillera in the municipalities of Raquira, Tinjaca and Sutamarchan (Boyaca), and Velez, Bolivar, Piedecuesta and Santa Barbara (Santander).

¹⁷ in the municipalities San Luis, Medellin, Gomez Plata, Carolina, Angostura, Guadalupe, Amalfi, Campamento, Yarumal, Valdivia, Briceño and Liborina (Antioquia).

¹⁸ in its northern end in the municipalities Ituango, Valdivia, Taraza, Buritaca, Canasgordas, Frontino, Giraldo and Santa Fe de Antioquia (Antioquia). Further south in a semi-continuous stripe in Valle del Cauca in municipalities Buenaventura, Dagua, La Cumbre, Vijes, Restrepo, Yotoco, Calima, RioFrio, Bolivar, El Dovio, Roldanillo, La Union, Toro, Versalles, Argelia and El Cairo, and some few more areas in Choco in municipalities Litoral de San Juan, Sipi and San Jose del Palmar.

Tyrant flycatchers (Tyrannidae) – E' index



ant flycatchers (Tyrannidae) – ESE index

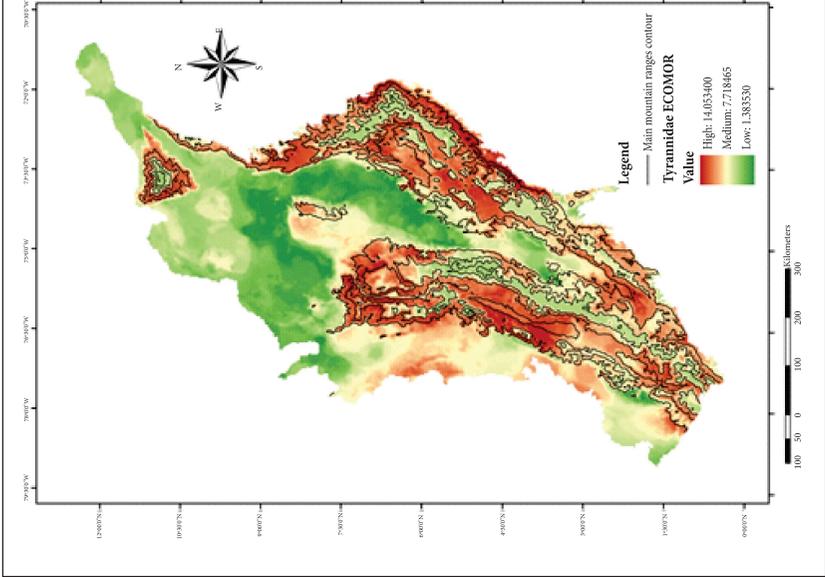


Figure 5.3.4.3.2. Equivalent–species ecomorphological diversity index (ESE index) and ecomorphological groups equitability (E' index) distribution in West Colombia for tyrant flycatchers (Tyrannidae). Habitat suitability modelling: second generation.

of the mountain ranges received “missing value” due to the absence of at least one functional group, as explained before for hummingbirds. Moreover, several high-score areas appeared in the Pacific lowlands in Nariño, Cauca and Choco and around the Serrania del Baudo. Otherwise, low-score areas north of the Andes and in the mid Magdalena valley were less common, although they were mostly replaced by “missing value” areas. Finally, it is important to add that for this family several areas with remarkably high E' index values emerged in the Serrania de San Lucas, on the western slopes of the Eastern Cordillera in west Boyaca and Cundinamarca and in the Central Cordillera in the adjacent foothills below its eastern slope in central-west Antioquia, sparsely around the Ruiz-Tolima Volcanic Complex, in the eastern slopes in south Tolima, and west and east of the Huaca Massif in Nariño. In addition, a few more areas appeared in the Western Cordillera in Serrania de los Paraguas and south of Munchique, as well as many more small areas in all the three Andean ranges.

In addition, it is interesting to highlight that for each family not all functional groups were equally important and had the same spatial distribution. Thus, results from this study suggest that, overall, for hummingbirds the functional groups related to species using the upper undergrowth and medium levels for both gleaning insects and invertebrates from leaves and taking nectar from open corollas (UMFTNBII and UMNECOCL) occupied a major proportion of the total modified equivalent-species for the family. Those accounting for nearly 74% of the map total in the ESE index (Table 5.3.4.3.1). On the other hand, although all functional groups had their highest scores in the main mountain ranges, the distribution of these areas varied in each case (Figure 5.3.4.3.3). In this sense, for example it is possible to note that groups related to canopy and borders (CBHII, CBFII and CBNECOCL) had a relatively extended and more even distribution in the Andes and the Sierra Nevada de Santa Marta; while the two remaining groups, those related to the upper undergrowth and medium levels (UMFTNBII and UMNECOCL), extended in some few areas into the Pacific lowlands in the Choco, Cauca and Nariño and in Serrania del Baudo.

In contrast, for tyrant flycatchers, modified equivalent-species were relatively more evenly distributed in a major number of functional groups, suggesting “apparently” higher ecomorphological diversity for this family than for hummingbirds. Functional groups related to species that glean insects and invertebrates from leaves in both the upper undergrowth and medium levels, and in the canopy and borders (UMFTNBII and CBFII) added up to $\approx 37\%$ of the map total in the ESE index. Another $\approx 33\%$ was distributed among functional groups related to species that hawk insects and invertebrates in both the upper undergrowth and medium levels and in the canopy and borders (UMHII and CBHII), and that take fruits in the canopy and borders (CBF) (Table 5.3.4.3.1). Otherwise, as also seen for hummingbirds, the distribution in the country of the potentially highest-ranking areas for each functional group varied

Table 5.3.4.3.1. Modified equivalent–species map totals for each functional group in hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae) in West Colombia. Habitat suitability modelling: second generation.

Guild name	Family			
	Trochilidae	%	Tyrannidae	%
UMHII	18,181.9	8.1	47,594.3	10.7
CBHII	10,096.4	4.5	47,007.5	10.6
GLUHII			15,241.0	3.4
GLUFII			51,580.2	11.6
UMFTNBII	73,572.5	32.8	84,845.2	19.1
CBFII	10,138.1	4.5	80,704.1	18.2
UFTNBVII			2,996.3	0.7
MCFTNBVII			18,283.6	4.1
GLUFF			9,369.3	2.1
UMFF			34,048.0	7.7
CBF			52,599.4	11.8
UMNECOCL	91,174.9	40.7		
CBNECOCL	20,813.8	9.3		
Total	223,977.6		444,268.9	

Undergrowth and Medium Level Hawking Insectivore and Invertebratvore; CBHII, Canopy and Borders Hawking Insectivore and Invertebratvore; GLUHII, Ground and Lower Undergrowth Hawking Insectivore and Invertebratvore; GLUFII, Ground and Lower Undergrowth Foliage Gleaner Insectivore and Invertebratvore; UMFTNBII, Upper Undergrowth and Medium Level Foliage and Thin Branches Gleaner Insectivore and Invertebratvore; CBFII, Canopy and Borders Foliage Gleaner Insectivore and Invertebratvore; UFTNBVII, Undergrowth Foliage and Thin Branches Gleaner Vertebratvore and Invertebratvore; MCFTNBVII, Medium Level and Canopy Foliage and Thin Branches Gleaner Vertebratvore and Invertebratvore; GLUFF, Ground and Lower Undergrowth Foliage Frugivore; UMFF, Upper Undergrowth and Medium level Foliage Frugivore; CBF, Canopy and Borders Frugivore; UMNECOCL, Undergrowth and Medium Level Nectarivores – Open Corolla Licking; CBNECOCL, Canopy and Borders Nectarivores – Open Corolla Licking.

UMFTNBII

CBHII

UMHI

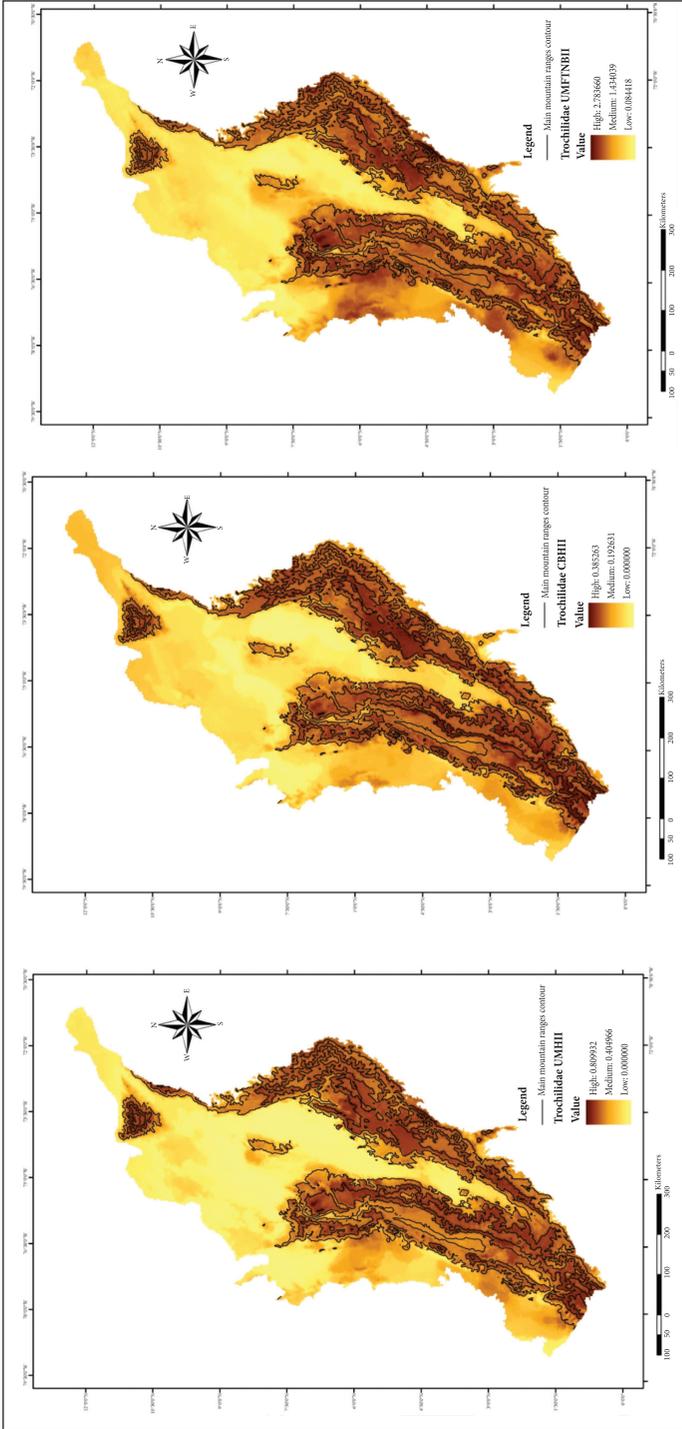


Figure 5.3.4.3.3a. Modified equivalent–species distribution in West Colombia for each functional group defined for hummingbirds (Trochilidae). Habitat suitability modelling: second generation. UMHII, Undergrowth and Medium Level Hawking Insectivore and Invertebrate; CBHII, Canopy and Borders Hawking Insectivore and Invertebrate; UMFTNBII, Upper Undergrowth and Medium Level Foliage and Thin Branches Gleaner Insectivore and Invertebrate.

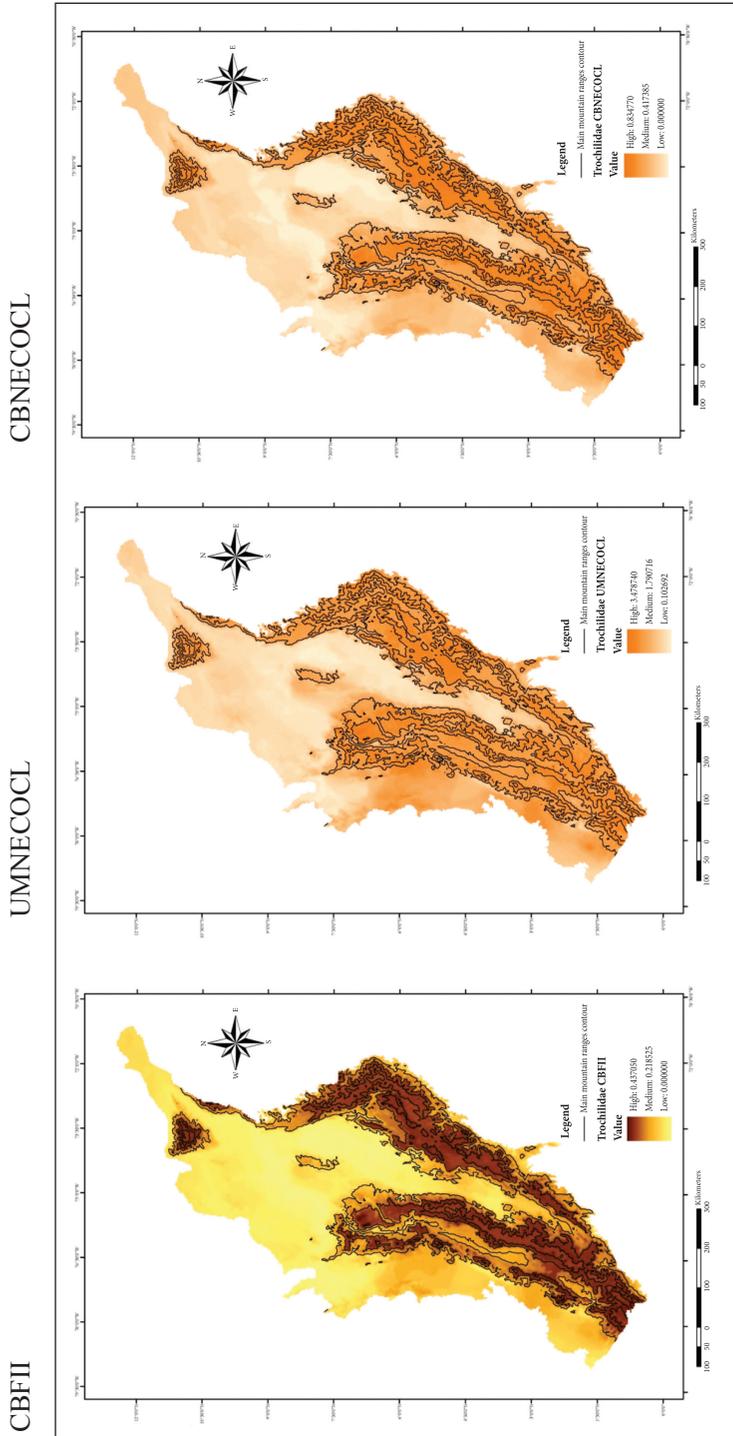


Figure 5.3.4.3b. Modified equivalent-species distribution in West Colombia for each functional group defined for hummingbirds (Trochilidae). Habitat suitability modelling: second generation. CBFII, Canopy and Borders Foliage Gleaner Insectivore and Invertebrate; UMNECOCL, Undergrowth and Medium Level Nectarivores – Open Corolla Licking; CBNECOCL, Canopy and Borders Nectarivores – Open Corolla Licking.

(Figure 5.3.4.3.4). However, for tyrant flycatchers, patterns were less extensive and continuous into the Andes and the Sierra Nevada de Santa Marta, being more restricted within the range of $\approx 1,000$ – $3,000$ m of elevation. As for example it occurred for some groups such as those related to species that hawk and/or glean insects and invertebrates in the canopy and borders (CBHII and CBFIII), and the upper undergrowth and medium level (UMHII), which exhibited varying degrees of patchiness in the distribution of areas with high scores within that elevational range. Similarly, groups related to frugivorous habits (GLUFF, UMFF and CBF) seem to maintain a similar general pattern as the one described, but include in some cases areas in the lowlands west of the Western Andes in Serrania del Baudo and in southwestern Nariño. Moreover, groups that forage insects and invertebrates on the ground and the lower undergrowth (GLUHII and GLUFII), and that glean insects and invertebrates from leaves in the upper undergrowth and medium levels (UMFTNBII) exhibited an even more restricted distribution (Figure 5.3.4.3.4). Finally, from the functional groups including small vertebrates in their diets, the group embracing species that forage in medium levels and the canopy (MCFTNBVII) behaved similarly to frugivorous related groups; whilst the group that includes species foraging in the undergrowth (UFTNBVII) exhibited a unique extensive and uniform pattern covering areas in the mountains below 2,000 m and the lowlands west of the Andes and the Caribbean Region.

The spatial analysis of the differences between standardised maps¹⁹ of plain richness and the ESE index revealed interesting patterns that suggest a dichotomy between areas with potentially high levels of ecomorphological singularity and areas where is clear ecomorphological redundancy (Figure 5.3.4.3.5). Results of this analysis evidenced areas with high ecomorphological singularity to be located in the Andean slopes, the Sierra Nevada de Santa Marta and in several areas in the lowlands. For hummingbirds, areas with high singularity were found mainly above 2,000 m in a semi-continuous stripe in the Eastern Cordillera, and in the Central and Western cordilleras in two main blocks in the north and south with some areas spread in between. Furthermore, several areas below 2,000 m, emerged in the eastern slopes of the Central Cordillera in south Antioquia, Caldas and north Tolima, and in the south, east of the Huaca Massif, in Caqueta, Cauca and Putumayo, and in the Pacific side in central-western Nariño. This was also true, in the high valleys of the Patia and Cauca rivers in Cauca, and in the Pacific slope of the Western Cordillera and some adjacent lowlands in Antioquia, Risaralda, Choco, Valle del Cauca and Cauca. Otherwise, most areas below the 2,000 m isocline and the foothills of the main

¹⁹ Maps were standardised using the maximum value of any cell of a set of related maps (*i.e.* plain richness current conditions and future scenarios projections and ecomdiversity current conditions and future scenarios projections), obtaining values between 0–1.

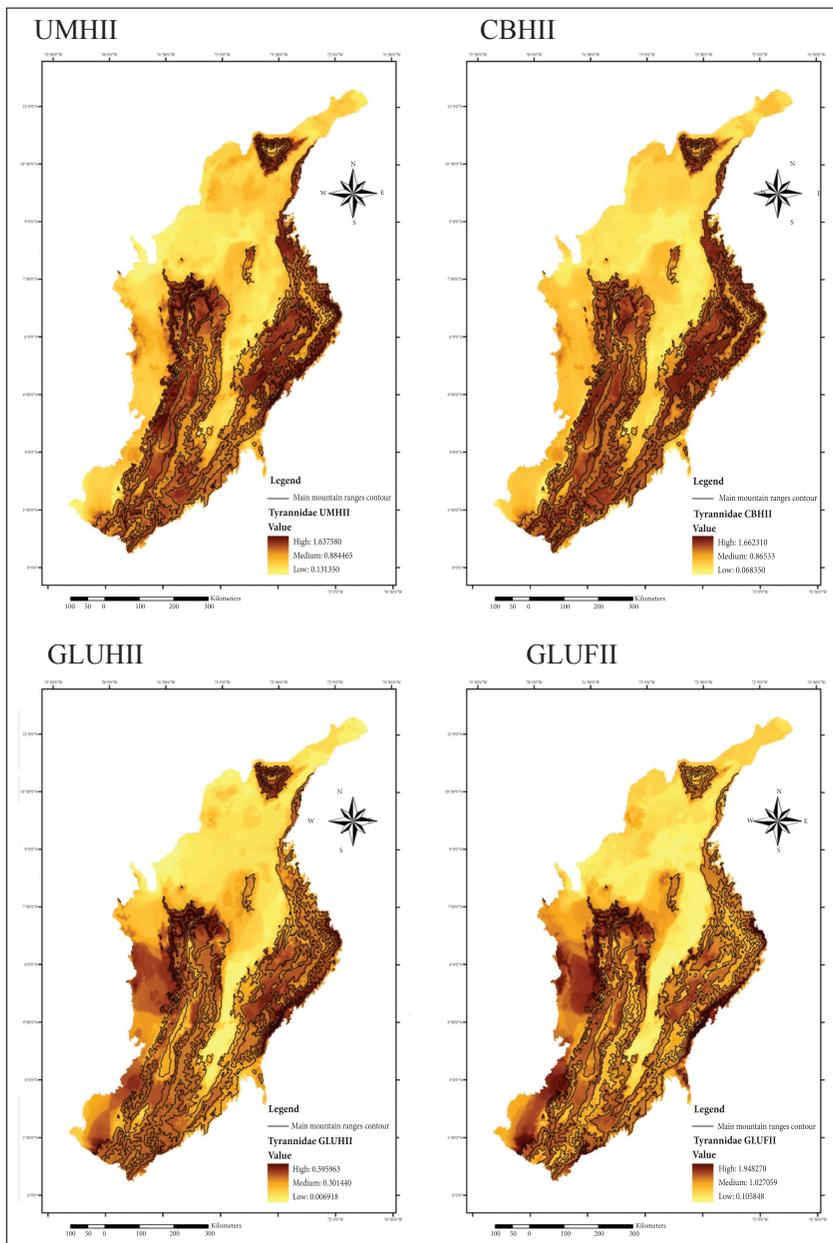


Figure 5.3.4.3.4a. Modified equivalent–species distribution in West Colombia for each functional group defined for tyrant flycatchers (Tyrannidae). Habitat suitability modelling: second generation. UMHII, Undergrowth and Medium Level Hawking Insectivore and Invertebrativore; CBHII, Canopy and Borders Hawking Insectivore and Invertebrativore; GLUHII, Ground and Lower Undergrowth Hawking Insectivore and Invertebrativore; GLUFII, Ground and Lower Undergrowth Foliage Gleaner Insectivore and Invertebrativore.

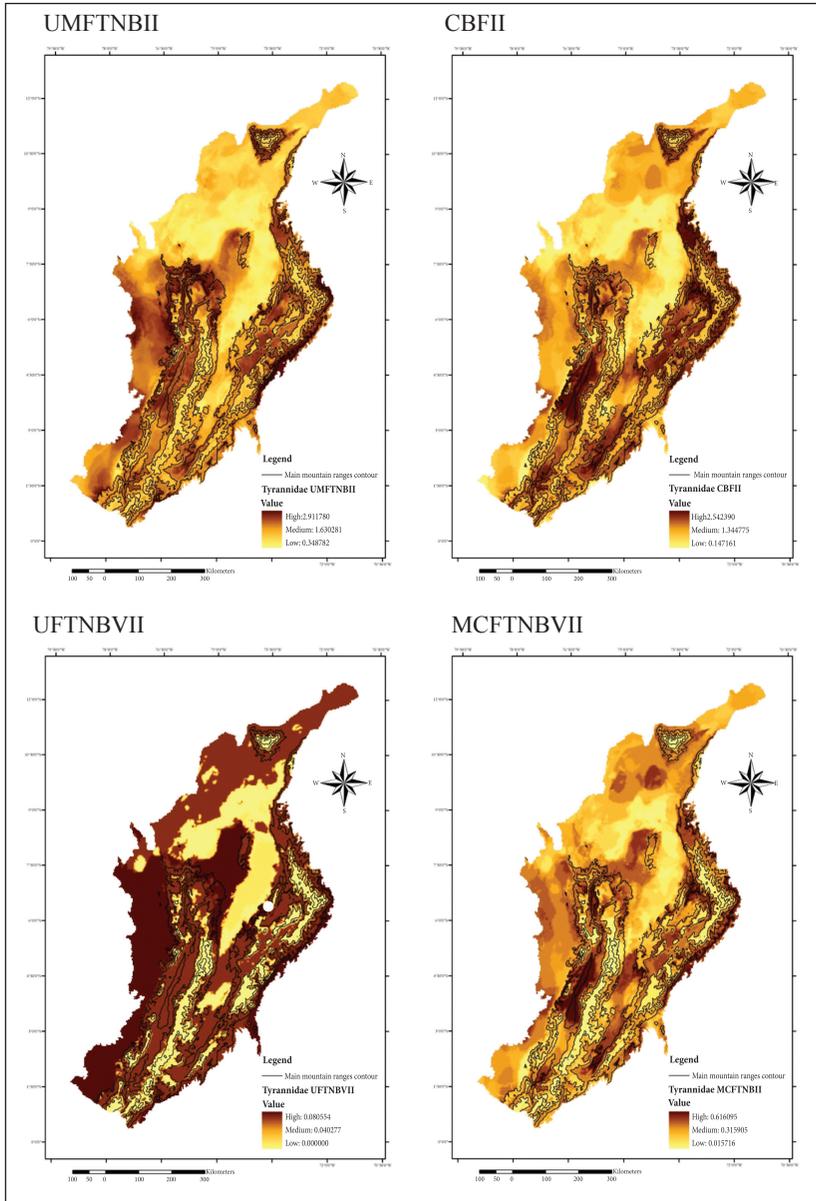


Figure 5.3.4.3.4b. Modified equivalent–species distribution in West Colombia for each functional group defined for tyrant flycatchers (Tyrannidae). Habitat suitability modelling: second generation. UMFTNBII, Upper Undergrowth and Medium Level Foliage and Thin Branches Gleaner Insectivore and Invertebrativore; CBFII, Canopy and Borders Foliage Gleaner Insectivore and Invertebrativore; UFTNBVII, Undergrowth Foliage and Thin Branches Gleaner Vertebrativore and Invertebrativore; MCFTNBVII, Medium Level and Canopy Foliage and Thin Branches Gleaner Vertebrativore and Invertebrativore.

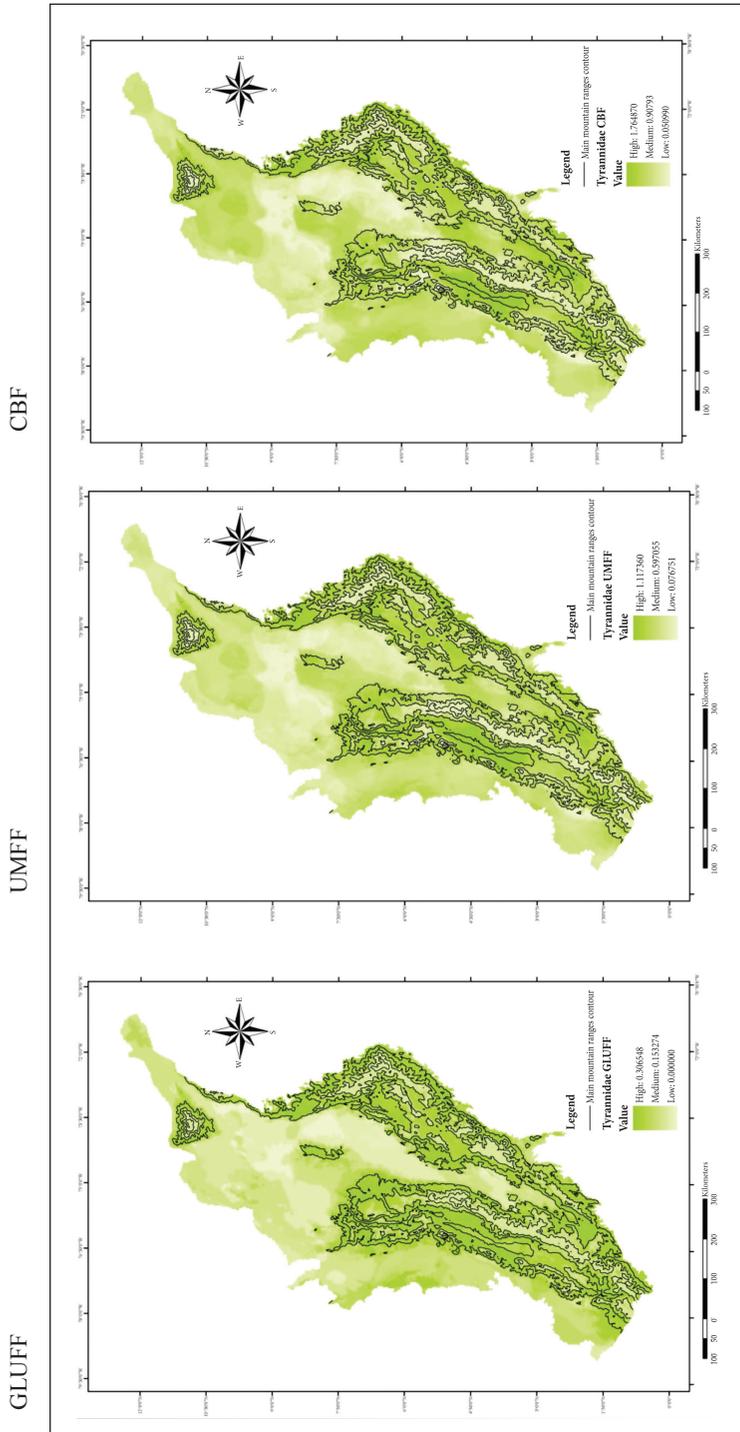


Figure 5.3.4.3.4c. Modified equivalent-species distribution in West Colombia for each functional group defined for tyrant flycatchers (Tyrannidae). Habitat suitability modelling: second generation. GLUFF, Ground and Lower Undergrowth Foliage Frugivore; UMFF, Upper Undergrowth and Medium level Foliage Frugivore; CBF, Canopy and Borders Frugivore.

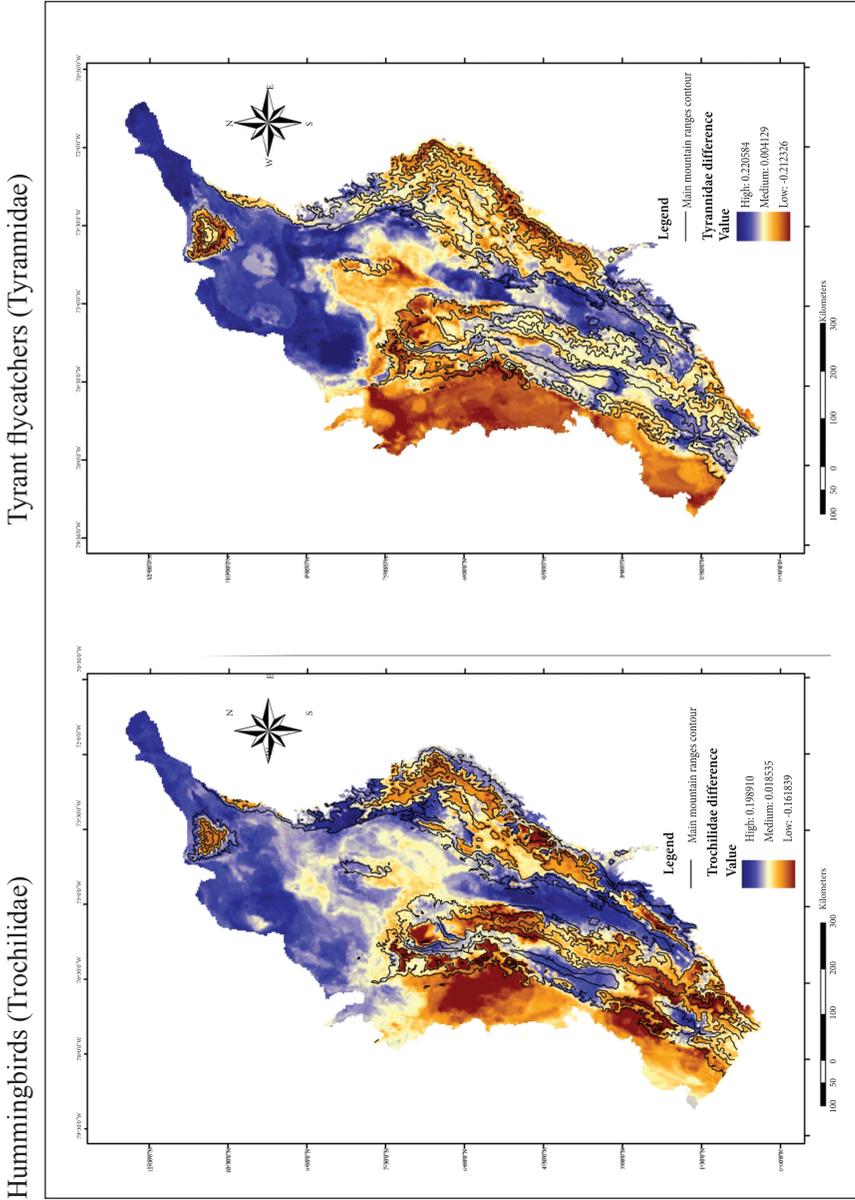


Figure 5.3.4.3.5. Spatial distribution of the difference between standardised plain richness and standardised ESE index maps (plain richness – ESE index) in West Colombia for hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae). Habitat suitability modelling: second generation.

mountain ranges showed no difference between plain richness and ecomdiversity, whilst most lowlands in the Caribbean and inter–Andean valleys corresponded to areas with high ecomorphological redundancy. On the other hand, tyrant flycatchers patterns were very similar. However, patterns of areas with potentially high singularity were more restricted within the range $\approx 1,000\text{--}3,000$ m of elevation in the Andes, and more extensive and uniform in the Pacific foothills and adjacent lowlands as well as in some areas north of the Western and Central cordilleras and east of the Serrania de San Lucas. Contrary to what was observed before, potential areas of high singularity in the south of the Central and Western Cordilleras were less common, although emerged some additional areas in the eastern slope of the Eastern Cordillera in Santander, Boyaca and Cundinamarca, and in the western slope of the Central Cordillera in Caldas, Risaralda and Quindio.

Finally, it is interesting to highlight that the ratio of total ecological singularity (negative differences) to total ecological redundancy (positive differences) in West Colombia is not equal for both families. In this sense, this ratio is about 1:4 for hummingbirds, whilst it is near 1:1 for tyrant flycatchers (Table 5.3.4.3.2).

Table 5.3.4.3.2. Ecological singularity to ecological redundancy ratio based on differences between standardised plain richness and standardised ESE index maps in West Colombia for hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae).
Habitat suitability modelling: second generation.

	Family			
	Trochilidae	%	Tyrannidae	%
Difference				
Positive	2,898.8	78.7	1,953.8	53.2
Negative	-782.2	21.3	-1,717.2	46.8
Absolute total	3,681.0		3,671.0	

5.3.4.4. Evaluation of Richness and rarity maps

Evaluation of final richness and rarity maps was performed in three different ways: 1) using 496 point samples and comparing with values from maps generated using the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (496–WHM), 2) using 76 point samples and comparing with values from maps generated using ProAves’ Migratory Monitoring Program Database – PMAMN Database (76–PMAMN), and 3) using “approximately equal surface interval bands” (AEQSIB) and comparing with values from maps generated using the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (AEQSIB–WHM). This section

will describe results obtained from each evaluation, for both diversity variables, at each taxonomic level in separate subsections. In each subsection, we will present a brief description of the general spatial patterns observed in differences between WHDBD Database based maps (reference) and MAXENT–BioMap based modelled maps (model) and will then provide detail on the results obtained from the three different approaches used to assess the uncertainty of model predictions.

Family richness

Regarding plain richness, at family level, reference maps showed higher values than model maps in several areas in the Pacific lowlands²⁰, in the Caribbean²¹ lowlands, in most of the mid Magdalena valley²² and in the Andean slopes and foothills²³. Additionally, in the highest portion of the Sierra Nevada de Santa Marta and the Serrania del Perija. On the other hand, model maps exhibited higher values than reference maps in most of the high–mid Cauca valley, the high Magdalena valley and the Patia and Dagua valleys, as well as some of their associated slopes in the Andean ranges (Figure 5.3.4.4.1).

When maps were sampled and tested statistically, differences between reference and modelled maps were significant (496–WHM, Three Factor ANOVA, $p < 0.05$). Here it is important to note that neither the “reference” nor “modelled” maps are perfect measures of reality – but both are estimates, with “reference” maps obtained from the information processed from the WHDBD Database being also the result of a non–explicit spatial “modelling” process. In this sense, results showed consistently that estimated mean values of richness were higher in reference maps than in model maps for all three avian subsets. It is important to highlight that differences to reference maps were also significant when we used the data subset retaining only post 1950 accessions and that differences were observed between models when all accessions and accessions post 1950 were used to map all taxa and non–marine avian subsets,

²⁰ In central–west and west Nariño, central–west and north Cauca, south and north Choco in the Atrato river valley.

²¹ In the valleys of the Sinu, San Jorge, Taraza, Cauca and Nechi rivers in northwest Antioquia, Cordoba, south Sucre and central Bolivar. Additionally, in some lowland areas located southwest and southeast from Sierra Nevada de Santa Marta and in the central–north Guajira.

²² From northeast Caldas and northwest Cundinamarca to southeast Bolivar and south Cesar.

²³ In the Pacific slope of the Western Cordillera in Nariño, Cauca, Valle del Cauca and Choco. Also north of the Western Cordillera and in the highest sections of it in some parts of Serrania de los Paraguas, Cerro Tatama and Paramo de Frontino. In the Central Cordillera in the Ruiz–Tolima Volcanic Complex and north east of it. (continues at bottom of next page)

In the Eastern Cordillera, northwest of Serrania de La Macarena in the municipality of Mesetas (Meta), and from Paramo de Sumapaz north to Sierra Nevada del Cocuy and further north to the area around Nudo de Santurban and paramos de Las Cruces, La Cabrera and Tama. In addition, in several sparse areas in the three Andean ranges.

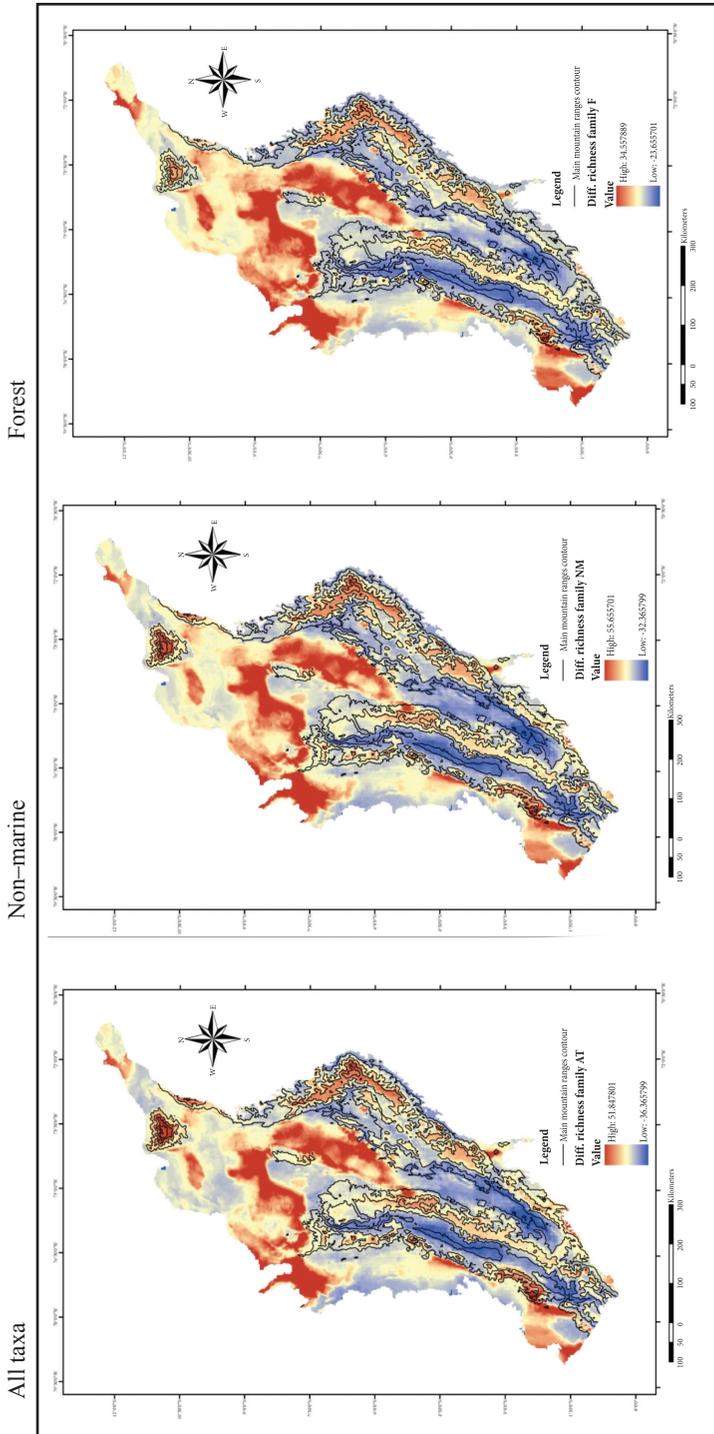


Figure 5.3.4.4.1. Spatial distribution of the difference in plain richness between WHDBD Database based maps (reference) and MAXENT–BioMap based modelled maps (model) in West Colombia at family level (reference - model). Habitat suitability modelling: second generation.

but not for the forest subset (Figure 5.3.4.4.2). On the other hand, when ProAves field data were used for validation, results also showed significant differences between reference and model maps (76–PMAMN, Three Factor ANOVA, $p < 0.05$). Thus, ProAves surveys and mist-net data combined, showed differences in relation to most other treatments, exhibiting intermediate values (Figure 5.3.4.4.3). Nonetheless, there

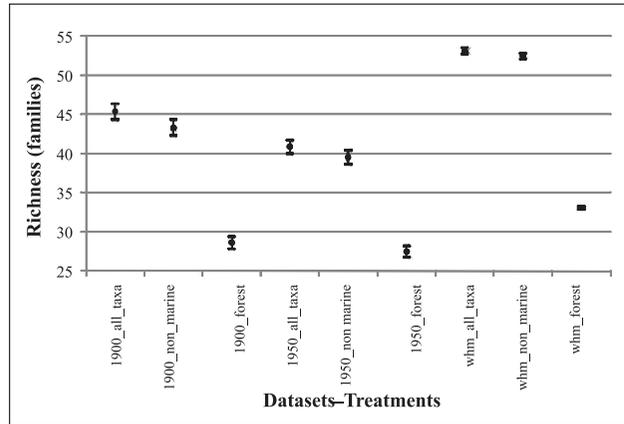


Figure 5.3.4.4.2. Confidence interval of the mean at the 95% probability for estimated family richness when using different data groups and avian subsets. Analysis based on 496 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

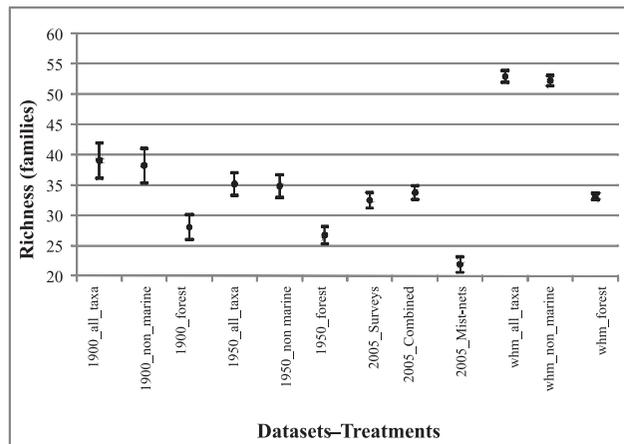


Figure 5.3.4.4.3. Confidence interval of the mean at the 95% probability for estimated family richness when using different data groups and avian subsets. Analysis based on 76 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “2005”, ProAves field data; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

were no significant differences when they were compared to model maps generated for all taxa and non-marine avian subsets using post 1950 accessions and to the reference map for the forest avian subset. Additionally, there were no differences in the estimated values of richness between models produced based on all accessions and accessions post 1950 (Figure 5.3.4.4.3).

Using the AEQSIB-WHM approach reference maps showed higher values in the mountains than model maps for all taxa and non-marine avian subsets. Whilst model maps showed higher values than reference maps in the same subsets in a few coastal areas in the Pacific and Caribbean and in the low Atrato, low Sinu, low Cauca and low Magdalena valleys; as well as in most of the country for the forest avian subset. When tested statistically, observed differences in the elevational gradient of total band richness between reference and model maps were significant for all avian subsets of both models produced based on all accessions and on accessions post 1950 (Wilcoxon Test, $p < 0.05$). Thus, overall, reference maps exhibited higher values than the models for all taxa and non-marine avian subsets, whilst for the forest subset the pattern was reversed. In addition, it is interesting to note that the elevational pattern of family richness in West Colombia resembled a humpback-shaped (sinusoidal) curve. This pattern differed slightly between data and avian subsets used. It was more marked for the non-marine data subset in the reference maps, and less evident in the models when all accessions were used. According to these results, there is a peak (plateau) of family richness in the country roughly between 500–1,500 m of elevation. Differences were bigger when only accessions post 1950 were used, and they increased significantly above 2,000 m for all taxa and non-marine avian subsets, whilst observed differences decreased when the forest subset was mapped (Figure 5.3.4.4.4).

Otherwise, when the 496-WHM approach was used to evaluate correlations between the several maps generated using different data and methodologies, results showed no correlation or very low and negative correlations between reference and model maps for plain richness estimates (Table 5.3.4.4.1). Nevertheless, correlations between model maps produced using all accessions and maps based on just post 1950 accessions exhibited high and positive correlation coefficients, as was expected. In contrast, when the AEQSIB-WHM approach was used, correlations between reference and model maps for the total band richness estimates were positive in most cases. Moreover, the majority of coefficients were relatively high for correlations between reference maps and model maps based on all accessions, and between the forest avian subset of reference maps and model maps based on only post 1950 accessions. In addition, it is interesting to note that coefficients exhibited the highest values for correlations between reference maps and the forest avian subset of model maps based on all accessions. Finally, under this approach, correlations between model maps

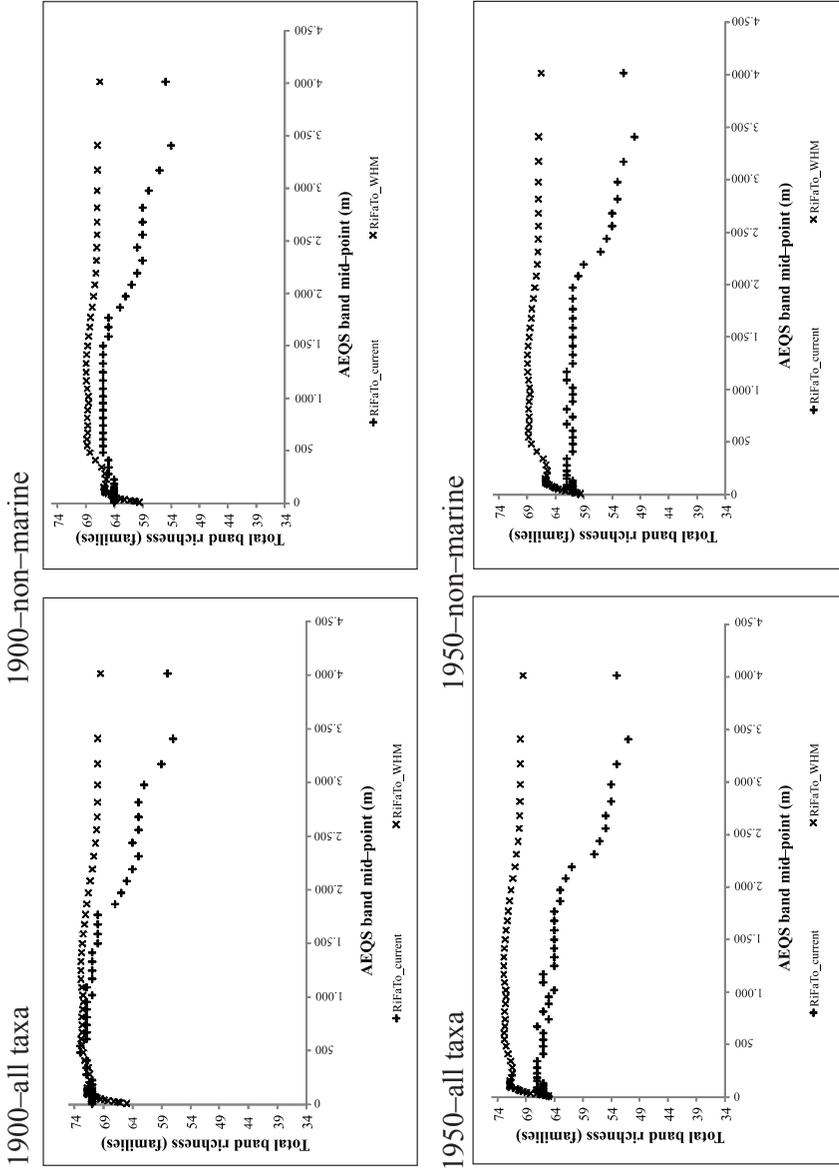
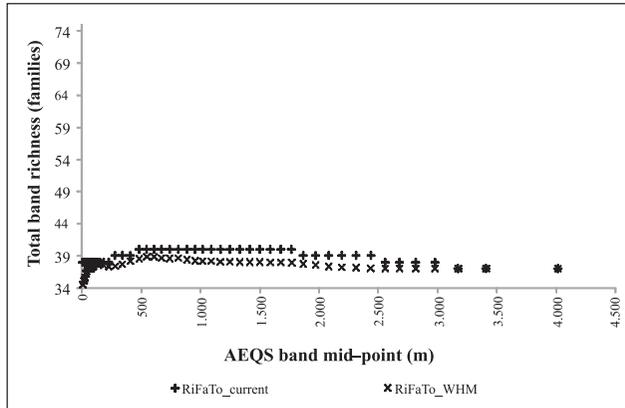


Figure 5.3.4.4.4a. Elevational gradient in estimated total family richness when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

1900–forest



1950–forest

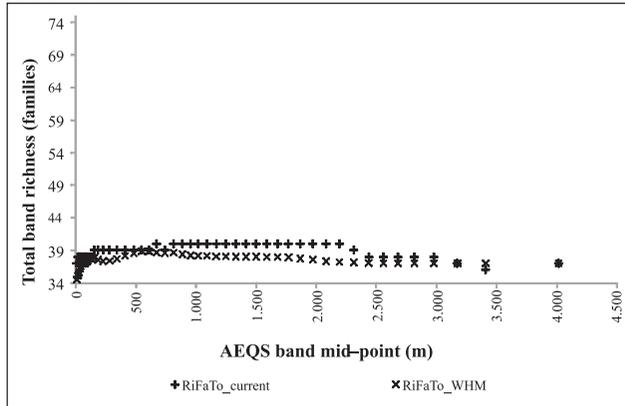


Figure 5.3.4.4b. Elevational gradient in estimated total family richness when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

based on all accessions and maps produced using only post 1950 accessions were relatively low, although they showed medium to high values in some occasions. As for example when correlating all taxa and forest avian subsets of models based on all accessions with their corresponding subsets in the models produced with only post 1950 accessions (Table 5.3.4.4.1).

Genus richness

At genus level, differences between reference and model maps were similar to patterns described previously at the family level, although with some remarkable

Table 5.3.4.4.1. Correlations between reference and model maps for family richness estimates produced using approaches 496–WHM and AEQSIB–WHM in West Colombia. Habitat suitability modelling: second generation.

	496–WHM approach ¹			AEQSIB–WHM approach ²		
	All accessions MAXENT–BioMap model maps			All accessions MAXENT–BioMap model maps		
WHM–reference maps	All Taxa	Non– Marine	Forest	All Taxa	Non– Marine	Forest
All Taxa	-0.042			0.489**		
Non–Marine		-0.110*			0.580**	
Forest			-0.007			0.843**
Post 1950 accessions MAXENT–BioMap model maps						
All Taxa	0.859**			0.745**		
Non–Marine		0.893**			0.590**	
Forest			0.903**			0.872**
	Post 1950 accessions MAXENT–BioMap model maps			Post 1950 accessions MAXENT–BioMap model maps		
WHM–reference maps	All Taxa	Non–Ma- rine	Forest	All Taxa	Non– Marine	Forest
All Taxa	-0.166**			0.121		
Non–Marine		-0.192**			0.015	
Forest			-0.004			0.753**

Spearman's ρ correlation coefficients. * indicates an associated probability < 0.05 and ** an associated probability < 0.01

¹ 496 point samples, comparing versus the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (496–WHM)

² “Approximately equal surface interval bands”, comparing versus the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (AEQSIB–WHM)

disparities, especially in areas where model maps exhibited higher values than reference maps. As described for family richness, at the genus level, reference maps showed higher values than model maps in some areas in the Pacific and Caribbean lowlands, and in the Andean slopes and foothills although less so than at family level. Also in the highest portion of the Sierra Nevada de Santa Marta and Serrania del Perija. On the other hand, model maps exhibited higher values than reference maps,

extensively more than at family level, in the Andean slopes below $\approx 2,000$ m and in the Serrania del Baudo, the high–mid Cauca valley and the high Magdalena valley (Figure 5.3.4.4.5). Areas where reference maps had higher values than model maps towards the Pacific and in the highest parts of the Sierra Nevada de Santa Marta and the Central and Eastern Cordilleras decreased or disappeared as taxa more restricted to forest were mapped. In addition, areas in the lowlands in the northern half of the country increased significantly when the non–marine avian subset were mapped, but increased slightly in comparison to all taxa when the forest avian subset was mapped and decreased slightly when the strictly forest avian subset was mapped. Conversely, areas where model maps had higher values than reference maps decreased when the non–marine avian subset was mapped, especially in the Pacific slopes, the high Cauca and Magdalena valleys and in the northern half of the Eastern Cordillera. Otherwise, areas increased as taxa more restricted to forest were mapped, including the northern half of Serrania de San Lucas and some small areas in the foothills around Sierra Nevada de Santa Marta.

Similarly, at genus level, observed differences were significant when maps were sampled and tested statistically (496–WHM, Three Factor ANOVA, $p < 0.05$). However, in this case estimated mean values of richness for reference maps were higher than model maps just when the non–marine avian subset was mapped, it was lower when the strictly forest avian subset was mapped, and did not show differences when all taxa and forest avian subsets were mapped. In contrast, but similar to that observed for family richness, it is interesting to note that differences were consistently significant when the data subset just retaining accessions collected post 1950 was used. Differences were observed also between models generated using all accessions and accessions post 1950 through all avian subsets (Figure 5.3.4.4.6). On the other hand, when ProAves field data were used, results showed significant differences between reference and model maps when the strictly forest avian subset was mapped (76–PMAMN, Three Factor ANOVA, $p < 0.05$). Otherwise, the pattern was in agreement to the one described in this paragraph for the previous approach using the WHBDD Database (496–WHM). In addition, in this case there were differences in the estimated values of richness when comparing models produced based on all accessions and only accessions post 1950, although those were relatively small. Finally, it is interesting to note that combined ProAves surveys and mist–net estimations of richness were lower than all other treatments (Figure 5.3.4.4.7).

When used AEQSIB–WHM evaluation approach, reference maps showed higher values than model maps extensively in the main mountains ranges, including also the Serrania del Baudo, Serrania de San Lucas, Serrania de La Macarena, Serrania de Los Motilones, Serrania del Perija and Sierra Nevada de Santa Marta, as well as the inter–Andean Cauca River valley. Those areas were held relatively constant between

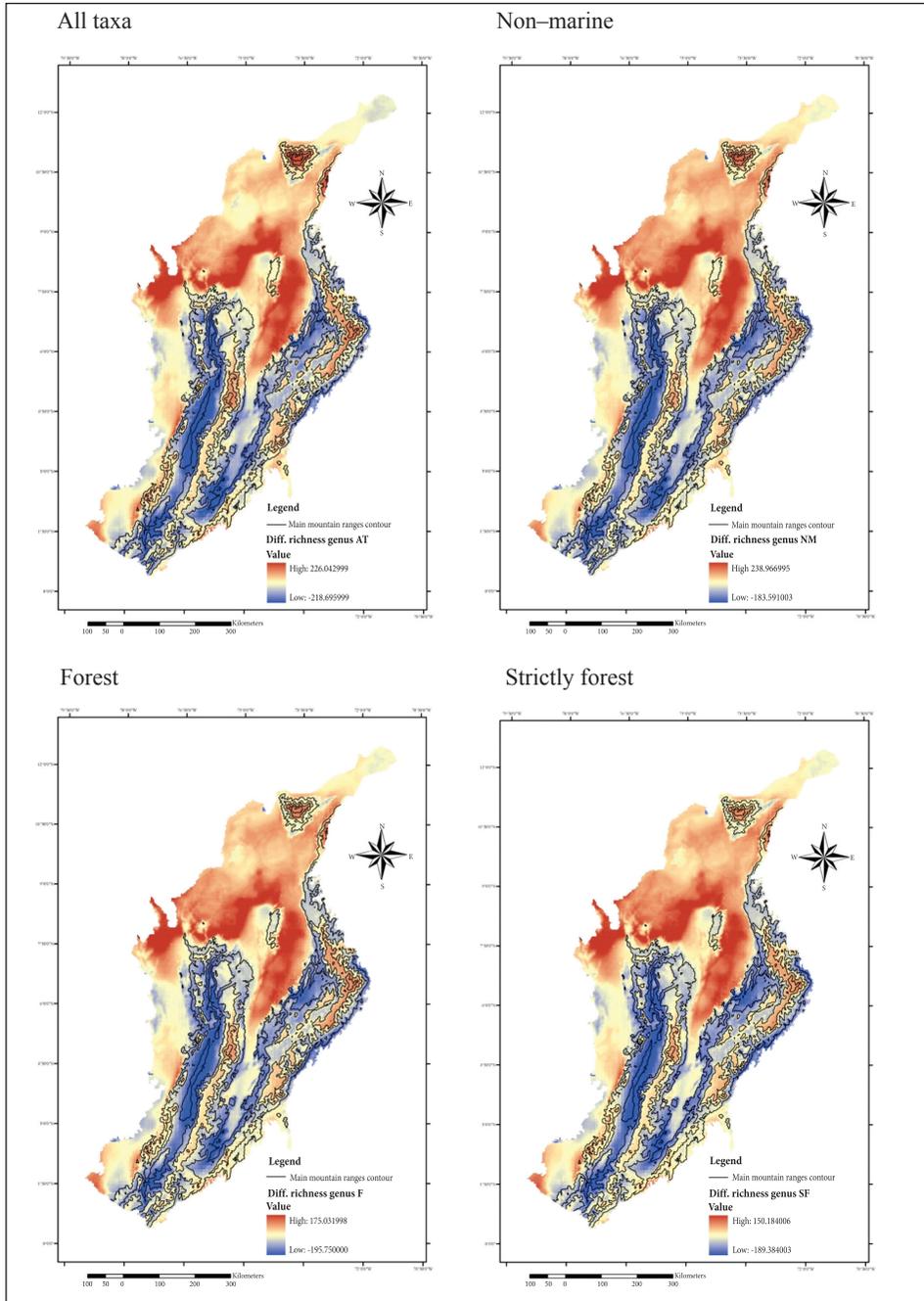


Figure 5.3.4.4.5. Spatial distribution of the difference in plain richness between WHDBD Database based maps (reference) and MAXENT–BioMap based modelled maps (model) in West Colombia at genus level (reference - model). Habitat suitability modelling: second generation.

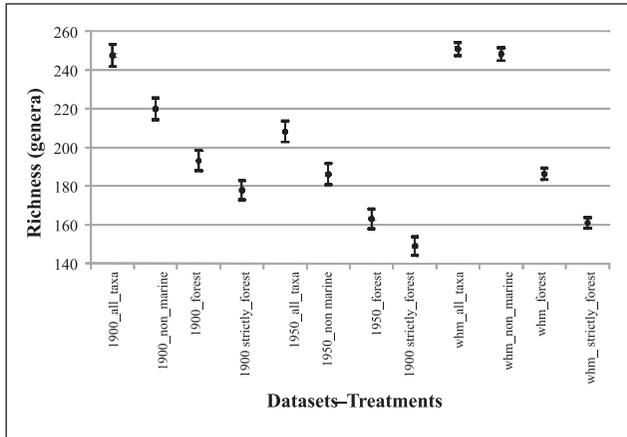


Figure 5.3.4.4.6. Confidence interval of the mean at the 95% probability for estimated genus richness when using different data groups and avian subsets. Analysis based on 496 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

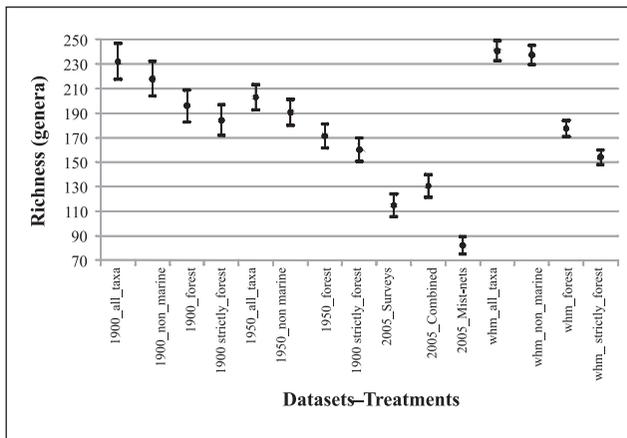


Figure 5.3.4.4.7. Confidence interval of the mean at the 95% probability for estimated genus richness when using different data groups and avian subsets. Analysis based on 76 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “2005”, ProAves field data; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

the different mapped avian subsets, with the exception of the non-marine subset, for which areas extended to adjacent lowlands. Including the inter-Andean Magdalena River valley, around Sierra Nevada de Santa Marta, Serrania de Simerua, Serrania

de Jarara and Serrania de Macuira. Otherwise, model maps showed higher values than reference maps when mapping the forest avian subset in very few and sparse areas in the low Magdalena valley and in La Guajira. Also when mapped the strictly forest avian subset in several coastal areas in the Pacific and the Caribbean, and in the Atrato, Sinu, low Cauca and low Magdalena valleys, similarly as seen before at family level. When tested statistically, observed differences in the elevational gradient of total band richness between reference and model maps were significant for all avian subsets of both models produced based on all accessions and on accessions post 1950 (Wilcoxon Test, $p < 0.05$). However, differently to what was observed at the family level, at the genus level reference maps exhibited higher values than the models through all avian subsets and data groups (Figure 5.3.4.4.8). In addition, in this case the elevational pattern of richness in West Colombia resembled a humpback-shaped curve more so than at family level. Although, as before, slightly different between different data and avian subsets. As also reported for family richness, results showed there is a peak (plateau) of genus richness in the country roughly between 500–1,500 m of elevation. Nonetheless, in this case reference maps exhibited a peak in a narrow section of bands between 500–1,000 m of elevation, while in model based maps this extends even to bands at 2,000 m of elevation, after which values fall. Similarly as seen at family level, differences were bigger when using accessions post 1950 only, increasing ostensibly above 2,000 m for all taxa and non-marine avian subsets. Finally, observed differences decreased when avian subsets more restricted to forest were mapped (Figure 5.3.4.4.8).

When the 496-WHM approach was used to evaluate models, correlation analyses reproduced the same patterns observed at family level. Although, different, correlations at genus level were, in most cases, significant and had higher values than those observed previously (Table 5.3.4.4.2). Thus, correlations between reference and model maps for plain richness estimates showed very low and negative coefficients in all cases, and correlations between model maps produced using all accessions and maps based on just post 1950 accessions exhibited high positive correlation coefficients. On the contrary, when the AEQSIB-WHM approach was used, correlations between reference and model maps for the total band richness estimates were high and positive.

Family rarity

Patterns of difference between reference and model maps in family rarity, measured as the weighted endemism score, exhibited dissimilarities between avian subsets. Once again, it is important to note that the weighted endemism score used as reference here is based on imperfect data and subject to error in the same way the model results are, and therefore a comparison reflects errors in both. Thus, when all taxa were mapped, reference maps showed higher values than model maps in a narrow discontinuous

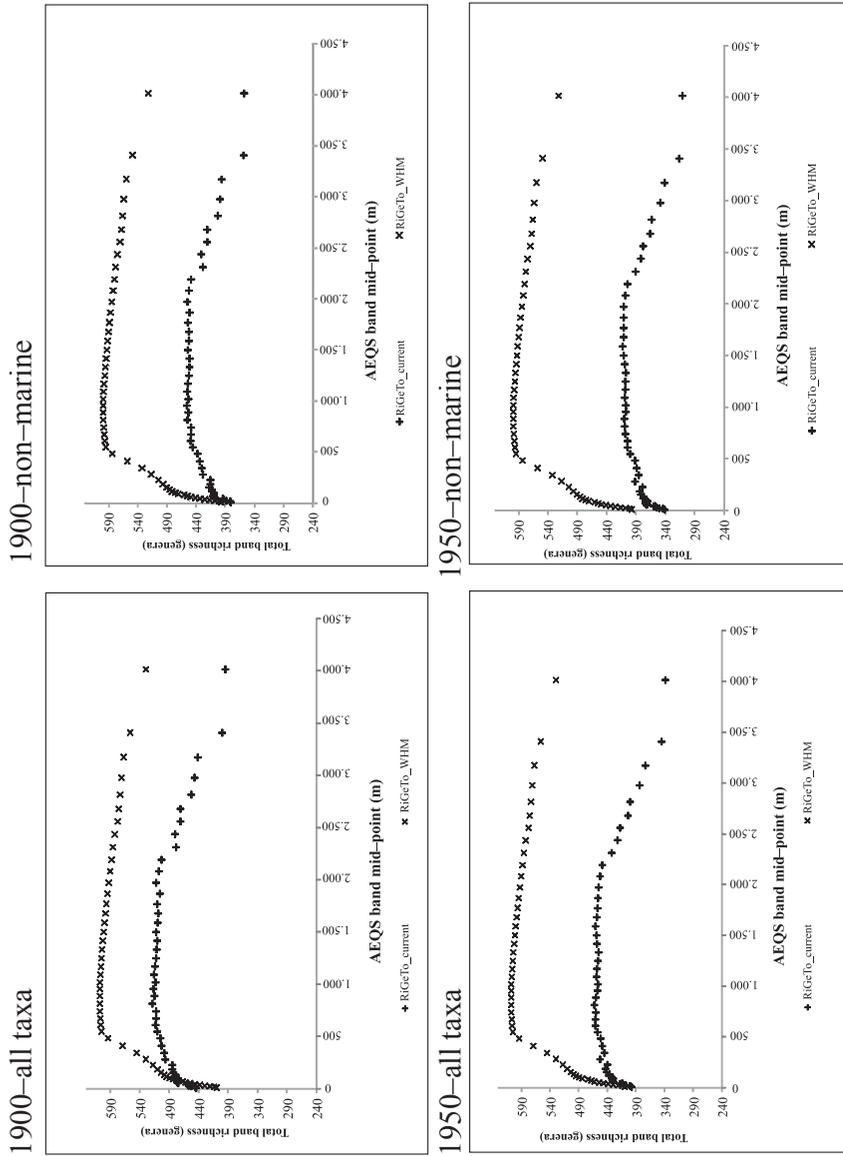


Figure 5.3.4.8a. Elevational gradient in estimated total genus richness when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

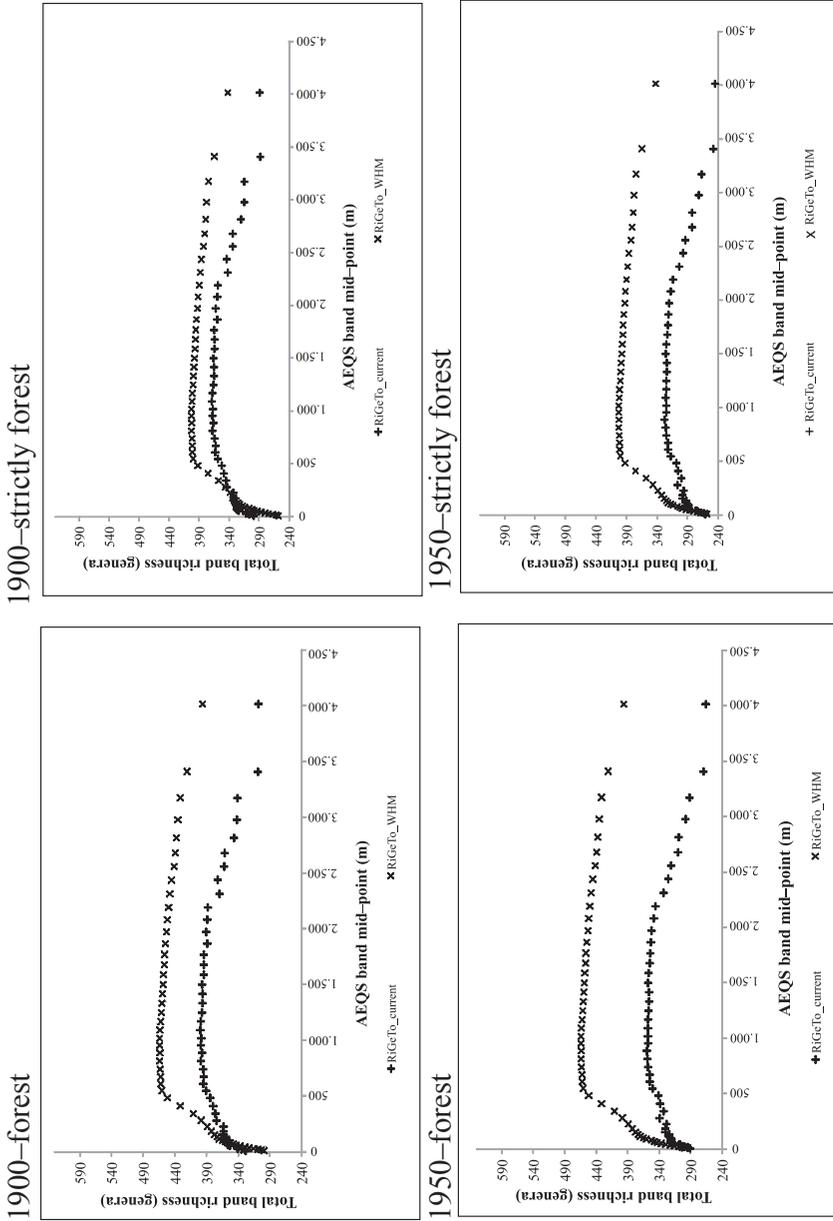


Figure 5.3.4.4.8b. Elevational gradient in estimated total genus richness when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

Table 5.3.4.4.2. Correlations between reference and model maps for genus richness estimates produced using approaches 496–WHM and AEQSIB–WHM in West Colombia. Habitat suitability modelling: second generation.

		496–WHM approach ¹				AEQSIB–WHM approach ²			
		All accessions				All accessions			
		MAXENT–BioMap model maps				MAXENT–BioMap model maps			
WHM–reference maps	All Taxa	Non–Marine	Forest	Strictly Forest	All Taxa	Non–Marine	Forest	Strictly Forest	
All Taxa	-0.270				0.849				
Non–Marine		-0.257				0.869			
Forest			-0.125				0.901		
Strictly Forest				-0.060 ^{ns}				0.900	
Post 1950 accessions									
		MAXENT–BioMap model maps				MAXENT–BioMap model maps			
All Taxa	0.940				0.956				
Non–Marine		0.957				0.951			
Forest			0.956				0.983		
Strictly Forest				0.958				0.978	
Post 1950 accessions									
		MAXENT–BioMap model maps				MAXENT–BioMap model maps			
WHM–reference maps	All Taxa	Non–Marine	Forest	Strictly Forest	All Taxa	Non–Marine	Forest	Strictly Forest	
All Taxa	-0.312				0.798				
Non–Marine		-0.276				0.790			
Forest			-0.119				0.864		
Strictly Forest				-0.045 ^{ns}				0.870	

Spearman's ρ correlation coefficients. ^{ns} indicates an associated probability > 0.05 and therefore a non-significant correlation. Otherwise, all associated probabilities were lower than 0.01.

¹ 496 point samples, comparing versus the "Western Hemisphere Digital Bird Distribution Database – WHDBD Database" (496–WHM)

² "Approximately equal surface interval bands", comparing versus the "Western Hemisphere Digital Bird Distribution Database – WHDBD Database" (AEQSIB–WHM)

strip in coastal areas in both the Pacific and the Caribbean. Additionally, in a wide continuous strip in the Eastern Cordillera²⁴ and east from Serrania de San Lucas²⁵ (Figure 5.3.4.4.9). Otherwise, the rest of the country did not show major differences between reference and model maps. Coastal areas where reference maps had higher values than model maps disappeared when the non-marine subset was mapped, and the pattern changed completely for the forest subset. In that case, model maps exhibited higher values than the reference maps in most of the country, with the exception of a few areas in the low Atrato, low Cauca and mid-low Magdalena valleys (Figure 5.3.4.4.9).

When maps were sampled and tested statistically, observed differences were shown to be significant (496-WHM, Three Factor ANOVA, $p < 0.05$). However, in contrast to those for plain richness, results showed consistently for all three avian subsets that model maps had higher estimated mean values of rarity than reference maps. Similarly, results showed significant differences between models when both all accessions and accessions post 1950 were used, although in this case those were congruent through all avian subsets (Figure 5.3.4.4.10).

Similarly to richness, when AEQSIB-WHM was used, the total weighted endemism score in reference maps showed higher values than model maps in the mountains, this time usually above $\approx 2,000$ m of elevation, and in a narrow band in the lowlands for all taxa and the non-marine avian subsets. On the other hand model maps showed higher values than reference maps in the same subsets in adjacent areas to the main mountain systems and in several areas spread across the lowlands; as well as in most of the country when mapping the forest avian subset. When tested statistically, observed differences in the elevational gradient in total band weighted endemism score between reference and model maps were significant for all avian subsets of both models produced based on all accessions and on accessions post 1950 (Wilcoxon Test, $p < 0.05$), as occurred also for richness. Nonetheless, for rarity, reference maps exhibited higher values than the models through all avian subsets (Figure 5.3.4.4.11). Furthermore, it is interesting to highlight that the elevational pattern of total family rarity in Western Colombia exhibited very different tendencies for reference and model maps and between avian subsets. Thus, when all taxa and non-marine avian subsets were mapped, for model maps the pattern resembled a humpback-shaped curve, whilst in contrast for reference maps it resembled a “concave-u” shaped curve with an additional tail of values that decreased at high altitudes. Moreover, shapes were slightly different between different data and avian subsets. They were more

²⁴ From the areas nearby Paramo de Amarguras (north of Paramo de Sumapaz) to the zone in between Paramo de La Rusia and Paramo de Pisba.

²⁵ Between the northern portion of Serrania the San Lucas in Cerro San Agustin and Serrania Iglesias and the foothills of the Eastern Cordillera in Cuchilla La Morena and Cuchilla La Osa.

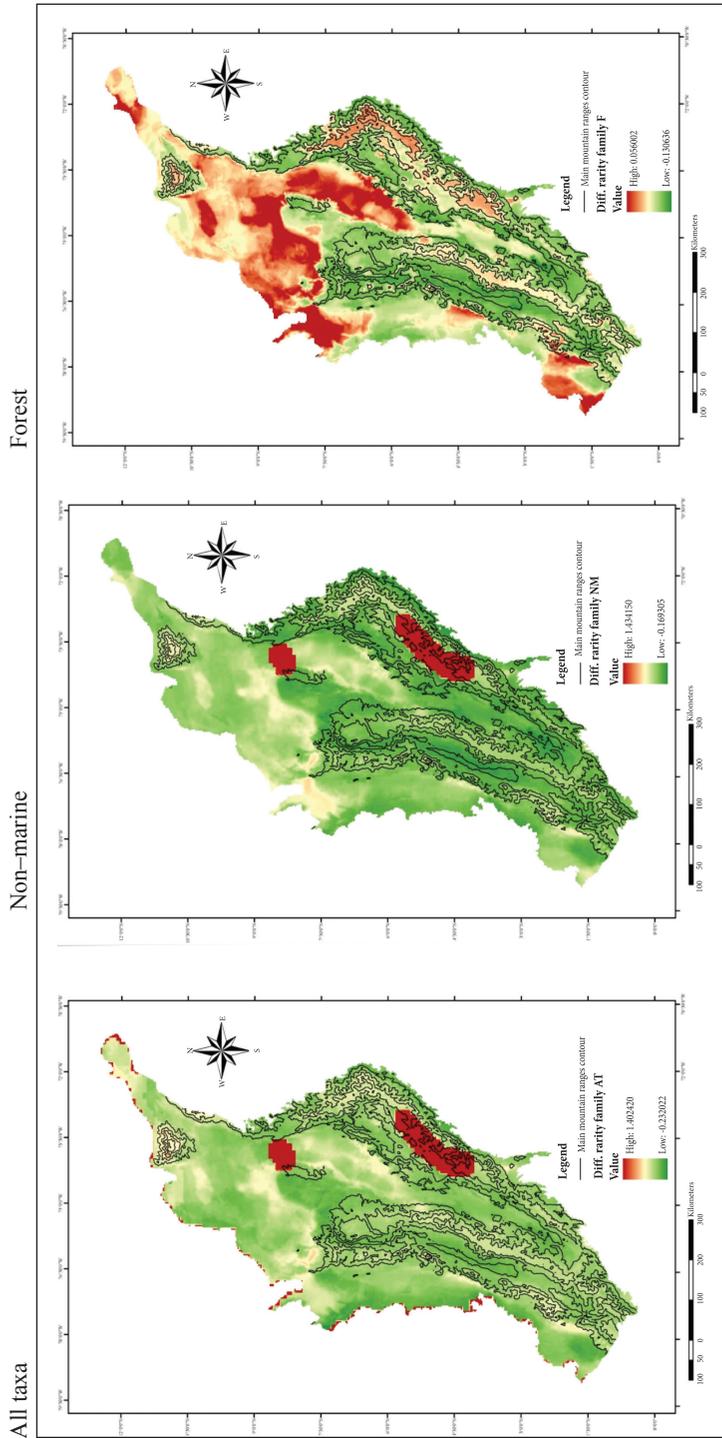


Figure 5.3.4.4.9. Spatial distribution of the difference in rarity (Weighted Endemism score) between WHDBD Database based maps (reference) and MAXENT-BioMap based modelled maps (model) in West Colombia at family level (reference - model). Habitat suitability modelling: second generation.

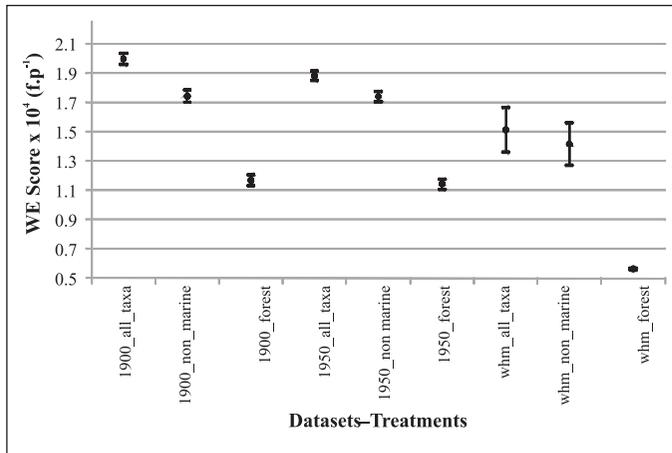


Figure 5.3.4.4.10. Confidence interval of the mean at the 95% probability for estimated family rarity (Weighted Endemism score) when using different data groups and avian subsets. Analysis based on 496 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

marked for the non-marine data subset in the reference maps and the forest subset, and less so in model maps when using post 1950 accessions and when mapping the all taxa subset, for which a tail of values increasing towards low elevations appeared. Otherwise, the forest avian subset of reference maps resembled almost a straight line with a very small positive slope. According to those results, reference maps exhibit two peaks of total family rarity in the country; a first one, at sea level and nearby areas, and a second one, between 2,500–3,000 m of elevation. On the other hand, model maps suggest there is a peak (plateau) of total family rarity in the country roughly between 500–2,000 m of elevation. This pattern is less clear when using model maps based just in post 1950 accessions, for which it seems rarity reaches a plateau around 500 m with a small increment between 2,500–3,000 m of elevation, and then decreasing at higher elevations. Contrary to what was observed for richness, differences to reference maps were slightly greater when using all accessions and observed differences increased when mapping the forest subset (Figure 5.3.4.4.11).

In addition, when the 496-WHM approach to evaluate models was used, results showed no correlation or very low, mostly, negative correlations between reference and model maps for rarity estimates (Table 5.3.4.4.3). However, correlations between model maps produced using all accessions and maps based on just post 1950 accessions exhibited medium to high positive correlation coefficients; presenting the highest coefficients for crossed correlations between the non-marine and the forest avian subsets of each data subset. When the AEQSIB-WHM approach

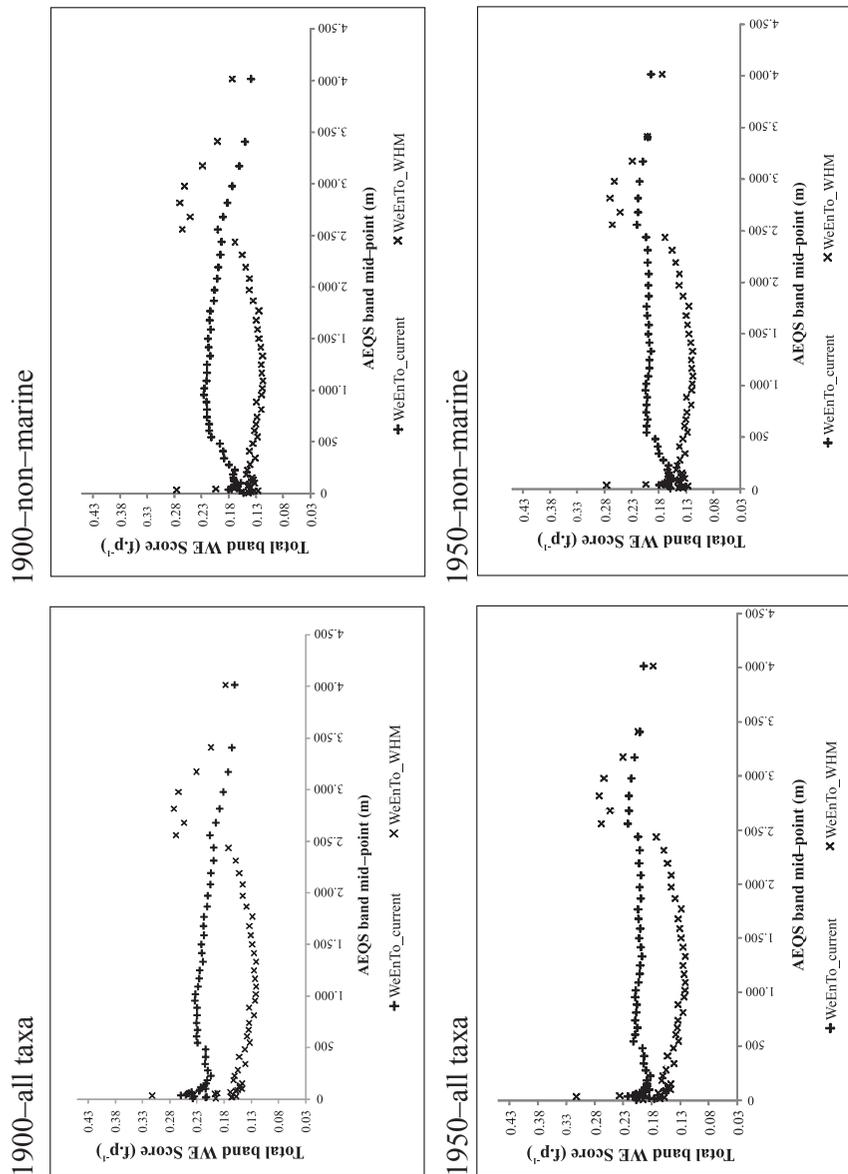
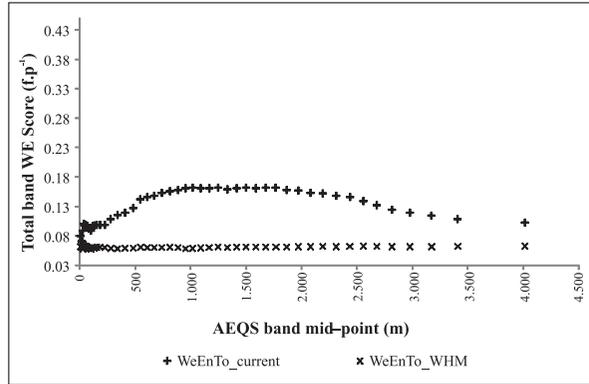


Figure 5.3.4.4.11a. Elevational gradient in estimated total family rarity (Weighted Endemism score) when used AEQSIB in West Colombia for reference (WeEnTo_WHM) and model (WeEnTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

1900–forest



1950–forest

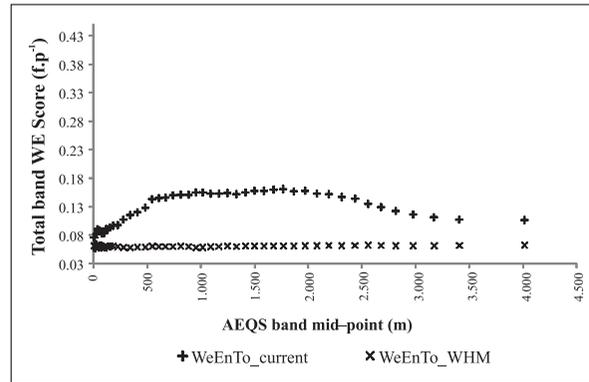


Figure 5.3.4.4.11b. Elevational gradient in estimated total family rarity (Weighted Endemism score) when used AEQSIB in West Colombia for reference (WeEnTo_WHM) and model (WeEnTo_Current) based maps. Data groups: 1900, models based on all accessions; 1950, models based on accessions post 1950. Habitat suitability modelling: second generation.

was used, correlations between reference and model maps for the total band rarity estimates exhibited a less clear pattern. In this case, correlations between model maps produced based on all accessions and reference maps were mostly low and negative. Nevertheless, the non-marine avian subset of reference maps and model maps generated using all accessions correlated with medium value coefficients. On the other hand, correlations between model maps produced based on only post 1950 accessions and reference maps were low and not always significant; and sometimes negative, whilst on other occasions positive. Finally, different to what was observed before for richness, correlations between model maps based on all accessions and maps produced using post 1950 accessions did not show a clear pattern. Thus, correlations between the all taxa subset of model maps based on all accessions and

model maps produced using only post 1950 accessions were very low and negative, whilst the rest were positive and exhibited medium to high correlation coefficients. It is worth highlighting that the non-marine avian subset of model maps produced using only post 1950 accessions and model maps based on all accessions correlated with medium value coefficients, whilst the forest avian subset of both model maps correlated with high value coefficients (Table 5.3.4.4.3).

Table 5.3.4.4.3. Correlations between reference and model maps for family rarity (Weighted Endemism score) estimates produced using approaches 496-WHM and AEQSIB-WHM in West Colombia. Habitat suitability modelling: second generation.

WHM-reference maps	496-WHM approach ¹			AEQSIB-WHM approach ²		
	All accessions			All accessions		
	MAXENT-BioMap model maps			MAXENT-BioMap model maps		
	All Taxa	Non-Marine	Forest	All Taxa	Non-Marine	Forest
All Taxa	0.017			-0.305**		
Non-Marine		-0.118**			-0.609**	
Forest			0.356**			0.026
Post 1950 accessions						
MAXENT-BioMap model maps						
All Taxa	0.625**			-0.289*		
Non-Marine		0.723**			0.610**	
Forest			0.917**			0.977**
WHM-reference maps	Post 1950 accessions			Post 1950 accessions		
	MAXENT-BioMap model maps			MAXENT-BioMap model maps		
	All Taxa	Non-Marine	Forest	All Taxa	Non-Marine	Forest
All Taxa	-0.230**			0.172		
Non-Marine		-0.291**			-0.011	
Forest			-0.253**			0.050

Spearman's ρ correlation coefficients. * indicates an associated probability < 0.05 and ** an associated probability < 0.01

¹ 496 point samples, comparing versus the "Western Hemisphere Digital Bird Distribution Database - WHDBD Database" (496-WHM)

² "Approximately equal surface interval bands", comparing versus the "Western Hemisphere Digital Bird Distribution Database - WHDBD Database" (AEQSIB-WHM)

Genus rarity

At genus level, reference maps exhibited higher values than model maps mainly in three zones in the Central and Western cordilleras²⁶ (Figure 5.3.4.4.12), in contrast with patterns reported at family level, for which such areas were concentrated mainly in the Eastern Cordillera. These same areas remained relatively unchanged when using different avian subsets. For the non-marine avian subset there was an increase in the northeast of Serrania de San Lucas and Serrania del Perija, whilst those areas disappeared and there was a slight reduction in the remaining areas when the forest and strictly forest subsets were mapped. Areas where modelled output values were higher than reference maps were very few and sparse (Figure 5.3.4.4.12). For the all taxa avian subset they were located in the eastern²⁷ and western²⁸ foothills of the Eastern Cordillera, in the mid Cauca Valley²⁹ and in a very few more areas in Valle del Cauca³⁰. Finally, it is important to add that those areas decreased when other avian subsets were mapped. For the strictly forest subset, areas were reduced in general and disappeared from Valle del Cauca. For the forest subset, a small portion in the Eastern Cordillera remained and for the non-marine avian subset, almost all disappeared, remaining a small area in north Caldas.

²⁶ In this case several patches emerged in the Central Cordillera in the Ruiz-Tolima Volcanic Complex and adjacent areas and further south in the municipalities of Chaparral, Rioblanco and Ataco in south central Tolima; as well as in the south in southwest Huila and the Central Bota Caucana, from Paramo de Los Coconucos towards south, including Paramo de Purace, Paramo del Buey, Paramo de Las Papas, Paramo del Letrero, Paramo de Cutanga, Paramo La Soledad, and the high Caqueta River valley, to the northern portion of Serrania de Los Churumbelos. Also, further south from the areas in between Paramo de Las Ovejas and Cerro Patascoy towards south, including Cerro Alcalde, Cerro Sucumbios, Cerro San Francisco, Cerro Palacio, Cerro La Quinta, Cerro Troya, and Paramo de Palacios, to Cerro Tigre and Cerro Pax. In the Pacific slope, in the foothills in south Choco in the municipalities of Sipi and Litoral de San Juan and in Calima in north Valle del Cauca, towards south to the border with Ecuador; extending as a continuous strip to the slopes below 2,000 m of the Western Cordillera in south central Valle del Cauca, Cauca and Nariño. Including partially some areas of well known importance such as Farallones de Cali, (continues at bottom next page).

Munchique and some of their adjacent buffer zones. Additionally, in the foothills northeast of Serrania de San Lucas and immediately adjacent lowlands in the mid Magdalena valley in the municipalities of Rioviejo, Arenal, Morales, Simiti (Bolívar), Gamarra, Aguachica (Cesar) and Puerto Wilches (Santander). As well as in an isolated spot in the Eastern Cordillera in the border of the municipalities of Choachi, Fomeque and Ubaque in Cundinamarca and in the foothills of Serrania de Perija in the municipalities of Fonseca, San Juan del Cesar, El Molino and Villanueva in La Guajira.

²⁷ In Cundinamarca, Casanare and Arauca.

²⁸ In the municipalities of Santa Elena del Opon, Landazuri, Velez and Bolívar in south central Santander.

²⁹ In municipalities of Jardín (Antioquia), Riosucio, Anserma (Caldas), Guatica, Quinchía, Belén de Umbria and Mistrato (Risaralda).

³⁰ In the municipalities of San Pedro, Buga and Ginebra.

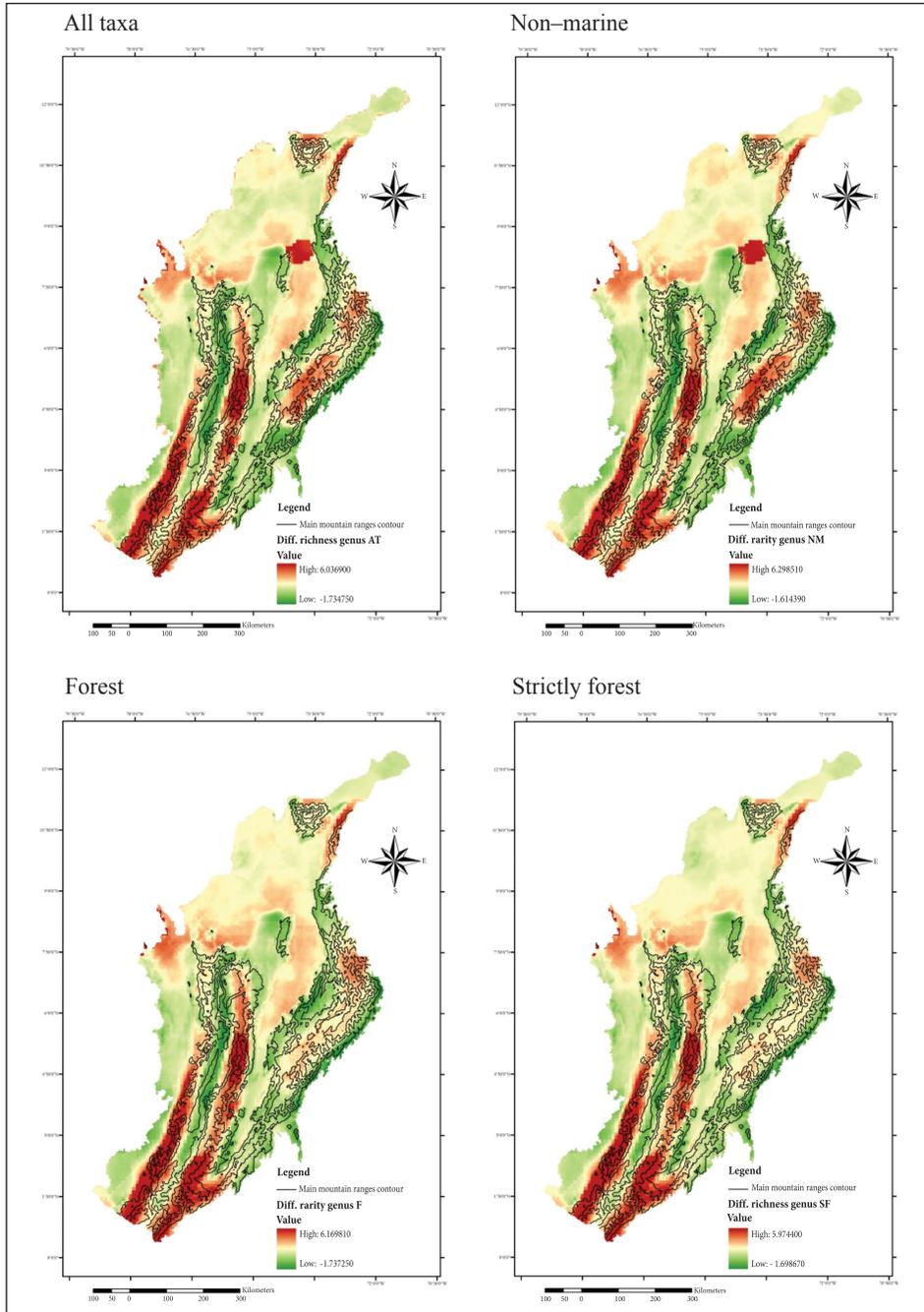


Figure 5.3.4.4.12. Spatial distribution of the difference in rarity (Weighted Endemism score) between WHDBD Database based maps (reference) and MAXENT–BioMap based modelled maps (model) in West Colombia at genus level (reference - model). Habitat suitability modelling: second generation.

Once more, at genus level, differences between maps were shown to be significant (496–WHM, Three Factor ANOVA, $p < 0.05$). Nonetheless, contrary to the tendency observed for family rarity, at this level, the mean rarity of reference maps had a tendency to show higher values than modelled values, although differences were only significant for the non–marine avian subset. Otherwise, reference maps exhibited consistently higher values than models when used only accessions collected post 1950 were used. Furthermore, differences between models were detected when both all accessions and accessions post 1950 were used through all avian subsets (Figure 5.3.4.4.13).

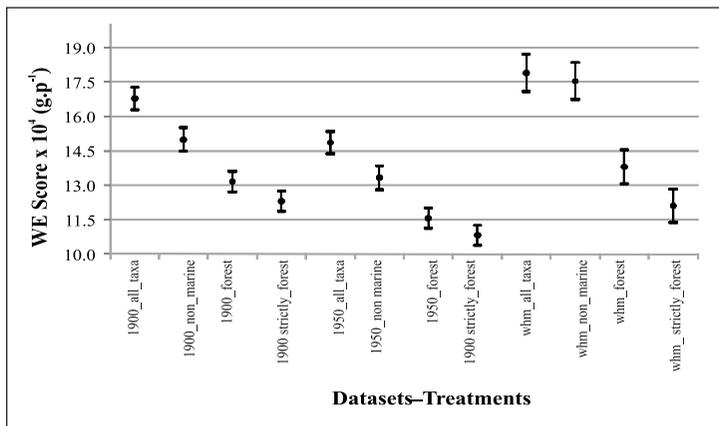


Figure 5.3.4.4.13. Confidence interval of the mean at the 95% probability for estimated rarity (Weighted Endemism score) when using different data groups and avian subsets. Analysis based on 496 sample points selected at random in West Colombia. Data groups: “1900”, MAXENT models based on all accessions; “1950”, MAXENT models based on accessions post 1950; “whm”, reference maps based on WHDBD Database. Habitat suitability modelling: second generation.

When models were assessed along the elevational gradient (AEQSIB–WHM approach), reference maps showed higher values than modelled maps primarily in the main mountains ranges, in the slopes above 2,000 m and foothills below 1,000 m, as well as the inter–Andean Cauca River valley. Although, similar to family rarity more extensively than at that level. Those areas decreased and retracted into the highlands as avian subsets more related to forest were mapped, but extended vastly into the lowlands when the non–marine subset was mapped. On the other hand, model maps showed higher values than reference maps in a very thin semicontinuous belt at $\approx 1,000$ m. Those areas increased slightly when the forest avian subset was mapped and extended into the lowlands for the strictly forest avian subset, although not as much as it was observed at family level. When tested statistically, reported differences

in the elevational gradient for total band weighted endemism score between reference and model maps were significant for all taxa and non-marine avian subsets (Wilcoxon Test, $p < 0.05$), but not for forest related subsets (Figure 5.3.4.4.14). Moreover, differences were significant through all avian subsets when reference maps were compared to model maps produced based on post 1950 accessions only (Wilcoxon Test, $p < 0.05$). In contrast to family rarity, at this level, both reference and modelled maps exhibited an elevational pattern of rarity in Western Colombia that resembled a humpback-shaped curve; and, as before, exhibited slight variations between different data and avian subsets. Results showed there is a peak in total rarity in the country at about 3,000 m of elevation for the reference maps, which is relatively constant among all avian subsets. In contrast, for modelled maps, when all taxa and non-marine avian subsets were plotted the curves reached a plateau at about 2,500 m, whilst exhibited a peak (plateau) between 2,000–2,500 m when plotting forest related subsets, after which values decrease (Figure 5.3.4.4.14).

Results from correlation analyses of rarity at genus level evidenced a significant positive correlation between reference and model maps that was very coherent between approaches. Thus, when the 496-WHM approach to evaluate models was used, correlation analyses reproduced partially some of the patterns observed previously for family rarity. Correlations between model maps produced using all accessions and maps based on only post 1950 accessions exhibited high and positive correlation coefficients. However, correlation coefficients between reference and model maps were positive and had medium-high values (Table 5.3.4.4.4). Likewise, analyses performed using elevational bands (AEQSIB-WHM approach), showed high positive correlations; although, in this case coefficients were ostensibly higher than in any other analysis conducted.

5.4. Discussion

Avian diversity mapping exercises performed in this study used two different methodologies. In one hand, DIVA-GIS though relatively easy to use with a dataset such as the Darwin-Hernandez Database proved to be inadequate due to the strong correlations between richness and effort, whilst MAXENT results, particularly when limited to the west portion of the country, exhibited reasonable results. However, diversity patterns generated through MAXENT did not show complete agreement with ProAves field data and the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database”, revealing very contrasting patterns on some occasions as well as differences in magnitude.

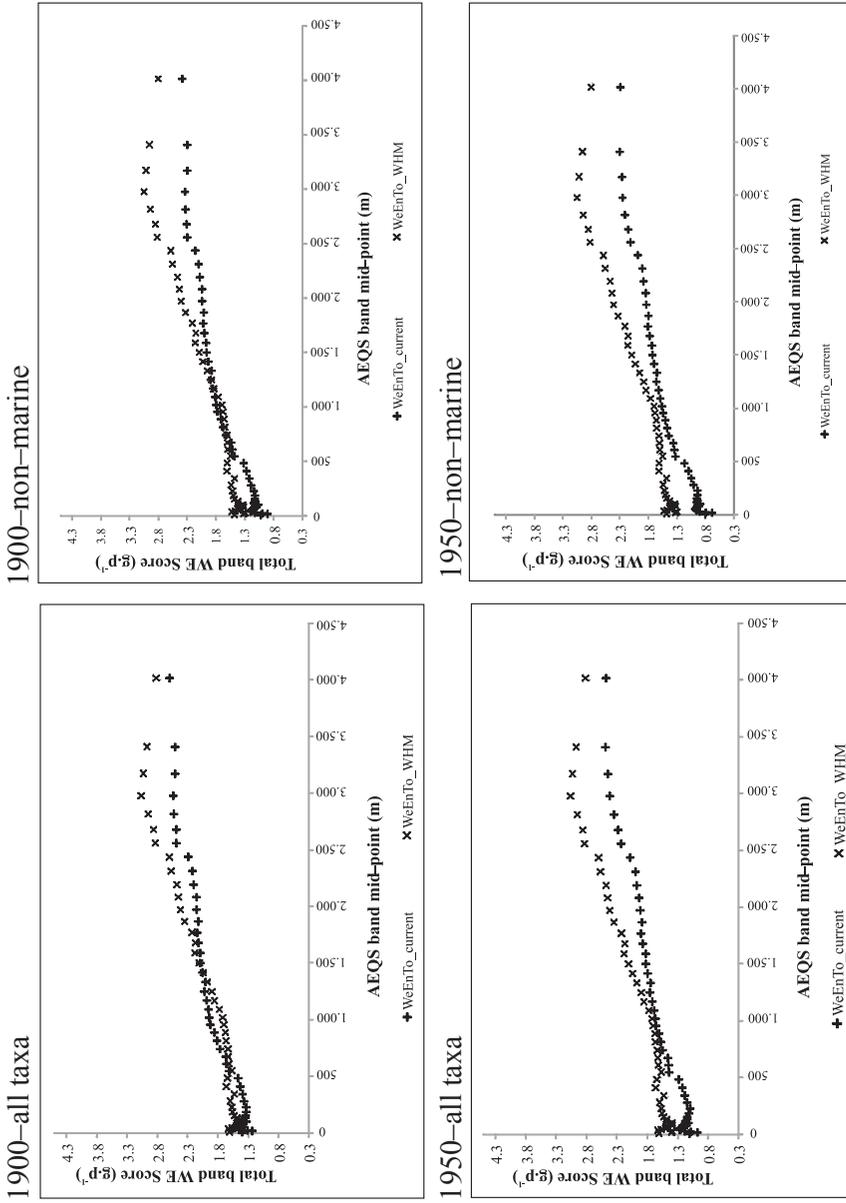


Figure 5.3.4.4.14a. Elevational gradient in estimated total genus rarity (Weighted Endemism score) when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

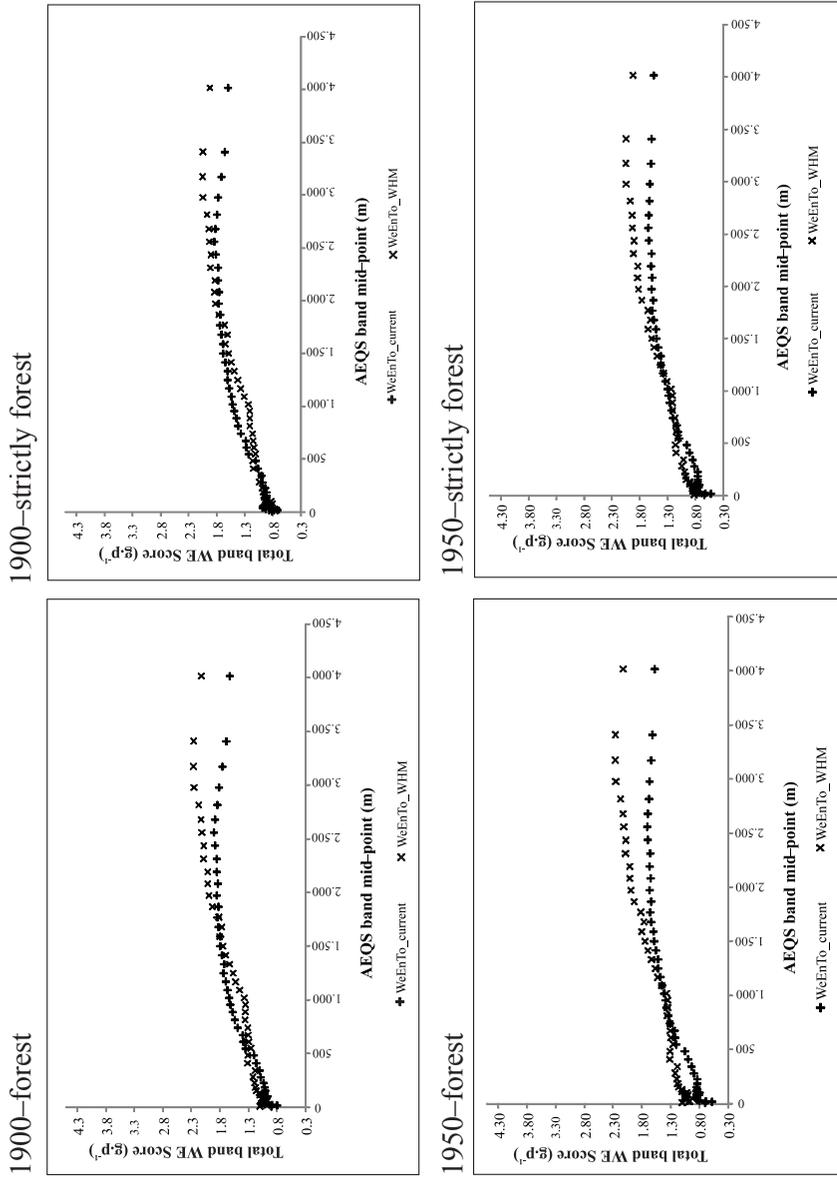


Figure 5.3.4.4.14b. Elevational gradient in estimated total genus rarity (Weighted Endemism score) when used AEQSIB in West Colombia for reference (RiFaTo_WHM) and model (RiFaTo_Current) based maps. MAXENT model data groups: “1900”, models based on all accessions; “1950”, models based on accessions post 1950. Habitat suitability modelling: second generation.

Table 5.3.4.4.4. Correlations between reference and model maps for genus rarity (Weighted Endemism score) estimates produced using approaches 496–WHM and AEQSiB–WHM in West Colombia. Habitat suitability modelling: second generation.

		496–WHM approach ¹			AEQSiB–WHM approach ²		
		All accessions			All accessions		
		MAXENT–BioMap model maps			MAXENT–BioMap model maps		
WHM–reference maps	All Taxa	Non–Marine	Forest	Strictly Forest	All Taxa	Non–Marine	Forest
All Taxa	0.652			0.944			Strictly Forest
Non–Marine		0.664				0.975	
Forest			0.662				0.912
Strictly Forest				0.719			0.942
Post 1950 accessions							
		MAXENT–BioMap model maps			MAXENT–BioMap model maps		
All Taxa	0.971			0.993			
Non–Marine		0.972				0.994	
Forest			0.946				0.984
Strictly Forest				0.954			0.987
Post 1950 accessions							
		MAXENT–BioMap model maps			MAXENT–BioMap model maps		
WHM–reference maps	All Taxa	Non–Marine	Forest	Strictly Forest	All Taxa	Non–Marine	Forest
All Taxa	0.626				0.943		Strictly Forest
Non–Marine		0.641				0.972	
Forest			0.664				0.948
Strictly Forest				0.718			0.970

Spearman's ρ correlation coefficients, all associated probabilities were lower than 0.01.

¹ 496 point samples, comparing versus the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (496–WHM)

² “Approximately equal surface interval bands”, comparing versus the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (AEQSiB–WHM)

5.4.1. DIVA–GIS mapping exercises

In general, DIVA–GIS maps generated using BioMap–Fil500 evidenced at all scales ($\approx 15\text{--}120$ km) a strong correlation between species richness and the number of specimens collected (Spearman's $\rho > 0.98$, $p < 0.01$), suggesting a logistic relationship ($R^2 > 0.95$ and $p < 0.05$ in all cases). Otherwise, the distribution of the density of collections per grid at all scales studied was positively skewed. The high number of grids where collected specimens summed less than 500 individuals oscillated between 75.9–99.5 % from the total number of pixels at the different studied scales. Similarly, when the whole dataset was used, the frequency distribution of the number of localities in effort classes determined by the number of collected bird specimens confirmed these results. About 80% of the localities had less than 50 bird specimens (Verhelst *et al.*, unpublished data). These results suggest unequivocally a generalised spatial undersampling in all the territory.

Similarly to other studies that have used DIVA–GIS, in this study sampling bias was a main limitation to this methodology. Foley *et al.* (2008), mapping the distribution and richness of mosquitoes in the Neotropics at $1^\circ \times 1^\circ$ grain size, showed a discrepancy of about 35% between two different richness estimator curves (Incidence–based Coverage and Chao2) and the actual species accumulation curve. These authors consider this as a clear indication of patchiness in the distribution of effort, which may be especially accentuated for rare species. Despite this finding, they do not assess explicitly its effects on their richness maps. Hijmans & Spooner (2001), studying the distribution of wild potatoes in the Western Hemisphere at $50 \text{ km} \times 50 \text{ km}$ grain size, found a strong correlation between the number of observations and the number of species (correlation coefficient = 0.74), which suggested a logistic relationship ($R^2 = 0.65$). They concluded in their study that wild potatoes show a richness pattern that is contrary to the general tendency known for most plant and animal groups; thus, finding the richest areas away from the Equator. Although, they consider their results may be influenced by recorder effort bias, they believe their richness maps are a good reflection of the actual natural pattern and that there is no causal relationship between observed species number and the number of observations. Otherwise, reversing the argument, these authors believe this relationship is caused by what they call “hotspot bias”, and thus it reflects higher sampling in very diverse areas rather than undersampling elsewhere. In other studies conducted in south India, Parthasarathy *et al.* (2006) mapped the diversity of the genus *Piper* in the Western Ghats using a $50 \text{ km} \times 50 \text{ km}$ grain size. However, in this study there is no indication of any assessment of sampling or effort bias. Furthermore, Graham & Hijmans (2006) although recognising the potential effects of sampling and effort bias in diversity patterns, fail to address its possible impact in their results when mapping comparatively the richness of the terrestrial herpetofauna in California (United States) using different methodologies.

Hijmans *et al.* (2000), assessing the representativeness of genebank collections of wild potatoes from Bolivia, identify four main types of sampling bias: species, species–area, hotspot and infrastructure. Species bias results from some species being included in the sample more frequently than others either because of biological causes such as major abundances or higher conspicuousness and/or human induced censuses such as for instance the collector preferences on particular groups or species. Species–area bias refers to an uneven representation in the sample of the total geographical range of a species, having only included particular areas of the total range. Hotspot bias denotes the overrepresentation of certain areas due to repetitive visits of collectors to areas already visited by others and identified as areas of high diversity. Finally, infrastructure bias considers uneven spatial sampling due to differences in access and facilities, which produces a pattern of aggregation of samples near towns and roads and undersampling of remote areas.

DIVA–GIS raw maps of the density of collection in the country suggest a spatial bias in sampling and effort towards the west and north of Colombia. In this manner, it is expected that different sources of biases, such as those mentioned by Hijmans *et al.* (2000) may be present in the dataset mapped (BioMap–Fil500). A further inspection of the spatial placement of localities of collection suggests that most collections were taken near departmental capitals and possibly along or near roads (Figure 5.4.1.1). In this sense, localities appear ostensibly clumped around Bogota, Cali and Popayan, and to a lesser degree in the proximity of Santa Marta, Cucuta, Bucaramanga, Medellin and Villavicencio. Furthermore, at regional level it seems there is a clear correspondence between the average degree of intervention of the natural ecosystems and the total number of specimens collected and richness (Table 5.4.1.1). Both sources of evidence would point to infrastructure bias as the type of bias having the greatest influence in richness estimations. Historically, since colonial times, access to continental areas of Colombia was possible from several coastal towns in the Caribbean and along the courses of the Magdalena and Cauca Rivers reaching the Inter–Andean valleys and the interior of the country, principally the Andean region. As an immediate consequence, species mainly distributed in the Colombian Orinoco and Amazon regions may be under– and/or unevenly–represented, generating also species–area bias in the dataset. Otherwise, although localities in the Caribbean compared with the Andean region have no differences regarding the average degree of intervention of the natural ecosystems (see Table 5.4.1.1 for details, Confidence Interval for the Mean, $p < 0.05$), the number of specimens taken from the Andean region is more than three fold those taken from the Caribbean region. This can be explained partially by the fact that the Andean region is about twice the area of the Caribbean. Nonetheless, when the effort was weighted by area, dividing the number of specimens by each region area, the Andean region still exhibits a significant difference in relation to the Caribbean (Table 5.4.1.1). It is suggested that this may indicate an additional

overrepresentation of the Andean region due to Hotspot bias. The Andes, well known for its high diversity due to its altitudinal gradient since the times of A. von Humboldt and A. Bonpland, attracted naturalists and collectors during the 19th and 20th centuries (Von Humboldt, 1805; Perez–Arbelaez, 1981), resulting in an over–representation of the region in natural history collections taken from Colombia and possibly also in other Andean countries. The few specimens collected for most endemic and rare species, representing about 70% of the known species in those categories, have less than 50 specimens collected each and these do not necessarily come from different

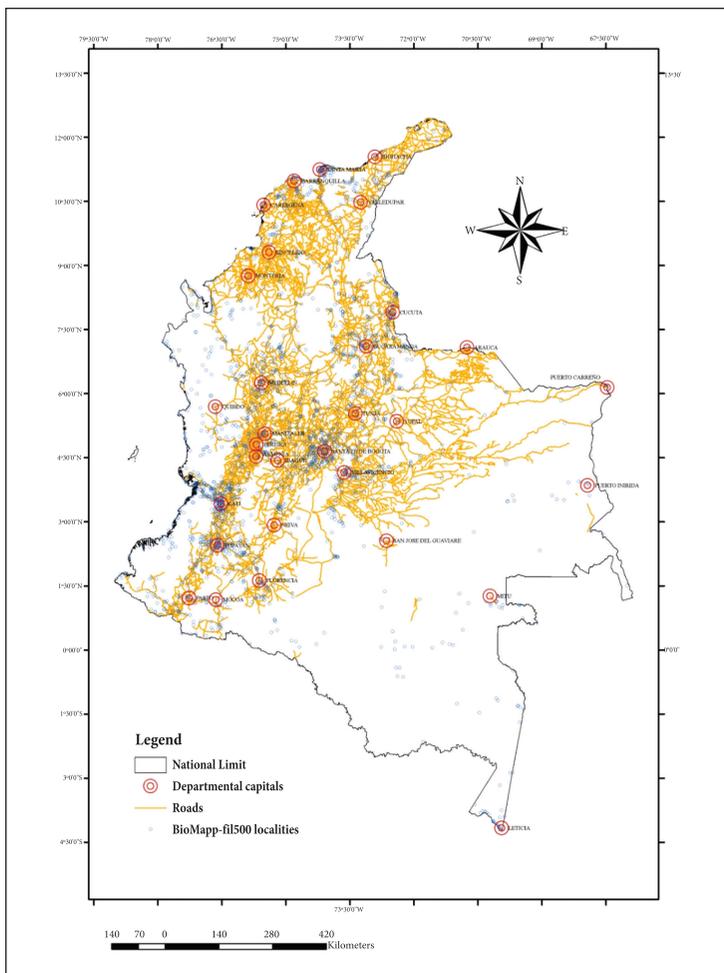


Figure 5.4.1.1. BioMap–Fil500 localities of collection positioning in relation to departmental capitals and major roads in Colombia. Infrastructure bias may constitute the major source of bias in the dataset and therefore in effort and richness estimations.

localities (Verhelst *et al.*, unpublished data). This suggests that species bias may affect also this dataset.

Table 5.4.1.1. Summary of regional effort, richness and intervention of natural ecosystems¹ in Colombia based on BioMap–Fil500 dataset.

Region	Total richness–#species	Total effort–#specimens	Area (km ²)	Specimens/Area per 100 km ² (#specimens)	Effort–#localities	Mean Human–footprint Index ^{2,3} (± SD)	Road density ⁴ per 100 km ² (#pixels)
Amazon	750	11,864	452,432.2	2.6	229	15.8 ± 11.8	0.9
Orinoco	772	12,758	191,493.3	6.7	293	26.0 ± 13.1	9.4
Pacific	792	21,162	80,197.1	26.4	341	27.8 ± 10.7	1.7
Caribbean	822	28,621	116,565.4	24.6	444	36.9 ± 12.5	18.7
Andean	1,277	97,467	300,894.6	32.4	2257	36.2 ± 15.0	15.6

¹Based on values for the Human–footprint Index (WCS–CIESIN, 2002), extracted for localities present in BioMap–Fil500 dataset.

² The Human–footprint Index (WCS–CIESIN, 2002) is part of the “Last of the Wild Project” conducted by Wildlife Conservation (WCS) and the Center for International Earth Science Information Network (CIESIN), estimates human pressure on terrestrial ecosystems combining the expected influence of land use, infrastructure and population density normalising it in relation to remnant areas of each ecosystem. The index is presented as a percentage with values ranging from 0–100.

³ The regional mean value for the Human–footprint Index is correlated with the effort, either measured as the total number of specimens or localities, and consequently with observed regional richness (Spearman’s $\rho = 0.9$, $p = 0.037$ in the three cases).

⁴ Calculated based on a map of roads obtained from Conservation International Colombia in 2004 (unpublished data)

5.4.2. Habitat suitability modelling: first generation

Results from the first generation of models produced using MAXENT showed a relatively good model performance. AUC values for individual models were near those reported before in the literature (Elith* *et al.*, 2006; Graham & Hijmans, 2006; Graham *et al.*, 2008). All models showed a predictive power better than random for the test sample, having AUC values usually above 0.7. Just in a few cases observed model performance fell below 0.7, reaching values lower than 0.6 on very few occasions. Hence, from model performance alone it was expected, at this point, that richness models produced as the addition of the modelled ranges for individual taxa may represent real richness patterns observed in Colombia. However, during the second stage this proved not to be as straightforward as assumed initially (see section 5.4.3.4). Moreover, the fact that richness maps could not be validated against other independent assessments or data sources represented the main caveat at this stage.

Despite this, the assessment and attenuation of spatial bias in sampling effort is a characteristic of this study that strengthens the robustness of the models obtained, and has probably not been performed before in any other study at country level for Colombia.

It is important to notice two more particularities of this study in the modelling of avian richness patterns for Colombia. First, in this study, models were produced at taxonomic levels that are not used in any other previous study. Higher order taxonomic levels may be relevant in relation to reducing error propagation related to uncertainty in the georeferences. Since genera and families might show broader geographical ranges, errors caused by georeferencing uncertainty are expected to have less impact than at species level. Even less impact may be expected if we consider results from Graham *et al.* (2008), who recently showed that moderate levels of error (up to 5 km) do not affect MAXENT predictions at the species level. Although, the use of higher taxonomic levels permits us to group more data together and to build up more robust models, it does involve losses of taxonomic detail, which may be of some relevance in systematic conservation planning. However, in other groups it has been proven a strong correlation between diversity at different taxonomic levels (Gaston, 1996a), which grants confidence to assume that diversity maps generated here at higher taxonomic levels must reflect also, at least broadly speaking, species diversity patterns in the country. Second, though this first generation of modelling exercises used the most complete dataset for the country, models were produced from a sub-sample of the dataset with the most accurate records, which may represent a shortcoming. However, if we consider that the total database represents about 99% of the bird species reported within the boundaries of the country, and about 79% of the families and 71% of the genera present were modelled, it may be considered that this sample includes a very important fraction of the avian taxa known for Colombia. Moreover, since MAXENT exhibits high predictive power with samples as small as 5 presence points (Pearson *et al.*, 2007), the inclusion of taxa for which there were less than 15 presence points during the second generation allowed us to achieve a higher representation of the total avian taxa for the country (see section 5.4.3).

Previous studies have shown that areas identified as having high richness do not necessarily overlap with endemic areas. Orme *et al.* (2005), studying all the 9,626 extant bird taxa at a $1^{\circ} \times 1^{\circ}$ grain size, found that globally there is no concordance between hotspots of richness, endemism and threat. Their analysis showed an overlap of 7.5% between the areas of highest richness and endemism, and 2.5% of agreement between all the three types of hotspots. Furthermore, Contreras-Medina & Luna-Vega (2007), reached a similar conclusion at the country level, studying at a $1^{\circ} \times 1^{\circ}$ grain size the richness and endemism of gymnosperms in Mexico. In contrast, results from this study showed that both at family and genus levels a major proportion ($\approx 62\%$ –

99%) of the areas identified as having high richness in the country fall within the endemic bird areas (EBAs) defined by Stattersfield *et al.* (1998) (Figure 5.4.2.1). However, a significant degree of variability was evidenced in the proportion these areas of high richness represent from the total area covered by the different EBAs present in the country ($\approx 2\text{--}47\%$), which depended on the particular threshold used to define the areas of high richness in each case (see Table 5.4.2.1). Furthermore, not all EBAs overlapped equally in relative terms with areas of high richness. In this sense, at the family level the EBAs of the Darien Highlands, Northern Central Andes and Central Andean Paramo captured poorly areas of high richness, whilst at genus level those EBAs as well as the Colombian East Andes and Choco EBAs overlapped poorly with areas of high richness.

5.4.3. Habitat suitability modelling: second generation

Prior to beginning this round of model generation, the effects of sample size, number of replicates and grain size on model performance was tested. Results showed that sample size exerted a significant effect on model accuracy, increasing accuracy as sample size increases, confirming the findings of previous studies (Stockwell & Peterson, 2002; Hernandez *et al.*, 2006; Pearson *et al.*, 2007). Additionally, several studies have shown the benefits of using a modelling technique such as MAXENT with a low number of samples. In this sense, Hernandez *et al.* (2006) testing the effect of sample size on model performance on one invertebrate and 17 vertebrate species in California (USA), using four different modelling techniques, found that MAXENT achieves better values of accuracy with samples fewer than 25 point occurrences compared with other modelling methodologies such as GARP, DOMAIN and BIOCLIM. Likewise, Pearson *et al.* (2007) studying 13 endemic species of gecko from Madagascar of the genus *Uroplatum*, established that when modelling with a limited dataset (< 25 localities), MAXENT outperforms GARP with samples fewer than 10 point occurrences. Furthermore, the same authors demonstrated that when experimentally reducing localities, both the number and the particular point occurrences included influenced model accuracy.

On the other hand, Stockwell & Peterson (2002) modelling the geographical ranges of 103 Mexican bird species, evidenced that GARP outperforms other methodologies such as Logistic Regression and Vegetation Surrogate Models. In this sense, the machine-learning technique GARP reached values of accuracy near 90% of the maximum (accuracy ≈ 0.63) at samples as low as 10 point occurrences and maximum values (accuracy ≈ 0.7) at roughly 50 point occurrences, whilst other methodologies showed a poorer performance, reaching similar accuracy values above 100 point occurrences.

In this study, results showed that the number of point occurrences where accuracy values near the maximum occurs vary between taxonomic levels. Thus, at family

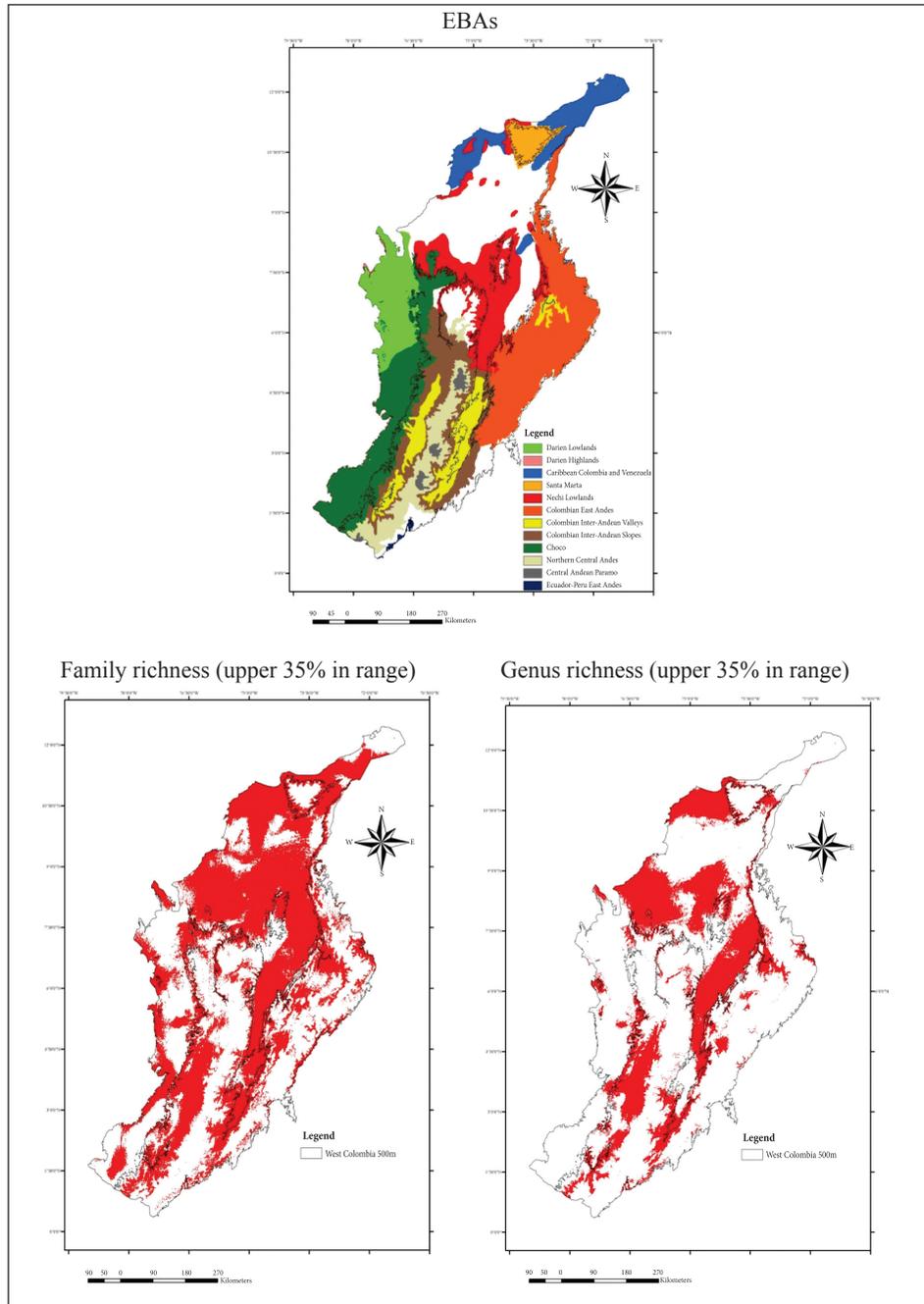


Figure 5.4.2.1. Endemic bird areas according to Stattersfield *et al.* (1998) and areas identified as having high richness in West Colombia.

Table 5.4.2.1. Overlap between areas identified as having high richness and Endemic Bird Areas defined by Stattersfield *et al.* (1998) at family and genus levels when using different thresholds for richness. Areas were calculated in pixels: 1 pixel = $0.008333^{\circ} \times 0.008333^{\circ} \approx 1 \text{ km}^2$ at the latitudes Colombia is located.

EBA Name	Family richness						
	EBA total area	Upper 35% overlap	% from EBA area	Upper 25% overlap	% from EBA area	Upper 15% overlap	% from EBA area
Darien Lowlands	40,025	14,467	36.14	6,457	16.13	474	1.18
Darien Highlands	666	94	14.11	17	2.55	0	0.00
Caribbean Colombia and Venezuela	35,921	23,774	66.18	16,821	46.83	9,827	27.36
Santa Marta	13,015	7,718	59.30	5,865	45.06	2,557	19.65
Neechi Lowlands	67,734	49,706	73.38	37,975	56.06	13,318	19.66
Colombian East Andes	92,751	27,758	29.93	8,215	8.86	1,405	1.51
Colombian Inter-Andean Valleys	35,988	30,866	85.77	21,708	60.32	7,067	19.64
Colombian Inter-Andean Slopes	55,698	25,232	45.30	9,813	17.62	2,756	4.95
Choco	78,246	32,755	41.86	16,123	20.61	2,205	2.82
Northern Central Andes	34,733	4,574	13.17	415	1.19	8	0.02
Central Andean Paramo	4,833	67	1.39	1	0.02	0	0.00
Ecuador-Peru East Andes	1,140	327	28.68	136	11.93	0	0.00
Total high-richness area included	297,401	176,144		63,375			
Total overlap EBAs-richness	217,338	123,546		39,617			
Total overlap EBAs-richness in relation to high-richness area included (%)	73.1	70.1		62.5			
Total overlap EBAs-richness in relation to total EBAs area (%)	47.2	26.8		8.6			

Table 5.4.2.1. Continued.

EBA Name	EBA total area	Genus richness					
		Upper 35% overlap	% from EBA area	Upper 25% overlap	% from EBA area	Upper 15% overlap	% from EBA area
Darien Lowlands	40,025	3,635	9.08	1	0.00	0	0.00
Darien Highlands	666	1	0.15	0	0.00	0	0.00
Caribbean Colombia and Venezuela	35,921	8,923	24.84	4,319	12.02	714	1.99
Santa Marta	13,015	3,982	30.60	726	5.58	2	0.02
Neehi Lowlands	67,734	38,055	56.18	13,076	19.30	337	0.50
Colombian East Andes	92,751	7,729	8.33	2,106	2.27	252	0.27
Colombian Inter-Andean Valleys	35,988	23,747	65.99	14,183	39.41	5,700	15.84
Colombian Inter-Andean Slopes	55,698	16,804	30.17	5,791	10.40	370	0.66
Choco	78,246	12,711	16.24	4,094	5.23	150	0.19
Northern Central Andes	34,733	2,151	6.19	172	0.50	0	0.00
Central Andean Paramo	4,833	9	0.19	0	0.00	0	0.00
Ecuador-Peru East Andes	1,140	233	20.44	17	1.49	0	0.00
Total high-richness area included		163,831		56,814		7,621	
Total overlap EBAs-richness		117,980		44,485		7,525	
Total overlap EBAs-richness in relation to high-richness area included (%)		72.0		78.3		98.7	
Total overlap EBAs-richness in relation to total EBAs area (%)		25.6		9.7		1.6	

level, AUC values near 90% of the maximum were achieved at 154 point occurrences, while maximum values (AUC \approx 0.8) were obtained at maximum sample sizes at 671 point occurrences. Moreover, the relationship of accuracy to sample size, although logistic, resembled a linear tendency, increasing the accuracy constantly as sample size also increased. In contrast, at genus and species levels AUC values near 90% of the maximum were reached respectively at 76 and 51 point occurrences, while maximum values (AUC \approx 0.85) were obtained above 100 point occurrences. Moreover, the relationship of accuracy to sample size was clearly logistic, increasing accuracy significantly as sample size increased initially but declining in its rate of increase as more samples were added. At species level, a decrease in accuracy at large sample sizes was noticeable, showing a slight humpback-shaped curve in several cases. Nevertheless, in all cases models generated for this particular experiment exhibited accurate values greater than 0.72, which denotes good discriminatory powers. It is hypothesised here, that the described differences result from a complex interaction between sample size (*i.e.* total number of data points) and sample prevalence (*i.e.* proportion of data points representing taxon occurrences).

Model performance can vary from one taxon to another due to differences in their ecology or to artefacts generated during the modelling process (McPherson *et al.*, 2004). A main ecological feature that may exert an important effect in this sense is the geographical range of the modelled taxa and how it is reflected in the samples used both for training and evaluating models. In this context, McPherson *et al.* (2004) modelled the ranges of 32 bird endemic species in South Africa, Lesotho and Swaziland using Logistic Regression and Discriminant Analysis to study the effects of range size, sample size and sample prevalence on model performance. Results from their study showed that when using approximate natural prevalence, different patterns of model accuracy appear in relation to range size for different evaluation measures. For instance, in their study an evaluation estimator such as the Cohen's Kappa changed proportionally with changes in range size, while AUC remained constant. In addition, the same authors demonstrated that other methodological artefacts appear due to the influence of sample size and prevalence; producing models with the highest accuracy at larger sample sizes and intermediate values of prevalence.

In the present study, the three different taxonomic levels reflect geographical ranges of different sizes, increasing from species to family. Considering that both the area of study and the number of pseudo-absences (10,000 background points) used in the modelling process was held constant. Higher values of accuracy at similar training sample sizes, as well as the faster saturation of the curves (*i.e.* faster surpass of the inflexion point where the curve slope decreases) of the accuracy-sample size relationship at lower taxonomic levels can be explained in terms of sampling prevalence in each case. Thus, lower taxonomic levels (*i.e.* species and genus) reflect

a higher sampling prevalence caused by their smaller range sizes, and therefore obtain better model accuracies.

Table 5.4.3.1. Number of models and taxa represented in different modelling exercises conducted in this study at both family and genus taxonomic levels.

Modelling exercises ¹	Total No. of models	Taxa represented	No. of Models with significant BTO ²	Taxa represented	No. models included in “best models subset”	Taxa represented
F1 15+	71	71	–	–	–	–
G1 15+	491	491	–	–	–	–
F2 12+	1,725	69	1,549	69	671	69
F2 12-	–	–	–	–	–	–
G2 12+	12,636	486	10,155	466	4,474	466
G2 12-	82	82	82	82	82	82
F’2 12+	1,690	65	1,348	63	596	63
F’2 12-	6	6	6	6	6	6
G’2 12+	10,348	398	7,371	380	3,113	380
G’2 12-	113	113	113	113	113	113
Total	27,162		20,624		9,055	

¹ Modelling exercises code: first letter represents the taxonomic hierarchy, F = family, G = genus; the number (second character) represents the MAXENT modelling generation, 1 = first generation, 2 = second generation; the last two numbers followed by a plus (+) or a minus (-) represent the number of localities used for modelling, 15+ = 15 localities and more, 12+ = 12 localities and more, 12- = from 5 to 11 localities; apostrophe (‘) represents models generated using not the entire filtered database (BioMap–BasicFilHP_v2) but just accessions post 1950 (BioMap–BasicFilHP_v2_1950).

² Binomial Test of Omission.

The second generation of models produced using MAXENT constituted a massive effort in modelling, which produced improved models. In this sense, 27,162 models were generated from which just over one-third (9,055 models) were selected to produce consensus geographical range maps and thus the final diversity maps (Table 5.4.3.1). Moreover, very importantly, the inclusion of models with less than 15 localities during the second generation permitted maintenance of the number of taxa modelled at family level an increase of 4–16% in taxa modelled at genus level. This augmented the percentage of taxa modelled from 71% to about 74–82% from the total of genera known for the country. These findings confirm the advantage of using a methodology such as MAXENT, which permits the generation of good quality predictions even with samples as small as five localities (Pearson *et al.*, 2007). Similarly, Pearson *et al.* (2007) suggested in the case of the bird atlas of Mexico

(Stockwell & Peterson, 2002) that the use of a methodology such as MAXENT instead of GARP would increase modelled taxa (species) from 65% to 88% of the total registered for the country, which represents a significant addition.

Results from this second modelling generation showed a better performance than models from the first generation (Figure 5.4.3.1). Likewise, as occurred in the first generation, on this occasion models generated at the genus level performed significantly better than at the family level, reflecting differences in both natural and sampling prevalence at the different levels. Furthermore, it is interesting to highlight that models included in the “best models subset”, as was implemented in this study (section 5.2.4.2), showed higher AUC values than the subset of models with significant Binomial Test of Omission ($p \leq 0.05$). Finally, model performance for the “best models subset” at genus level was particularly good, exhibiting AUC values than on average were higher ($\mu > 0.86$) than average values found in other studies conducted at species level (Confidence Interval for the Mean, $p < 0.05$). Such as for instance, Graham & Hijmans (2006), who reported an average AUC value of 0.82 (SD = 0.13, N = 159), when modelling the geographical range of 159 species of the terrestrial herpetofauna of California (USA).

As well as, Graham *et al.* (2008), who reported an average AUC value of 0.73 (SD = 0.11, N = 40), when studying the distribution of 40 different species of plants and vertebrates from four different zones of the world.

5.4.3.1. Richness and rarity patterns in West Colombia

According to maps generated during this second modelling generation the potentially richest bird areas in West Colombia are located in the foothills of the Magdalena and Cauca rivers, including the highest elevation portions of their valleys, several interior dry valleys and the slopes of the Andes below 2,000 m as well as in the foothills of the Sierra Nevada de Santa Marta and in Serrania del Baudo. This pattern is similar to that observed during the first generation modelling. During the first modelling generation, pockets of richness were less continuous in the Andean slopes and extended more into the low Cauca River and the mid- and low Magdalena River and in lowland areas near the Sierra Nevada de Santa Marta.

Although similar, richness patterns during this second generation modelling were not identical between either taxonomic levels or different subsets of the avifauna. In this sense, the intersection of all areas of highest potential richness at all levels was confined sparsely within a broken belt in the Andes slopes and foothills between ≈ 500 –2,000 m and the highest areas of Serrania de La Macarena and Serrania del Baudo. Furthermore, in general terms potential pockets of high richness seemed coarser at family than at genus level, extending over more areas, especially in the

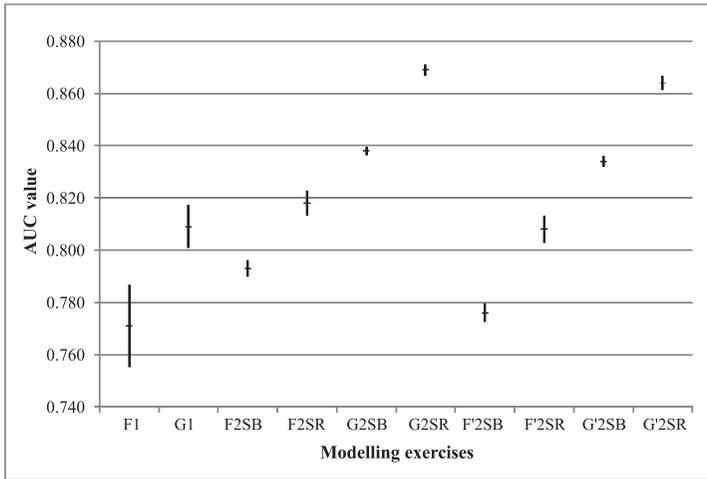


Figure 5.4.3.1. Confidence interval of the mean at the 95% probability for AUC values in different modelling exercises conducted in this study at both family and genus taxonomic levels. Modelling exercises code: first letter represents the taxonomic level, F = family, G = genus; the number (second character) represents the MAXENT modelling generation, 1 = first generation, 2 = second generation; the final two letters represent models subsets, SB = models with a significant Binomial Test of Omission, SR = models included in the “best models subset”; apostrophe (‘) represents models generated using not the entire filtered database (BioMap–BasicFilHP_v2) but just accessions post 1950 (BioMap–BasicFilHP_v2_1950). Calculations were based on models generated based on 12 or more localities, which represent $\approx 97\%$ of all models produced.

Central – and Western Cordillera, and coastal and nearby lowland areas around the Sierra Nevada de Santa Marta and the Serrania del Baudo, in the Caribbean and the Pacific regions respectively.

Avian rarity reflected contrasting patterns between different taxonomic levels. Thus, at family level areas with the highest scores resembled general patterns of richness, although they were more elevationally constrained to the foothills and slopes of the Andean cordilleras, including their extensions in the north, the Serrania del Baudo and the Sierra Nevada de Santa Marta as well as to thinner strips in the coastal areas both in the Caribbean the Pacific regions. At genus level, potential areas of high rarity lay mainly in the highest sections of the Eastern and Central Andes (including the Huaca Massif) and the Sierra Nevada de Santa Marta, between $\approx 2,000$ – $4,500$ m. As observed for richness, potential high rarity areas exhibited differences in pattern when mapped for different subsets of the avifauna.

Previous studies mapping vascular plant and bird diversity globally have shown roughly similar patterns for Colombia (Kier *et al.*, 2005; Mutke & Barthlott, 2005;

Orme *et al.*, 2005; Orme *et al.*, 2006; Storch *et al.*, 2006; Davies *et al.*, 2007a; Kreft & Jetz, 2007). In general, they point to the Andean and the Pacific regions as well as the Sierra Nevada de Santa Marta as the zones with the highest richness in the country. Despite this, visual inspection of diversity maps from those studies show several features of interest. For instance, Mutke & Barthlott (2005) map of vascular plant richness points to the Pacific Region from north Cauca up to the boundary with Panama and the eastern slope of the Andes in Caqueta, Putumayo and Nariño as the zones with highest richness, which harbour more than 5,000 spp/10⁴ km². Richness maps from other studies, which are not presented in broad categories, tend to less consistently represent these patterns; showing instead particular pixels with high richness (Figure 5.4.3.1.1). For example, in Kreft & Jetz (2007) predictive model of vascular plant richness based on environmental variables, pockets of high richness are located in particular areas in the southern portion of the Andean Cordilleras, the Serrania del Baudo and areas in the zone around the Sierra Nevada del Cocuy. Otherwise, Orme *et al.* (2005), Davies *et al.* (2007a) and Storch *et al.* (2006) global bird richness maps point to some areas in the southern portion of the Andes, especially towards the eastern slopes. Not surprisingly, grids of very high richness in raw maps correspond to areas around some of the departmental capitals such as Bucaramanga, Cucuta, Bogota, Villavicencio, Cali, Popayan, Florencia, Mocoa and Pasto. These areas are well known for being intensively collected. This suggests that in those maps, at least for areas modelled in Colombia, sampling and effort bias have not been removed. In fact, there is no indication that the authors addressed explicitly those sources of bias in their geographical ranges database. Nonetheless, Kreft & Jetz (2007) although not assessing sampling and effort bias, do remove spatial autocorrelation in their model using “kriging” and “co-kriging”. Consequently, patterns changed significantly, pointing to few areas in north Choco and east Amazonas as the zones with highest richness in the country. Likewise, Storch *et al.* (2006) after generating a predictive model based on environmental variables and correcting for autocorrelation found different patterns. In this case, the zones of highest richness appear roughly in Nariño, Choco, the northern portion of the Western and Central cordilleras, in the Eastern Cordillera in Norte de Santander and in the area from Sierra Nevada del Cocuy to Macarena and the surrounding lowlands, as well as in the most northeastern part of the Colombian Amazon, near the border with Venezuela. Davies *et al.* (2007a), also produced a similar model correcting by autocorrelation although they did not presented as a figure map predictions in such article and at present time we do not know which changes occur in diversity spatial distribution in Colombia in that study.

It is important to note that richness maps produced in these studies have been generated at $\approx 1^\circ \times 1^\circ$ grain size ($\approx 10,000$ – $14,400$ km²), which may be an appropriate scale to study certain phenomena globally but rather limits their use at the national scale.

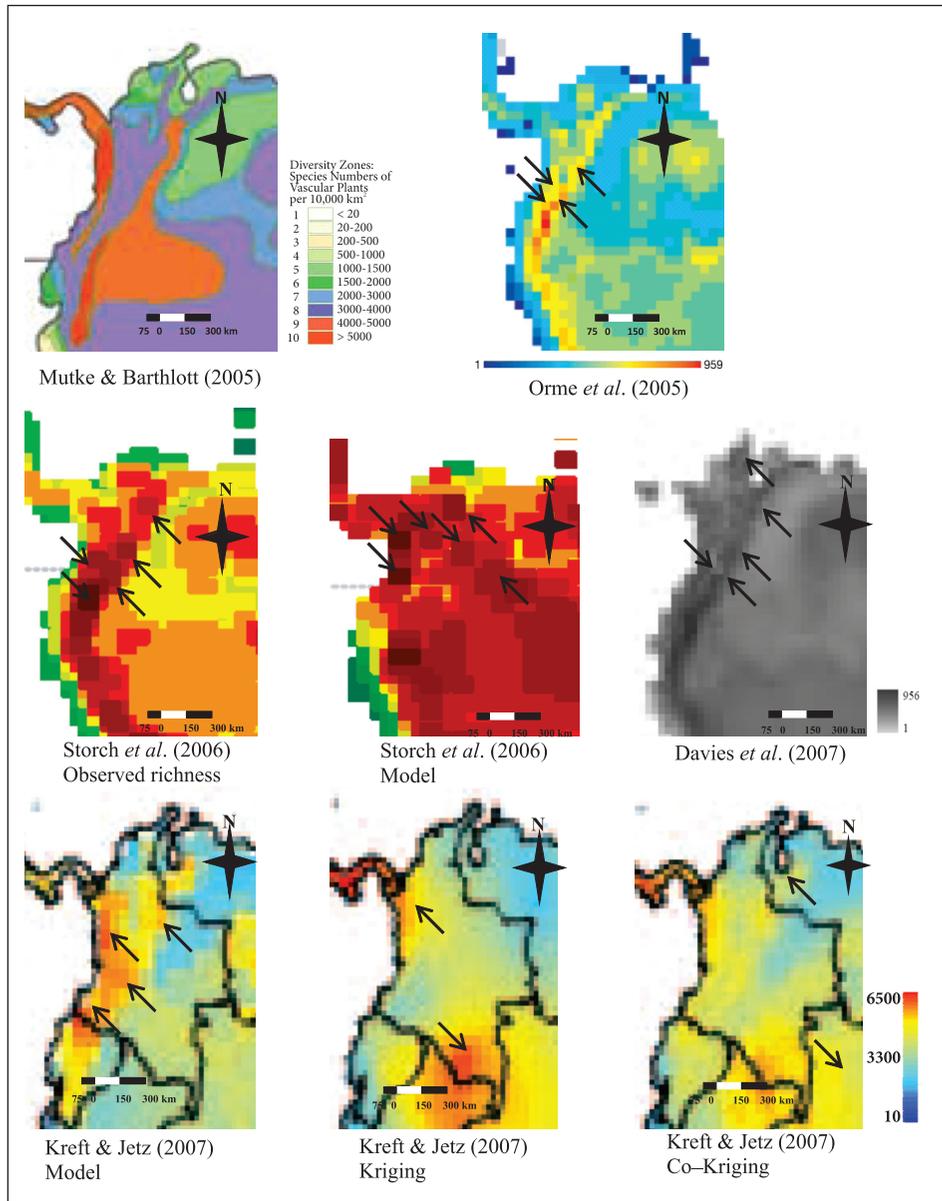


Figure 5.4.3.1.1. Samples of richness patterns for Colombia generated by previous studies mapping vascular plant (Mutke & Barthlott, 2005; Kreft & Jetz, 2007) and bird (Orme *et al.*, 2005; Storch *et al.*, 2006; Davies *et al.*, 2007a) diversity globally. Diagonal arrows point to particular areas of high richness in presented maps.

This is especially the case when conservation practitioners intended to use them to inform conservation planning and biodiversity inventory. In this sense, richness maps elaborated at higher resolution in this study (9 km²) using the Darwin–Hernandez Database and MAXENT represent an important advance in biodiversity science for Colombia. However, evaluation of richness and rarity maps produced in this second generation modelling against maps elaborated using the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” and “ProAves’ Migratory Monitoring Program Database – PMAMN Database”, suggest both richness maps based on modelled geographical ranges (MAXENT) and maps based on expert knowledge (WHDBD) must be used cautiously.

Overall in West Colombia results suggested that “MAXENT–based” maps (the models) showed a tendency to underestimate family richness and genus rarity, whilst they tended to overestimate family rarity and genus richness in relation to “expert–based” maps (the reference). Nevertheless, a detailed inspection of the confidence intervals for the averages obtained after extracting separately 496 localities at random and 76 localities where ProAves Foundation has been conducting field studies, revealed a more intricate pattern of differences between the several mapping exercises performed using different data and avian subsets. In this sense, when differences were tested using the 496 random localities, average richness of model maps generated using all accessions showed consistently lower values than their reference map counterparts at family level, but only for the non–marine avian subset at genus level. Otherwise, at genus level there was no difference in average richness for the forest subset and average richness was higher than its reference map counterpart in the strictly forest subset. In contrast, models generated using accessions post 1950 exhibited consistently lower values than their reference map counterparts. This pattern was retained when differences were tested by extracting values from ProAves’ 76 localities at family level. However, it changed at genus level, and thus differences in average richness became smaller or non–existent. It is worth highlighting that average family richness estimated from ProAves field data (surveys and mist–nets) did not have differences in relation to the forest subset and showed lower values than non–forest related avian subsets of reference maps. Moreover, ProAves field data exhibited intermediate values in relation to model maps. In contrast, at genus level both model and reference maps exhibited consistently higher average richness values than estimations from ProAves field data. This suggests that both “MAXENT–based” and “expert–based” richness maps overestimate actual local richness, especially for non–forest avian subsets. On the other hand, rarity, that was tested only using the 496 random localities, showed consistently that average scores for model maps were higher than values for their reference counterparts at family level. On the contrary, at genus level, average values for model maps were lower than those values observed

for reference maps; although, differences were significant just for the non-marine avian subset.

It is interesting to note that the spatial distribution of differences between model maps generated based on all accessions and reference maps showed contrasting patterns in the location of areas where the biggest differences for both richness and rarity were observed. In general, richness in model maps showed lower values than reference maps in some areas in the lowlands, mainly in the low Atrato, low Cauca and mid-low Magdalena valleys, and the highest parts of the main mountain ranges. Richness in model maps had higher values than reference maps in the mid-high Cauca and high Magdalena valleys and associated foothills. This pattern was relatively similar between taxonomic levels and avian subsets, although it tended to be slightly more extensive at genus level and for forest related subsets. At family level, rarity in model maps showed lower values in the Altiplano Cundiboyacense and surroundings and in the lowlands between the Serrania de San Lucas and the Eastern Cordillera. In addition, for all taxa avian subsets emerged as a discontinuous band bordering both Pacific and Caribbean coasts. This probably reflects the inclusion of marine taxa, which have restricted distribution in comparison to continental taxa. At genus level, patterns were very consistent between avian subsets showing minor variations. Thus, rarity in model maps showed lower values than reference maps in the Pacific slopes of the Andes and immediately adjacent lowlands in Cauca and Nariño, in the Ruiz-Tolima Volcanic Complex and around, in few areas in the south Central Cordillera, in the northeast foothills of the Serrania de San Lucas and immediately adjacent lowlands and in few areas in Serrania del Darien. Otherwise, rarity in model maps had higher values than reference maps in very few and sparse areas in the country.

Patterns of richness and rarity in “approximately equal surface interval bands” (AEQSIB) along the elevational gradient of West Colombia were very variable exhibiting some interesting dissimilarities between taxonomic levels and avian subsets. Thus, although total richness showed a “humpback” tendency with elevation at both taxonomic levels, this was less pronounced at family level. Family richness exhibited a peak at about 500–1,500 m, while at genus level this plateau extended roughly to 2,000 m. Moreover, it is important to highlight that differences in total richness between reference maps and models generated using only post 1950 accessions were greater than those observed with models generated using all accessions, and that differences between curves grew when non-forest related taxa were mapped, becoming particularly wide above 2,000 m of elevation. On the other hand, rarity patterns were markedly dissimilar at family level between reference and model maps, although they presented similar tendencies at genus level and between avian subsets. Thus, for model results rarity showed a “humpback” tendency with elevation, whilst for reference maps it resembled a “concave-u” shaped curve with

an additional tail of values that decreased at high altitudes. It is worthy noting that this tail emerged at $\approx 2,500$ m and above this elevation both models and reference map patterns became similar. However, the forest taxa subset differed from this pattern, remaining almost constant and thus resembling a line with a very low slope. At genus level, patterns were similar between reference and model maps through all avian subsets, reflecting a humpback-shaped curve negatively skewed, which was more marked for forest-related taxa. Also, similarly as was observed previously for total richness, differences between reference and model curves were greater for models generated using only post 1950 accessions and grew slightly when non-forest related taxa were mapped, widening slightly above 2,000 m of elevation.

In addition, correlation analysis conducted for both richness and rarity showed different extents of agreement between reference and model maps at different spatial scales. Thus, correlations ran for richness based on values extracted from the 496 random localities revealed poor agreement between reference and model maps for local values. In general, Spearman's ρ coefficient values were low, negative and not significant many times. Conversely, correlations ran in AEQSIB bands showed better agreement; exhibiting usually significant positive coefficients, although not always with high values. On the other hand, agreement between reference and model maps for local values of rarity showed a pattern similar to the one observed for richness, although coefficients had slightly higher values. In a very different way, at genus level agreement between reference and model maps increased markedly showing statistically significant Spearman's ρ coefficients with medium to high values.

Despite of the importance richness maps have in ecology and biogeography, few studies have tested differences between maps created for the same region using different methodologies and datasets. Differences found in this study reflect some of the findings of Graham & Hijmans (2006), who mapped the richness of terrestrial amphibian and reptiles in California comparing resulting maps from different methodologies. As we do, they found that different approaches lead to different patterns of richness. Their results also showed that maps derived from counts within grids (DIVA-GIS) had the lowest values of richness, whilst maps derived from "explicitly-modelled" ranges resulted in the highest estimations of richness and those derived from "expert-drawn" ranges exhibited intermediate values. Although, here there was no direct comparison with the first maps obtained through DIVA-GIS, it is clear those maps tended to underestimate richness at high resolutions due to sampling bias. Furthermore, the significant evidence of effort bias here suggests, in agreement with Graham & Hijmans (2006), that maps derived from counts within grids probably do not reflect accurately patterns of richness, and possibly are useful only as a general reference methodology at coarse grain sizes. Otherwise, contrary to the findings of Graham & Hijmans (2006), in this study richness maps derived

from “expert–drawn” ranges exhibited consistently higher values on average than maps derived from “explicitly–modelled” ranges at the family level. This was not always the case for the different avian subsets mapped at genus level, which showed no difference for all taxa and forest avian subsets, higher values for the non–marine subset and lower values for the strictly forest avian subset.

Graham & Hijmans (2006) explain their differences arguing that in their study “explicitly–modelled” ranges predicted greater range sizes than other methodologies due to higher errors of commission, which result from a failure of models to incorporate factors other than climate limiting ranges; such as biological interactions and dispersal capabilities as well as barriers to dispersal. Agreeing with these authors, although overprediction due to commission error is undesirable, inflating the overall richness forecast, it may be interesting to address areas where differences have occurred to test biotic and abiotic hypotheses that may explain the observed divergence. In contrast, the fact that in this study, patterns of difference were the opposite at family level suggest the dominance of omission errors at this level, while at genus level results suggest commission and omission errors were more balanced overall. Average absolute differences in richness were roughly less than 10 families and 20 genera, which is relatively small error. However, there are particular zones where absolute differences were extremely high, reaching maximum values of about 50 families and 200 genera. It is hypothesised here that these differences are mainly due to: 1) the lack of appropriate sampling effort for particular zones in the country, 2) increased omission errors in taxa with few sample localities, and 3) the failure to model some taxa due to total lack of data. As proven elsewhere in this study, the country may be still considered spatially undersampled. Moreover, within the purged dataset used from the Darwin–Hernandez Database 30 families and 439 genera were modelled with less than 100 point localities, which, despite the excellent performance proven for MAXENT represents a very small number of samples for the entire Colombian territory (Figure 5.4.3.1.2). In addition, another 9 families and 73 genera had less than 5 point localities and therefore were not included in modelling exercises.

Differences between diversity maps generated also may have arisen from uncertainties in the climatic datasets used. Although WorldClim climatic surfaces are of a relative higher resolution than other climatic datasets, and they were produced using more accurate elevational information and more data on individual meteorological stations, still they do not capture all variation existing at very high resolutions such as 1 km, especially for precipitation related variables in the mountains (Hijmans *et al.*, 2005a). Consequently, inaccuracies in climatic datasets used as basis for habitat suitability modelling may have profound effects on resulting maps and on overall modelled diversity. Despite climatic data limitations and apparent elevational bias in

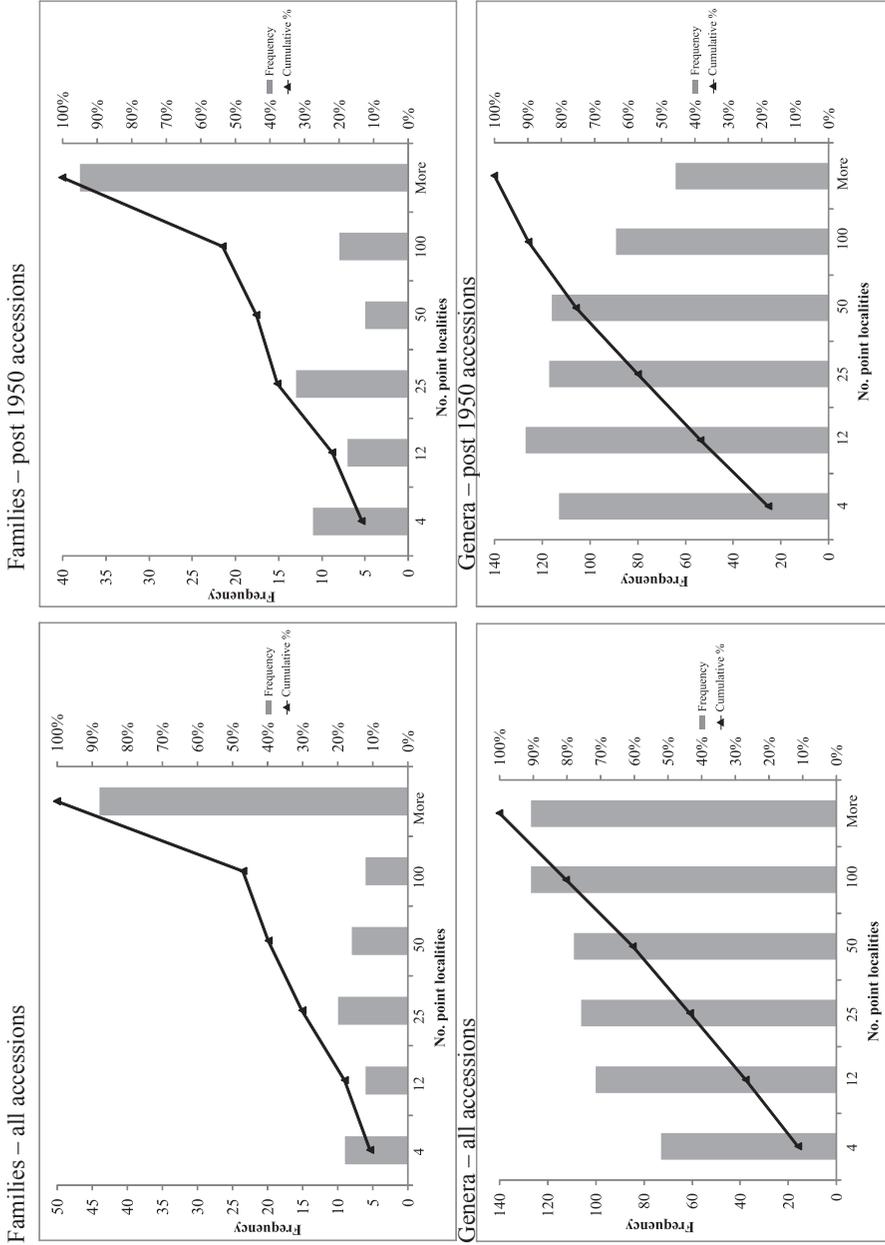


Figure 5.4.3.1.2. Frequency of taxa modelled using MAXENT within different samples classes. Habitat suitability modelling: second generation.

meteorological stations positioning, it is worth mentioning that Hijmans *et al.* (2005a) maps of density of meteorological stations situates most stations in Colombia west of the Andes, which suggests better climatic predictions for the Caribbean, Andean and Pacific regions than for the Orinoco and Amazon regions. According to the same authors, the use of satellite remote sensed datasets might produce improved high-resolution climatic predictions. However, possibly this may not be very meaningful as long as uncertainties in biological data georeferencing are not improved or corrected, which in the way most georeferencing has been done until now (*i.e.* retrospective georeferencing) seems not possible to certain extent.

The thorough assessment of differences between datasets and methods as conducted in this study is helpful to better understand how sampling and effort bias is affecting diversity estimation in particular zones of the country. Additionally, it is useful to direct particular attention to areas of high diversity, but also to areas showing the greatest differences between methods and thus the greatest uncertainty. First, because these may reflect areas where diversity was underestimated due to incomplete sampling, making it necessary to consider them for future inventory efforts. Second, because they can point out new areas expected to be of high diversity, but overlooked previously because of the inherent incomplete knowledge of some “expert-drawn” ranges.

Described differences in rarity scores between reference and model maps have an origin in two main causes. First, rarity, estimated here as the Weighted Endemism Score, is sensitive to patterns of omission and commission in each individual taxon range projected. It thus decreases in areas where taxa are omitted and on the contrary increases where more taxa are predicted as present.

Second, since the weighted contribution for each taxon in a cell was calculated by dividing by the total number of pixels representing the range in the whole of northern South America, it is expected that the index is also sensitive to total omission and commission errors generated in each one of the final modelled consensus range maps. Moreover, since model building only used data from Colombia, at the regional scale it is very likely that omission error was increased due to sampling bias and insufficient sampling. Nevertheless, results suggest that this affected particular areas and that it had a greater impact at family than at genus level, where omission and commission errors seemed more balanced.

Hence, differences in rarity maps may have arisen as result of a complex interaction between these factors. For instance, for family rarity, areas such as the Altiplano Cundiboyacense and the lowlands and foothills between the northeastern slope of Serrania de San Lucas and the Eastern Cordillera, had higher scores in reference than in model maps. Whereas for the area near Serrania de San Lucas it could be hypothesised that undersampling is the cause, the same idea cannot be supported for

the Altiplano Cundiboyacense, which has been relatively well explored. In that case, it is more likely that differences were created by a greater commission error outside of Colombia in the models generated for the particular families that inhabit this area within the country. On the other hand, for genus rarity, the Altiplano Cundiboyacense did not show differences, but additional areas with higher scores in reference than in model maps emerged in the Ruiz–Tolima Volcanic Complex, in the Pacific slopes and foothills from the western foothills of Serrania de los Paraguas south to the border with Ecuador and in the Colombian Massif, as well as a few more areas in the Serrania del Darien, the northwestern foothills of Serrania del Perija and in the eastern slope of the Andes in the border with Ecuador. It may be that for areas in the eastern slope of the Andes, in the south, the cause is undersampling, while this is unlikely for the other areas. As stated before, it is more likely that differences in those were generated by greater commission errors outside Colombia in models developed for the particular genera inhabiting these parts of the country. Moreover, at family level differences in rarity between reference and model maps evidenced a narrow coastal band of high values for the all taxa avian subset, which very likely is a consequence of an increased rate of commission error in marine bird models. Otherwise, at the family level when forest taxa only were mapped a few areas where the reference map had higher values than the model emerged in the lower Atrato, mid–low Nechi, low Cauca and middle Magdalena valleys, which very likely corresponded to undersampled areas in the lowlands. Contrastingly, areas where the model exhibited higher scores than the reference map appeared extensively in most of the mountain ranges and adjacent lowlands, including most of the inter–Andean valleys; and likely caused by a greater level of commission errors at the country level and increased omission at regional level for forest related families models.

Additionally, it is interesting to highlight that Graham & Hijmans (2006) found that correlations between maps derived from different approaches showed low coefficients (< 0.5) at high resolutions (1 km), although those increased to medium–high values (≈ 0.7) at low resolutions (50 km). Results in this study exhibit a similar tendency in resulting differences between correlation coefficients when the richness local average and the total richness in AEQSIBs were tested. However, conversely at high resolution in this study correlations for richness maps were extremely low and negative, while they improved when analyses were performed in AEQSIBs (medium–high positive values), which is analogous to a larger grain since each elevational band in this approach has an areal extent of about 10,000 km². It is important to highlight that rarity at genus level exhibited better correlations between reference and model maps. This suggests that, despite the differences observed, rarity at genus level may possibly be considered the best mapping exercise in this study to take forward with projections for future climates.

Graham & Hijmans (2006) also believe that expert drawn maps tend to represent better (compared with modelled ranges) the current geographical range of a species. Nonetheless, frequently databases or secondary information sources from museums and herbaria hold point localities that lie outside the drawn ranges, and consequently represent extensions of the known ranges (Graham & Hijmans, 2006). This suggests that “expert-drawn” maps often do not cover thoroughly the area of occupancy or even the area of extension of some taxa. The same authors argue that some of those records correspond to old specimens collected in localities from where the particular taxa have been extirpated and this is probably the case for species such as the Yellow-eared Parrot (*Ognorhynchus icterotis*), thought to be distributed along the Andes of Colombia and Ecuador, but today extinct in Ecuador and known to occur in Colombia from no more than 5 localities (Salaman *et al.*, 2007c). However, both in Graham & Hijmans study, and here this it not the case for some accessions, which have been collected more recently. An example of this, are the many range extensions confirmed during the last 20 years due to new explorations in the field (Salaman *et al.*, 2007b). Clearly, this results in an inherent failure of “expert-drawn” range maps to include particular portions of the ranges due to lack of proper knowledge by experts. Thus, modelled maps might tend to reflect better the potential and/or historical spatial distribution of richness (Graham & Hijmans, 2006).

Results from this study showed that model maps generated using all accessions usually exhibited higher average values of richness than those generated using post 1950 accessions only. It is hypothesised here that much of this difference corresponds to a drastic reduction in accessions in the datasets used for modelling each time, which dell from $\approx 120,000$ to $\approx 60,000$ accessions; meaning changes in modelled taxa from a total of 74 to 71 families and 569 to 513 genera. Sampling and effort bias can influence model overfitting to particular regions that have been better sampled than others, overestimating richness in particular areas (Graham & Hijmans, 2006). Although, this source of bias was definitely reduced in this study for the filtered dataset with all accessions, it possibly reappeared in the subset that just retained accessions post 1950. To illustrate this point the difference in richness and rarity estimations between the two types of models for the forest avian subset at the genus level were mapped (Figure 5.4.3.1.3). These new results showed a marked similarity in patterns for richness and rarity, suggesting that differences could be principally consequence of data reduction, although both datasets possibly keeping a very similar spatial distribution and levels of sampling and effort bias. On the other hand, it is possible that some of these are the result of a synergistic effect between bias and real change due to climate and land cover change since the beginning of the 20th century. However, the separation of those effects is not an easy task. Possibly a more detailed analysis focusing on the Andean region in areas where collection has been more intensive may help to reveal some of the effects caused by each one of those factors.

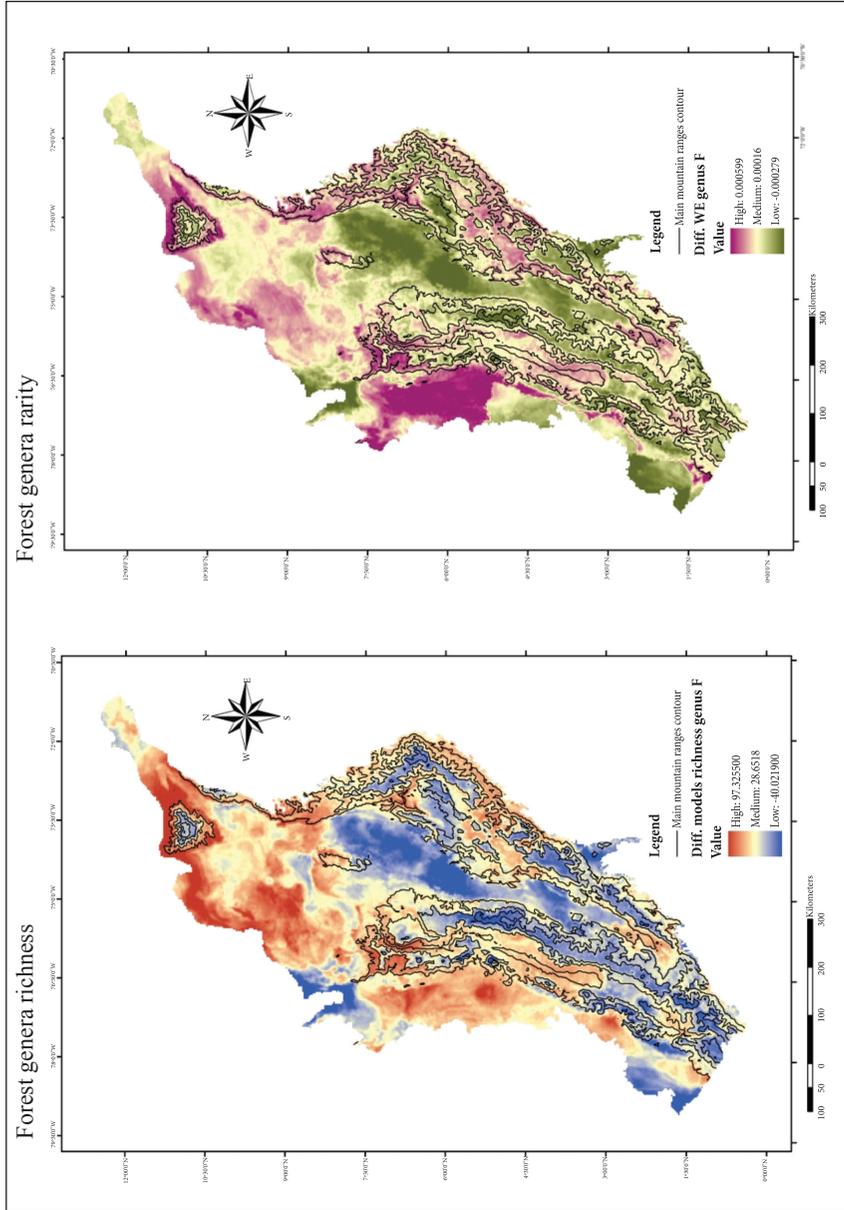


Figure 5.4.3.1.3. Spatial distribution of the difference in simple richness and rarity (Weighted Endemism score) between MAXENT–BioMap based modelled maps when using all filtered accessions and a subset just with accessions post 1950 in West Colombia at genus level for the forest avian subset (model all data - model post 1950). Habitat suitability modelling: second generation.

As also seen by Graham & Hijmans (2006) in their study, this section shows that diversity maps are sensitive to the different methodologies and datasets used to generate them. A possibility to advance mapping in Colombia could use, as recommended by the same authors, “hybrid” range maps created using habitat and niche modelling methods and “expert-drawn” range maps. This is very useful since hybrids exploit the potential to correct predictions from models, while limiting them for commission errors in areas where it is well known that certain taxa do not exist due to different reasons such as possible competitive exclusion with other related taxa, the presence of physical barriers and/or the taxon’s own dispersal capabilities.

5.4.3.2. *Ecomorphological avian diversity in West Colombia*

Results obtained when mapping ecomorphological diversity (ecomdiversity) showed patterns that are consistent with those observed for plain richness. Thus, most areas of high ecomdiversity emerged in the Andean region, the Sierra Nevada de Santa Marta and Serrania del Baudo. However, the families Trochilidae (hummingbirds) and Tyrannidae (tyrant flycatchers) showed some differences in the spatial distribution of ecomdiversity. There were also clear dissimilarities in patterns within each family between the “equivalent-species ecomorphological diversity index” (ESE index) and the “ecomorphological groups equitability” (E’ index).

The ESE index showed the highest values of ecomdiversity to be located in areas that were roughly between $\approx 2,000$ – $4,000$ m for hummingbirds, and between $\approx 1,000$ – $3,000$ m for tyrant flycatchers. Otherwise, for both families the majority of the Andean foothills and the Biogeographic-Choco (Pacific) Region exhibited medium values, whilst most lowlands in the Caribbean Region exhibited low values for hummingbirds and medium values for tyrant flycatchers. In addition, for both families, the lowest values in the ESE index appeared in the low Atrato, low Sinu, San Jorge, low Cauca, low Nechi and the mid Magdalena valleys.

On the other hand, the E’ index exhibited a similar general pattern. Nevertheless, areas with high ecomdiversity for hummingbirds extended relatively evenly in the Andes including also areas above $\approx 1,000$ m and the inter-Andean valleys. Additionally, some areas in the lowlands of the Pacific Region, in Nariño, and in the Caribbean Region from Antioquia to La Guajira also exhibited high ecomdiversity. For tyrant flycatchers additional high-ecomdiversity areas below $\approx 1,000$ m were included, although excluding the inter-Andean valleys and areas in the Andes above $\approx 3,000$ m. The inter-Andean valleys as well as most of the Caribbean Region acquired medium values, whilst the top of the mountain ranges received a “missing value”, due to the absence of at least one functional group. This same situation was seen for hummingbirds in the core of areas with the lowest values. Otherwise, most lowland

areas ranked in medium values keeping the lowest values in fewer areas in the low Atrato, San Jorge, low Cauca, low Nechi and the mid Magdalena valleys, although those were less clear for tyrant flycatchers.

It is important to note that overall functional groups did not contribute equally to the total ESE index and that they differed in their spatial distribution for each family. Accordingly, results evidenced that for hummingbirds the functional groups related to species using the upper undergrowth and medium levels for both gleaning insects and invertebrates from leaves and licking nectar from open corollas (UMFTNBII and UMNECOCL) occupied a major proportion of the total modified equivalent–species for the family ($\approx 74\%$ of the ESE index map total). Conversely, for tyrant flycatchers, modified equivalent–species were relatively more evenly distributed in a greater number of functional groups. For this family, functional groups related to species that glean insects and invertebrates from leaves in both the upper undergrowth and medium levels, and in the canopy and borders (UMFTNBII and CBFII) added up to $\approx 37\%$ of the ESE index map total. Additionally, another $\approx 33\%$ was distributed among functional groups related to species that hawk insects and invertebrates in both the upper undergrowth and medium levels and in the canopy and borders (UMHII and CBHII), and that take fruits in the canopy and borders (CBF).

In relation to functional groups spatial distribution patterns, results showed that for hummingbirds groups related to canopy and borders (CBHII, CBFII and CBNECOCL) presented high–scores in a relatively wider and more even zone in the Andes and the Sierra Nevada de Santa Marta. The two remaining groups, those related to the upper undergrowth and medium levels (UMFTNBII and UMNECOCL), extended in some few areas into the Pacific lowlands and in Serrania del Baudo. In contrast, tyrant flycatchers patterns for areas with high–scores were in general more restricted to the range $\approx 1,000\text{--}3,000$ m of elevation in the mountains. This was particularly the case for groups related to species that hawk and/or glean insects and invertebrates in the canopy and borders (CBHII and CBFIII), and the upper undergrowth and medium level (UMHII), which exhibited varying degrees of patchiness within those elevations. Functional groups related to frugivorous (GLUFF, UMFF and CBF) maintained a similar general pattern, although including some areas in the lowlands west of the Western Andes. Groups that forage insects and invertebrates on the ground and the lower undergrowth (GLUHII and GLUFII), and that glean insects and invertebrates from leaves in the upper undergrowth and medium levels (UMFTNBII) exhibited an even more restricted distribution in the Andes and the Pacific lowlands. Finally, from the functional groups including small vertebrates in their diets, the first one embracing species that forage in medium levels and the canopy (MCFTNBVII) behaved likewise to frugivorous related groups. On the other hand, the second group, which includes species foraging in the undergrowth (UFTNBVII), exhibited a unique

extensive and uniform pattern covering areas in the mountains below 2,000 m and the lowlands west of the Andes and the Caribbean Region.

Differences between standardised maps³¹ of plain richness and the ESE index evidenced a dichotomy between zones with potentially high levels of ecomorphological singularity and areas where ecomorphological redundancy is prevalent. For hummingbirds, areas with high singularity were mostly above 2,000 m elevation in a semi-continuous stripe in the Eastern Cordillera, and in the Central and Western cordilleras in the north and south. On the other hand, most areas below 2,000 m did not show major differences, whilst most lowlands in the Caribbean and inter-Andean valleys corresponded to areas with high redundancy. Tyrant flycatchers exhibited a similar spatial distribution. Nonetheless, areas of high singularity were more restricted within the range $\approx 1,000$ –3,000 m of elevation, as well as being more extensive and uniformly distributed in the Pacific Region and in the zone between the Andean and Caribbean regions. In contrast, areas of high singularity in the south of the Andes were less prevalent and a few additional areas in the eastern slope of the Eastern Cordillera and in the western slope of the Central Cordillera emerged.

In the literature a plethora of different indices to measure diversity are described. Different indices are rooted in different branches of biology, consequently reflecting the different conceptions of biodiversity in the fields from where they have originated. Among some of those, Harper & Hawksworth (1994) mention three general approaches: taxic, molecular and phylogenetic measures, which they consider are alternatives to the most widespread used index of biodiversity, “species richness”. Otherwise, in ecological research, the equitability of the species population numbers in a community has received enormous attention. In this sense, there is a wide spectrum of indices, which assess diversity through equitability. Some of them are for example: Simpson, Shannon–Wiener, Margalef, Brillouin, for alpha and gamma diversity, and Whittaker, Jaccard, Morisita–Horn and Sorenson for beta diversity, among others (Magurran, 2004).

More recently, after the CBD (1992) a paradigm shift in ecology has occurred, and research on measures of diversity relating the equitability of abundance between the species of a community has moved towards research in measures of functional diversity. These describe constituent elements of biodiversity which may affect ecosystem functioning. This is by no means an easy task and although advances have been achieved mainly in the theoretical aspects such as developing new biodiversity indices (Izsák & Papp, 2000; Roy *et al.*, 2004; Ricotta, 2005a, b; Ricotta, 2006, 2007), their application and use has remained limited to local scales. Furthermore,

³¹ Maps were standardised using the maximum value of any cell of a set of related maps (*i.e.* plain richness current conditions and future scenarios projections and ecomdiversity current conditions and future scenarios projections), obtaining values between 0–1.

integration of the complexities related to interactions between biodiversity elements still proves to be elusive.

Initiatives such as WorldMap (Brooks *et al.*, 2000; Williams, 2001) and DIVA-GIS (Hijmans *et al.*, 2005c) have advanced remarkably some of those limitations making available to the scientific community and the general public software that offers the opportunity to apply different diversity indices at large spatial scales once data are available. For example, DIVA-GIS can estimate additionally to simple richness, equitability indices such as Margalef, Simpson, Menhinick and Shannon-Wiener, while WorldMap can estimate several different indices such as rarity scores, β diversity and phenetic measures of diversity. These packages do not address functional diversity measures explicitly. Although, it is possible to use them in simple ways for that purpose, if for example functional diversity is estimated as the richness of functional groups defined *a priori*, to which species present in a particular dataset used should be assigned beforehand and the dataset arranged accordingly.

Ecomdiversity indices proposed in this study use a combination of conceptualisations rooted in classical ornithological studies and ecological studies in biodiversity. On the one hand, they apply a functional classification based on the “ecological guilds” concept *sensu* Root (1967), according to which, each “guild is defined as a group of species that exploit the same class of environmental resources in a similar way”. In this sense, functional groups in this study are characterised as feeding guilds, based solely in traits related to resources used and forms of exploitation. The term “functional group” has been used in the literature in different ways, generating certain confusion in its use. For instance, some authors consider both “ecological guild” and “functional group” as concepts that apparently developed in parallel reaching a remarkable similarity in meaning (Simberloff & Dayan, 1991). In contrast, other authors in more recent revisions think “functional group” should be used in a narrower sense to indicate a group of organisms characterised by having a similar response to perturbations or changes in environmental conditions (Gitay & Noble, 1997). Although it does not have to be the rule, logic dictates a close relationship between both terms, and taxa included in the same ecological guild are expected very likely to exhibit similar responses to alterations in environmental conditions (Gitay & Noble, 1997). On the other hand, the “ecomorphological groups equitability” (E' index) is calculated in this study as a modification of the Shannon-Wiener index (Magurran, 2004), used for the first time in ornithological research by R. MacArthur (H') to describe bird and plant diversity in different habitats in the United States (MacArthur & MacArthur, 1961; MacArthur, 1964, 1965), and nowadays used widely to study the equitability in the distribution of species abundance in natural communities.

Finally, although other studies such as Tuiller *et al.* (2006) have adapted the Shannon-Wiener index to map functional diversity, it is possible to highlight a

couple of important differences with this thesis. First, that study was conducted for vegetation, which is a group that has received a great deal of attention in this type of research, and second, in their estimation species are used as analogous to individuals to determine the equitability in the distribution of species among functional types. The present study is unique in exploring functional diversity in Colombia for the first time in an Animalia group. Furthermore, the use of equivalent species modified by a morphological index is exclusive to this study. This approach revealed different patterns in avian diversity distribution in Colombia in comparison to those observed when using the more widely used species richness index. In this way, results permitted a decoupling of different constituent elements of bird diversity that might be studied in relation to particular functions in the environment and thus associated to particular ecosystem services.

Though the ecomdiversity indices proposed here constituted a valuable and very interesting exercise in producing alternative measures of biodiversity, still errors in the accuracy of predictions in geographical range maps constitute a significant caveat to the diversity maps obtained. In this sense, the examination of differences in richness estimates between reference (WHDBD Database based) and model (MAXENT based) maps for both hummingbirds and tyrant flycatchers showed extremely negative values, indicating high overprediction in richness in model maps (Figure 5.4.3.2.1). Moreover, spatial patterns of difference were not homogeneous both in the country and between families. In general, model maps overestimated richness in the Andes. This was extensive through the three cordilleras, the Sierra Nevada de Santa Marta and Serrania del Baudo for hummingbirds and in a more restricted fashion for tyrant flycatchers, excluding major portions of the Central Cordillera, the Sierra Nevada de Santa Marta and the highest portions and the southeastern slopes of the Eastern Cordillera. For tyrant flycatchers the contrary was found and emerged several zones where richness was underestimated, especially areas of the Atrato, Sinu, San Jorge, Nechi, low Cauca and mid Magdalena river valleys, as well as in the highest portions of the Sierra Nevada de Santa Marta, Serrania del Perija and in the Ruiz–Tolima Volcanic Complex.

A more detailed examination of differences in prediction in modelled ranges of several taxa³² in relation to “expert–drawn” range maps suggested some interesting

³² Bronzy Hermit (*Glaucis aeneus*), Rufous–breasted Hermit (*Glaucis hirsutus*), Violet–tailed Sylph (*Agelaiocercus coelestis*), Long–tailed Sylph (*Agelaiocercus kingi*), Buff–tailed Coronet (*Boissonneaua flavescens*), Velvet–purple Coronet (*Boissonneaua jardini*), White–vented Plumeleeter (*Chalybura buffonii*), Bronze–tailed Plumeleeter (*Chalybura urochrysia*), Tufted–tit Tyrant (*Anairetes parulus*), Agile–tit Tyrant (*Anairetes agilis*), Bronze–olive Pygmy–tyrant (*Pseudotriccus pelzeni*), Rufous–headed Pygmy–tyrant (*Pseudotriccus ruficeps*), Streak–necked Flycatcher (*Mionectes striaticollis*), Olive–striped Flycatcher (*Mionectes olivaceus*), Ochre–bellied Flycatcher (*Mionectes oleagineus*), Tawny–breas-

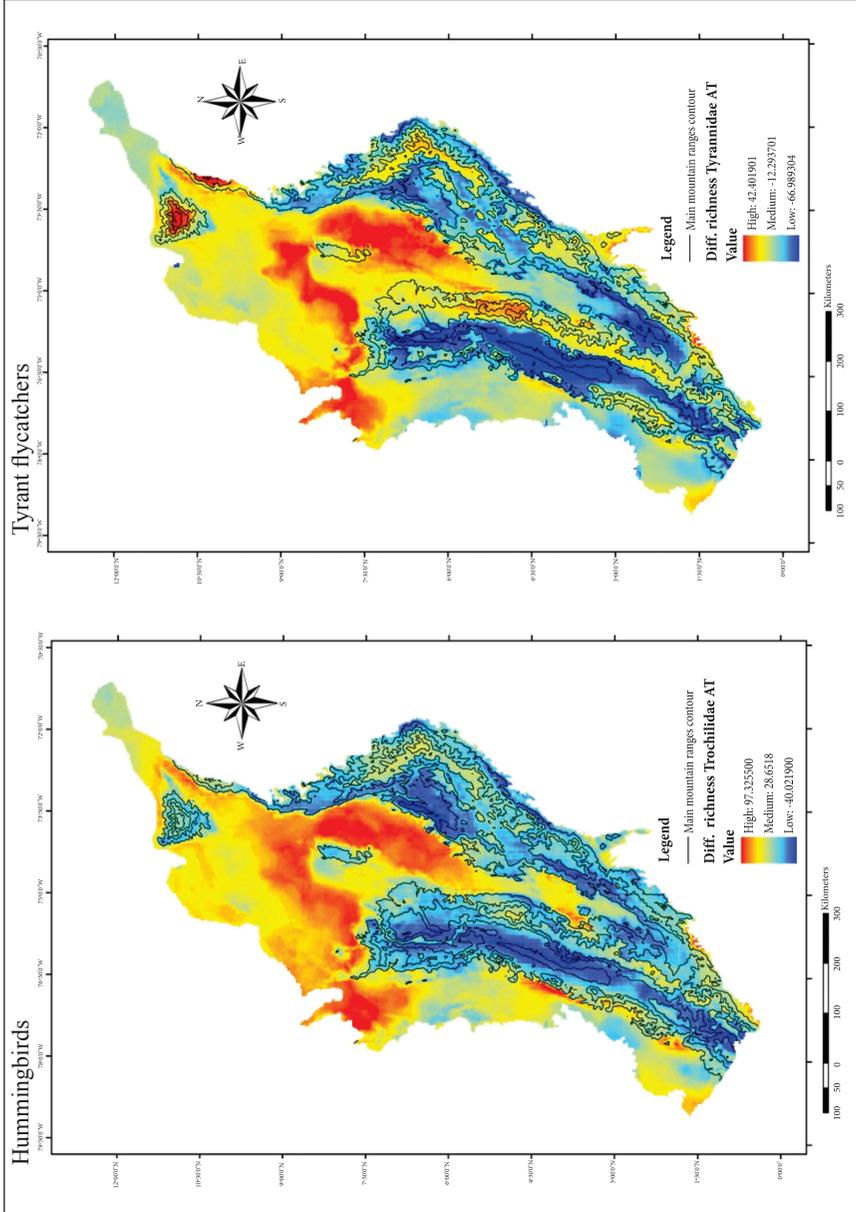


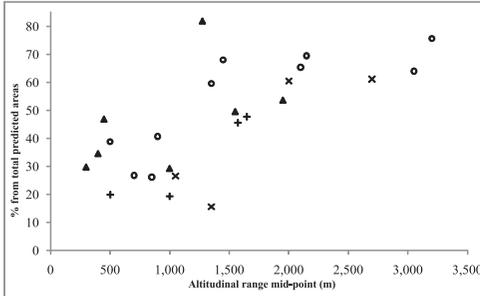
Figure 5.4.3.2.1. Spatial distribution of the difference in plain species richness between WHDBD Database based maps (reference) and MAXENT-BioMap based modelled maps (model) in West Colombia for hummingbirds (Trochilidae) and tyrant flycatchers (Tyrannidae) (reference - model). Habitat suitability modelling; second generation.

tendencies and permitted some conclusions regarding the most likely causes behind observed disparities. In general, these analyses showed that the proportional area predicted by MAXENT increases consistently for taxa whose elevational ranges lie at higher elevations, while conversely the proportional area predicted where both WHDBD Database maps and MAXENT maps coincide decreases (Figure 5.4.3.2.2). Moreover, the proportional area solely predicted by WHDBD Database maps tended to decrease; although for tyrant flycatchers taxa a “concave–u” pattern emerged with elevation. Otherwise, both species and genera followed similar patterns, although species showed higher overprediction in MAXENT range maps in all cases.

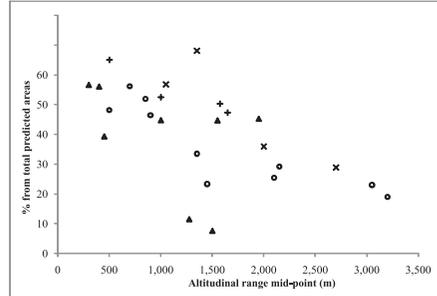
It is interesting to highlight that neither MAXENT nor WHDBD Database maps predictions were perfectly accurate. Highly accurate modelled geographical ranges are expected to exhibit both low omission and commission errors (Anderson *et al.*, 2003). Nevertheless, the magnitude of both errors may change depending on how spatially biased data occurrences used to model are and how comprehensively they represent the whole range of conditions under which the species occur (Graham & Hijmans, 2006). On the other hand, “expert–drawn” maps may include greater commission error than models since they are relatively coarse approximations of the “extent of occurrence” (*sensu* Gaston, 1994) of species geographical ranges (Graham & Hijmans, 2006). Conversely, depending on how thoroughly inventoried the area is and how well known the specific taxon under examination is, “expert–drawn” maps may include greater omission error than models. In this context, differences in prediction between MAXENT and the WHDBD Database geographical range maps in this study seem to indicate a very complex interaction of all the factors mentioned above, which possibly were different in each specific case. A couple of examples will help to illustrate this. For instance, the Bronzy Hermit (*Glaucis aeneus*) and the Rufous–breasted Hermit (*Glaucis hirsutus*) are two species of hummingbirds occupying mainly the lowlands in Colombia below 1,000 m of elevation. The Bronzy Hermit range is limited mostly to the Pacific Region, while the Rufous–breasted Hermit is widely distributed in the Caribbean, the inter–Andean valleys, the foothills of the eastern slope of the Eastern Cordillera and the Amazon Region (Hilty & Brown, 2001). Although, most of both ranges seem predicted correctly, there are several points to highlight (Figure 5.4.3.2.3). First, for the Rufous–breasted Hermit there are several areas between 1,000–2,000 m where the species is predicted to be present only by the WHDBD map, only by the MAXENT map, or by both types. Although, some of these may be artefacts created by grain resampling and conversion between formats, in most of these areas the species may actually occur, especially below 1,300 m (Verhelst *et al.*, 2001). It is interesting to note that MAXENT predicts presence in

ted Flycatcher (*Myiobius villosus*), Sulphur–rumped Flycatcher (*Myiobius barbatus*), Black–tailed Flycatcher (*Myiobius atricaudus*).

MAXENT–only predicted areas
(Spearman's $\rho = 0.665$)



WHDBD Database–only predicted areas
(Spearman's $\rho = -0.606$)



MAXENT \cap WHDBD Database predicted areas

(Spearman's $\rho = -0.628$)

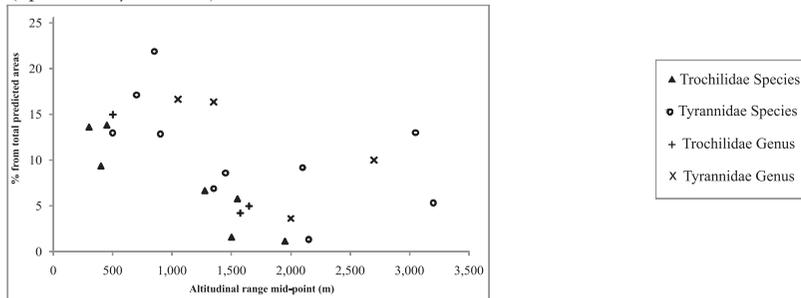


Figure 5.4.3.2.2. Proportion of MAXENT–only predicted areas of presence in relation to total suitable predicted areas by both WHDBD Database based range maps and MAXENT–BioMap based modelled range maps in the elevational gradient of West Colombia for 8 species (4 genera) of hummingbirds (Trochilidae) and 10 species (4 genera) of tyrant flycatchers (Tyrannidae). Bronzy Hermit (10), Rufous-breasted Hermit (139), Violet-tailed Sylph (24), Long-tailed Sylph (62), Buff-tailed Coronet (59), Velvet-purple Coronet (12), White-vented Plumeleteer (69), Bronze-tailed Plumeleteer (27); Tufted-tit Tyrant (9), Agile-tit Tyrant (5), Bronze-olive Pygmy-tyrant (21), Rufous-headed Pygmy-tyrant (19), Streak-necked Flycatcher (58), Olive-striped Flycatcher (128), Ochre-bellied Flycatcher (138), Tawny-breasted Flycatcher (18), Sulphur-rumped Flycatcher (50), Black-tailed Flycatcher (18). The number in parentheses is the total number of occurrences used for generating models. Habitat suitability modelling: second generation. All Spearman's ρ were significant at $p < 0.01$.

the Cauca valley correctly, where the species was formerly widely distributed (Hilty & Brown, 2001) and its presence confirmed in recent years by studies conducted by the National Centre for Coffee Research – CENICAFE (pers. obs.). In addition, if we consider that in the Andes elevation conditions may change rapidly, even in one horizontal kilometre, at the grain size used (9 km²) it may be considered very likely that averaging of conditions within the model grain may also lead in part to this pattern of overprediction. Second, the species is predicted to be present solely by the WHDBD map in several areas above 2,000 m, which clearly are erroneous,

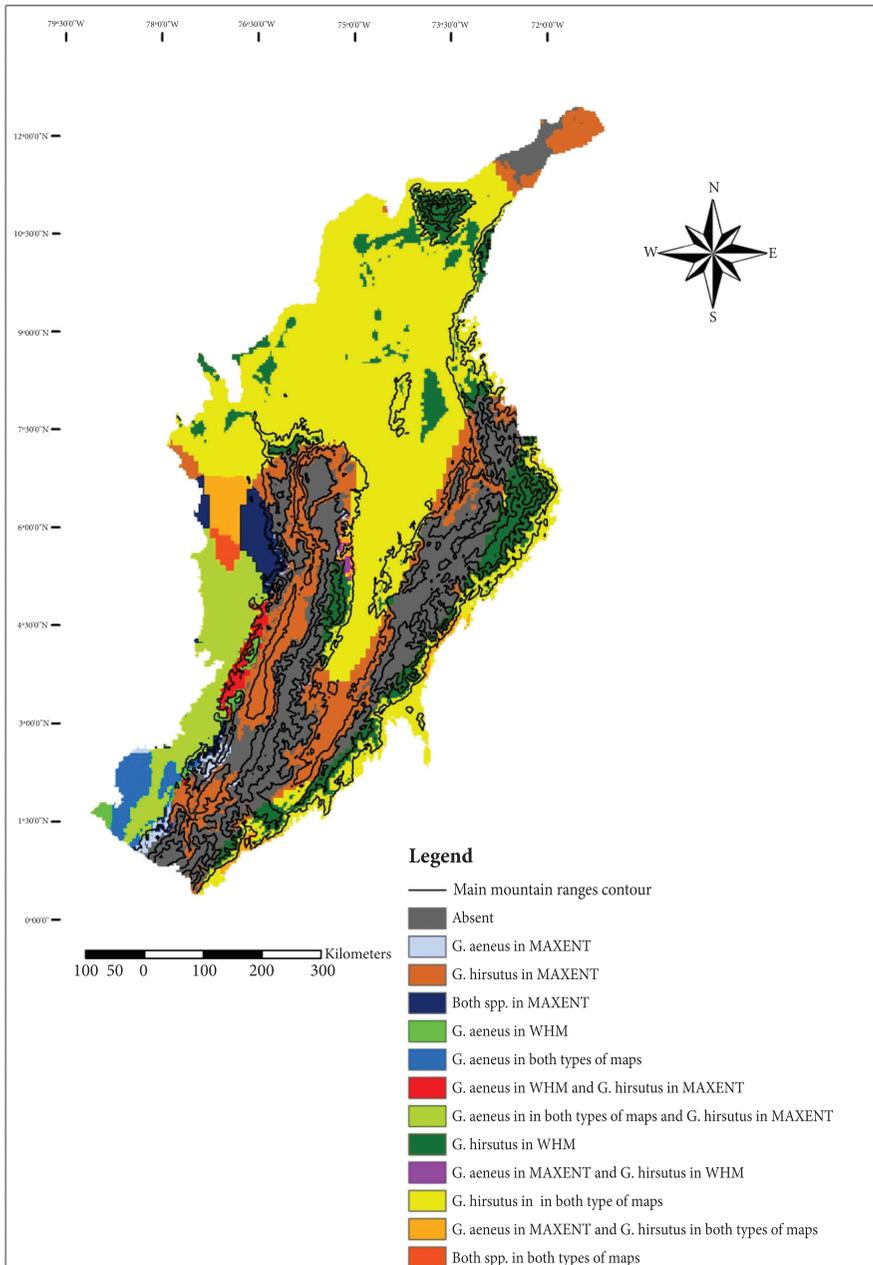


Figure 5.4.3.2.3. Bronzy Hermit and Rufous-breasted Hermit (*Glaucis*, Trochilidae) geographical ranges in West Colombia, predicted using MAXENT–BioMap and WHDBD Database. Habitat suitability modelling: second generation.

but that were correctly predicted as absent by the MAXENT map. Third, in contrast, there are some few areas in the Caribbean lowlands where the species is predicted to be present solely by the WHDBD map, which are very likely correct but were not predicted by the MAXENT map. Fourth, the species is predicted as present only by MAXENT map in the high Guajira, the Patia–Dagua valleys and the high Magdalena valley, where conditions are possibly too dry for the Rufous–breasted Hermit to exist. Particularly in La Guajira, although there are isolated spots such as for the example the Serrania de La Macuira and several small mountains south from it, where conditions are apparently climatically adequate but the species has not established populations. Otherwise, for the Bronzy Hermit we can note the same as for its congener in the first and second points, although mostly limited to the Pacific slope. It is interesting to highlight an area in the most southwestern portion of Nariño where the species is predicted as present by the WHDBD map but absent by MAXENT map.

On the other hand, species with mostly Andean ranges show a slightly different picture. The Long–tailed Sylph (*Agelaiocercus kingi*) and the Violet–tailed Sylph (*Agelaiocercus coelestis*) are two species of hummingbirds that occupy the mountain ranges in Colombia mostly above 1,000 m of elevation. The Violet–tailed Sylph range is limited mostly to the Pacific slope, while the Long–tailed Sylph is mostly distributed in the Central and the Eastern cordilleras and occurs sympatrically with its congener in the southern half of its range (Hilty & Brown, 2001). In this case, it is interesting to note that there are areas in the mountains above 1,000 m where both species are predicted by MAXENT, but not predicted by WHDBD maps (Figure 5.4.3.2.4). Some of these areas may possibly be zones where the species may occur. Thus, the Violet–tailed Sylph may occur further north in the Pacific slope of the Western Cordillera, whilst the Long–tailed Sylph may be present in the eastern slope of the Western Cordillera, both slopes of the Central Cordillera and the eastern slope of the Eastern Cordillera. In this sense, MAXENT prediction of the Violet–tailed Sylph in those areas is incorrect. Field data from the ProAves Foundation confirms the presence of the Long–tailed Sylph in the area of Frontino and in Jardin (Antioquia) in the eastern slope of the Western Cordillera and in Roncesvalles (Tolima) in the western slope of the Central Cordillera. In addition, ProAves also have documented the Violet–tailed Sylph in Jardin (Antioquia) and in Serrania de los Yariguies (Santander) in the Eastern Cordillera, which are possibly misidentifications. Furthermore, neither of these species are known to occur in the Sierra Nevada de Santa Marta, although according to the models climatic conditions are adequate for both species to exist.

Over–prediction in species that have predominantly Andean ranges can be exacerbated in cases of species with relatively small or restricted ranges. The Tufted–tit Tyrant (*Anairetes parulus*) and the Agile–tit Tyrant (*Anairetes agilis*) are two species of tyrant flycatchers found in high altitude Andean zones above 2,500 m. Both species occur sympatrically in the southern central Cordillera in Huila, Cauca, Putumayo and

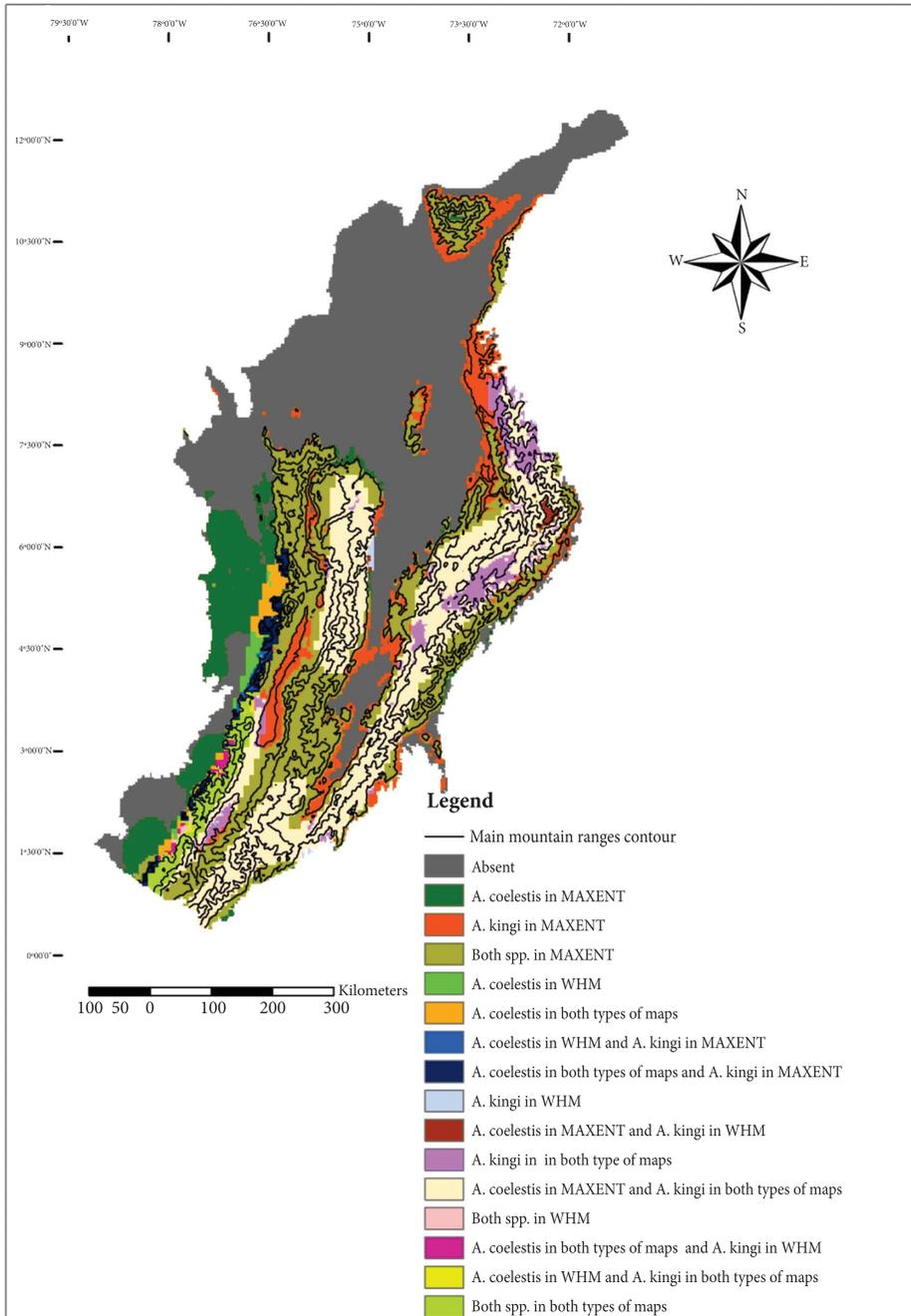


Figure 5.4.3.2.4. Long-tailed Sylph and Violet-tailed Sylph (*Agelaiocercus*, Trochilidae) geographical ranges in West Colombia, predicted using MAXENT–BioMap and WHM Database. Habitat suitability modelling: second generation.

Nariño, while the Agile-tit Tyrant is present additionally in the eastern Cordillera in Boyaca, Cundinamarca and the northwestern tip of Meta (Hilty & Brown, 2001). Although, MAXENT models for both species captured well most areas where the species were expected to occur according to WHDBD maps, a few areas solely predicted by WHDBD maps remained. Interestingly, for the Tufted-tit Tyrant these were mainly in the western slope of the Central Cordillera, while for the Agile-tit Tyrant these were located in the eastern slope of the Eastern Cordillera. Furthermore, models exhibited over-prediction in all the Andes and the Sierra Nevada de Santa Marta in areas above 2,000–3,000 m of elevation (Figure 5.4.3.2.5), extending slightly to lower elevations for the Tufted-tit Tyrant, which is actually known to occur at lower elevations. It is very unlikely that distant areas from the known ranges are occupied by the species, suggesting may be other reasons different to climate why they have not reached those zones. However, the Tufted-tit Tyrant surprisingly has been reported in at least three separate documents as present in the area around the Ruiz-Tolima Volcanic Complex in the 1980s and the 1990s (Pfeifer *et al.*, 2001), several hundred kilometres north from its known range limit. This suggests the actual range of the species may include other paramo areas from the Central Cordillera, where the species has been overlooked or has not been recorded due to a lack of inventories.

In summary, the examples discussed illustrate that inaccuracy in modelled maps in this study may arise from four main causes. First, insufficient sampling particularly in some areas in the lowlands may cause omission of zones where potentially the species may occur but it is not predicted due to a lack of samples for model training. Second, degradation of grain size leads to averaging of conditions within grids, which in the mountain ranges may result in a slight shift in the elevational belts where taxa are predicted, increasing commission error. Third, pure climatic based models fail to include in the modelling process other aspects of importance in defining geographical ranges, such as biological interactions, dispersal capabilities and barriers to dispersal, *etc.* (Soberon & Peterson, 2005; Graham & Hijmans, 2006). As a main consequence, commission error increases in the mountain ranges, due to a generalised projection of the potential conditions of existence of species along the whole three Andean cordilleras, the Sierra Nevada de Santa Marta and Serrania del Baudo, where the species for instance are not known to occur or are known to be replaced by a congener. Finally, each one of the main mountain ranges in Colombia has very singular climatic conditions that vary between slopes and even sometimes between adjacent valleys (Van Der Hammen & Ruiz, 1984; Van Der Hammen & Dos Santos, 1995; Cavelier, 1998; Van Der Hammen, 1998). Thus, for example any given species even if occupying all the three Andean cordilleras, the Sierra Nevada de Santa Marta and the Serrania del Baudo, usually occurs under a very specific set of climatic conditions in each mountain range, which often corresponds very well

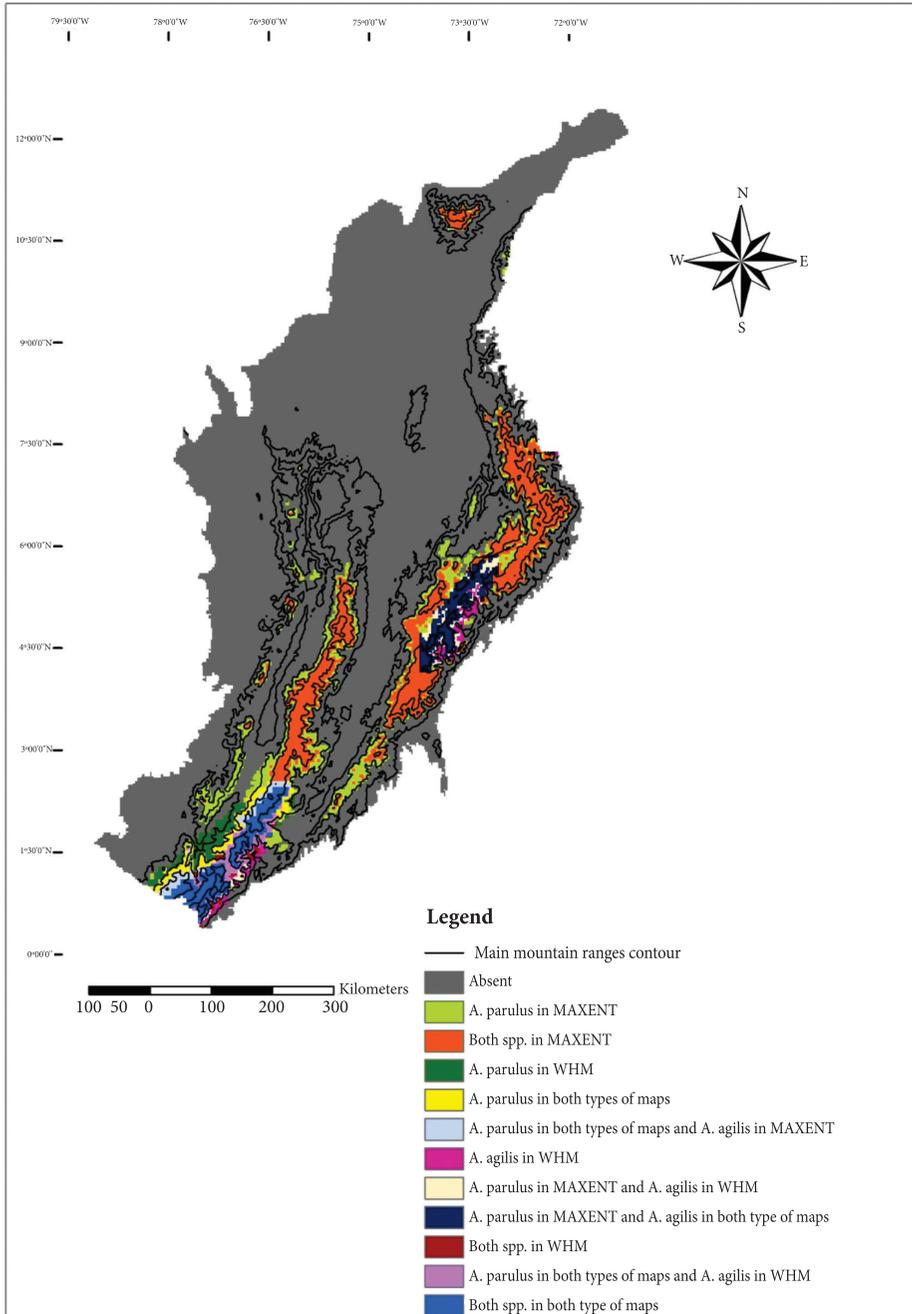


Figure 5.4.3.2.5. Tufted-tit Tyrant and the Agile-tit Tyrant (*Anairetes*, Tyrannidae) geographical ranges in West Colombia, predicted using MAXENT-BioMap and WHDBD Database. Habitat suitability modelling: second generation.

with the distribution of geographical races (Hilty & Brown, 2001). Furthermore, it is well known that similar components of the biodiversity may occupy slightly different altitudinal ranges in the different slopes of the cordilleras. For example, the limits between the Andean forests and the Paramo in the drier slopes of the Eastern Cordillera is between 3,300–3,500 m, at about 3,600–3,800 m in the wetter slopes of the Central Cordillera, and descends to nearly 3,000–3,200 m in the Pacific slope and the Sierra Nevada de Santa Marta, although these areas are relatively humid (Rangel-Ch., 1995, 1997, 2000, 2004). Similarly, for many species of Andean birds it has been documented that their ranges have lower limits in the Pacific slope and the Sierra Nevada de Santa Marta, while others extend their ranges at higher elevations in the wet slopes of the Central Cordillera (Hilty & Brown, 2001). In this sense, the addition of samples taken from different mountain ranges may increase commission error due to the mixing of conditions that apply to specific geographic regions in a generalised fashion over all mountain ranges. These same four causes of over-prediction can be expected to affect different taxonomic levels similarly, although, as showed before they were less prominent at genus level.

The mentioned patterns of over-prediction, particularly in the Andean Region, are in general agreement with observations made by Graham *et al.* (2010). These authors used MAXENT and “GIS expert-drawn” maps (*i.e.* GIS polygons created including all occurrences known and expert range maps) to study the extent to which potential modelled ranges are filled by the best-known range maps of occurrence for 70 endemic species in Colombia. Their results evidenced that the different cordilleras share – to certain extent – very similar conditions in specific areas and consequently, models exhibited high overprediction across cordilleras. This suggests the existence of adequate climatic areas to be occupied by particular species, although those have not been colonised due to other factors such as biotic interactions and dispersal limitations (Graham *et al.*, 2010). On the other hand, the same authors found that – usually at the cordillera level – model predictions are well matched by “GIS expert-drawn” maps, extending over the potential areas predicted as suitable. In this sense, the authors conclude that main discontinuities in elevation within the cordilleras do not act significantly as barriers to limit bird dispersal. Different mechanisms and processes influence range filling at these two spatial scales. Contrastingly, in this thesis there is evidence showing that areas predicted as suitable within cordilleras are not necessarily well matched by “expert-drawn” maps. For instance, the Tufted-tit Tyrant and the Agile-tit Tyrant occupy only a small fraction of the zones potentially predicted as suitable by MAXENT in the Central and the Eastern cordilleras. Moreover, it seems that the range of both species in the Central Cordillera is separated from the range of the Agile-tit Tyrant in the Eastern Cordillera by both a geographical and a climatic discontinuity approximately southwest of the Paramo de Sumapaz in the Eastern Andes as defined by Graham *et al.* (2010). This suggests the need to

continue exploring range filling in Colombian birds, especially in pairs or groups of related species, which may provide additional hints on mechanisms and processes responsible for bird range limits in the Colombian Andes.

This chapter summarises results obtained from the several mapping methodologies used to address bird diversity distribution in Colombia using the Darwin–Hernandez database from Project BioMap. From these, MAXENT habitat suitability models showed reasonable results. Thus, obtaining on average values for the AUC evaluation statistic of individual taxon models higher than 0.75. Moreover, diversity models seem to be independent of effort when heavily collected areas around Bucaramanga, Medellin, Bogota, Ibague, Cali and Popayan were resampled at random to reduce localities and analyses were limited to the western half of the country. During the second modelling phase, a significant increment in model accuracy was observed and AUC values were always greater at genus than at family taxonomic level; reaching AUC average values as high as 0.85. Otherwise, validation of MAXENT–based models of diversity against the WHDBD Database and ProAves field data showed that climatic models generated in this study do not show perfect agreement with the validation datasets, and therefore must be used cautiously. Observed differences are most likely the result of undersampling and effort bias in some regions of the country, such as areas between the Atrato River and the low mid–Magdalena valley and some areas in the Pacific Region as well as overprediction in the mountain ranges.

Despite the inaccuracies, the explicit modelling of diversity patterns in Colombia, using a large proportion of Colombian bird taxa, represents a major advance in biodiversity science in the country. Additionally, the Darwin–Hernandez database and MAXENT can be used in a similar way as conducted in this chapter to project geographical ranges onto future climate conditions (see the next chapter). Although possibly representing an optimistic scenario and limited by general assumptions made during the modelling process (Chapter 1, section 1.6), this constitutes a first set of hypotheses regarding potential impacts of future climate change on bird diversity in the country, against which future studies may compare their results. Furthermore, the comparative study of different types of maps as conducted here, as well as the continuation of studies refining functional measures of diversity represent an opportunity to advance further biodiversity knowledge in the country and bring closer the concepts of biodiversity and ecosystem services.

Other possible directions to continue research in this field may include the generation of hybrid maps based on both “explicitly–modelled” and “expert–drawn” maps and range filling in the whole dataset of maps generated in this study. This will help contribute to a better understanding of the mechanisms and processes defining range limits in birds in the Andes of Colombia and patterns of avian diversity in the country. Assisting, the generation of testable hypotheses related to the importance of abiotic

or biotic factors in shaping species geographical ranges in the north Andes of South America as Graham *et al.* (2010) have shown recently.

Overall, this chapter contributes to the first objective of the national strategy for birdlife conservation in Colombia (Renjifo *et al.*, 2001), which is to develop an information system to study and monitor bird diversity in the country. Specifically, to increase the quality and quantity of research related to all aspects of Colombian birdlife biology and to identify key conservation areas for Colombian birdlife, especially for threatened, endemic and migratory species.

Summary – This chapter assesses the potential impacts of future climate change on bird diversity in Colombia. For this purpose habitat suitability models using the Darwin–Hernandez Database and MAXENT modelling software were generated at family and genus taxonomic levels and projected onto future climate conditions generated from the HadCM3 model scenarios A2A and B2A for the years 2020, 2050 and 2080. In each case models were evaluated using 30% of the data that were available as 12 point samples or more and other parameters were kept as default in the programme. For each taxon, 25 replicates were built from which the best 10 models with highest AUC statistic, lowest training omission error and with a significant Binomial Test of Omission ($p \leq 0.05$) were selected to create consensus range maps. In turn consensus range maps were used to create richness and rarity maps for West Colombia under current and future climate conditions from which were selected a series of potential refugia of bird diversity on the basis of maximising diversity, minimising the difference between predicted and current conditions and selecting the areas where modelling was most robust. Predicted spatial patterns of diversity, differences and elevational patterns of diversity in West Colombia under climate change conditions were sensitive to the biodiversity index used, taxonomic level, avian subset and scenario used to generate predictions. For both indices, areas with the highest scores under future climate conditions were in or adjacent to the main mountain ranges. Under future climatic conditions, in West Colombia, richness is predicted on average to decrease, while rarity is expected to increase. This pattern was particularly evident when comparing current conditions to the most severe and/or distant in–time scenarios (B2A–2080, A2A–2050 and A2A–2080). Furthermore, bird richness under future climatic conditions is expected to be below values observed today at low and mid elevations, while it is projected to increase at high elevations. Otherwise, richness follows a humpback–shaped curve and rarity describes a slight sigmoidal curve. Rarity in future climatic conditions is predicted to decrease at low elevations, while it is predicted to increase at mid and high elevations. It is interesting to note that differences to current conditions were far clearer when modelling rarity. Thus, we observed consistent statistically significant increments in scores under more severe and/or distant in–time scenarios (B2A–2050, B2A–2080, A2A–2050 and A2A–2080). Both for family and genus level richness, potential refugia appeared

in the upper Tropical, Subtropical and Temperate zones between $\approx 1,000$ – $3,000$ m of elevation and in some areas in the Pacific and Caribbean lowlands. In contrast, family rarity areas tended to concentrate in the Temperate and Paramo zones, above $\approx 2,500$ m of elevation, although some appeared below that elevation, whilst at genus level potential refugia occupied mainly the upper Tropical and Subtropical zones and areas in the lowlands, particularly in the Pacific Region, where they appeared more extensively than in any other case. Interestingly, selected areas were usually more restricted at the genus level, although this pattern varied between avian subsets. Although, modelling exercises conducted in this study advance biodiversity science in the country, the analyses have limitations due to particular assumptions made during the modelling process. Results from this study suggest developments are needed in three main directions. First, advances in model sophistication are required, increasing both taxonomic and geographical scale, and integrating intra- and inter-population processes. Second, it is essential to decouple past and future impacts on biodiversity in Colombia in order to understand their potential interactions in future scenarios. Third, it is vital to use knowledge gained from scientific research on the impacts of climate change to plan, implement and feedback integrated conservation strategies.

6.1. Introduction

In addition to the direct impacts that human activity has produced on landscape biodiversity, the increment in the atmosphere of greenhouse gases and aerosols is warming up the globe at rates not seen ever before in the last 10,000 years (Hannah *et al.*, 2006). In general, in the earth-atmosphere system, total incoming energy from the sun is roughly balanced by outgoing energy from the system, and any factor affecting that balance potentially may affect climate (Albritton *et al.*, 2001). Radiative forcing, defined as the net radiative energy available in the system, may change due to three main reasons (Albritton *et al.*, 2001). First, as a response to concentration in greenhouse gases such as water vapour, carbon dioxide, ozone, methane and nitrous oxide, which create resistance to outgoing radiative energy increasing available radiative energy in the system. Second, as a response to concentration of different type of aerosols, either anthropogenic as those resulting from fossil fuels combustion or natural as those resulting from volcanic eruptions, which depending on its constitution may have different effects on radiative forcing, although in general it is negative. Third, because of cyclic variations in the earth's orbit, which cause changes in the incoming radiative energy from the sun. As consequence, during the next 100 years and beyond, human activities are expected to generate massive increments in temperature and changes in the hydrological cycle, which may have profound effects in global biodiversity, probably worse than those already seen if all stressors and causes of loss of biodiversity interact and impact on biodiversity synergistically (Hannah *et al.*, 2006).

Current climatic trends indicate that climate change effects are very likely under way (Hannah *et al.*, 2006). Different sources of evidence show increments in temperature during the last century and more intensively in the last 30 years (Hulme, 2006). Changes generated also include variation of the hydrological cycle in different regions and change in pattern of large-scale climatic phenomena such as El Niño–Southern Oscillation and the Northern Atlantic Oscillation (Hulme, 2006). In addition, extreme climatic events have become more frequent and severe in some regions, although it has been difficult to confirm it statistically in some areas (Hulme, 2006).

Models of future conditions and biodiversity allow exploration of possible climate change scenarios and their impacts on biodiversity as well as the possible solutions to its effects (Hannah *et al.*, 2006). General Circulation Models (GCM) are built based on complex mathematical equations describing the physical laws governing the redistribution of incoming radiative energy from the sun among major climate system components such as the earth's surface, the atmosphere and the oceans and its subsequent effects in climate (Albritton *et al.*, 2001). Paleoclimatic research has showed that regional changes in the past have been sometimes extreme and fast, on the order of 10 °C in few decades, while global changes, usually related to deep ocean circulation, have been of lower magnitude and occurring in much longer periods of time (Hannah *et al.*, 2006). In this sense, GCMs for future climate conditions predict changes of about 6 °C for the year 2100 (Root & Hughes, 2006). If we consider that the last 11,000 years have been unusually warm and stable, a change in conditions as suggested means that biodiversity will face conditions with no precedent in the recent geological past (Hannah *et al.*, 2006). This will represent in evolutionary terms a real adaptive challenge, more so if we consider the disproportionate speed at which this change may occur.

On the other hand, knowledge on the geographical range and ecophysiology of different species has been used to study biodiversity in relation to current climate conditions and then generate projections of it under future climates, aiming to understand the possible impacts of climate change on biodiversity (Hannah *et al.*, 2006). In this context, in its simplest form, effects on global vegetation have been studied using correlative models, and projecting known biome limits and plant types ecophysiological responses to GCM climates (Hannah *et al.*, 2006). Additionally, more complex Dynamic Global Vegetation Models (DGVMs), which connect land vegetation dynamics to major biogeochemical planetary cycles such as the water and carbon cycles have been developed (Bachelet *et al.*, 2003). Modelling both individual and population processes such as photosynthesis, transpiration, competition, growth and disturbance regimes (Sitch *et al.*, 2003). The models use plant functional types (PFT) rather than species due to the obvious difficulty in gathering and processing data at species level for continental or global scales (Thuiller *et al.*, 2006). Most of

these models predict temperate forest will move northward, while some areas in the tropics are expected to shift from humid forest to savannah (Hannah *et al.*, 2006). However, both biological (*i.e.* PFT) and geographical ($\approx 0.5^\circ \times 0.5^\circ$) resolution of these models is very coarse, limiting their usefulness. Furthermore, there is still a lack of studies connecting DGVMs with more detailed models of geographical range shifts at higher biological levels, and in turn linking those to ecosystem functional diversity (Thuiller *et al.*, 2006).

Furthermore, to model biodiversity at higher scales, both taxonomically and geographically, GCMs have been downscaled (62,500–160,000 km² to 100–2,500 km²) using diverse methodologies, and applying different habitat suitability or niche modelling techniques predicting possible shifts in range due to climate change (Hannah *et al.*, 2006). In general, these techniques combine species data with environmental layers and use different statistical methods to generate probabilistic surfaces, which reflect how suitable a particular set of environmental conditions is for the given taxon (Graham *et al.*, 2008). Thus, in the last 20 years different modelling techniques that use either only–presence or presence–absence data to predict species geographical ranges have emerged. Some of the most used in the literature are for instance BIOCLIM (Nix, 1986), DOMAIN (Carpenter *et al.*, 1993), GARP (Stockwell & Noble, 1992; Anderson *et al.*, 2002a; Anderson *et al.*, 2002b; Stockwell & Peterson, 2002; Anderson *et al.*, 2003), MAXENT (Dudik *et al.*, 2004; Phillips *et al.*, 2004; Phillips *et al.*, 2006), and Logistic Generalised Linear Models (GLM) and General Additive Models (GAMs) implemented in GRASP (Pearce & Ferrier, 2000; Guisan *et al.*, 2002; Lehmann *et al.*, 2002, 2003), *etc.* Models generated using those techniques hint at possible impacts on biodiversity as well as provide explicit spatial projections of biodiversity that can be used for conservation planning (Hannah *et al.*, 2006).

Changes in biodiversity due to climate change are already underway and there is a strong body of evidence of changes occurring in ranges, phenology and physiology of different species (Hannah *et al.*, 2006; Thuiller *et al.*, 2008). For example, it has been documented that some ranges have shifted towards the poles, and a few towards the equator, while, at the local scale, increments in temperature have resulted in increments in abundance of low latitude species and declines in high latitude species (Parmesan, 2006). In this sense, Parmesan & Yohe (2003) in a global meta–analysis of the effects of climate change including more than 1,700 species from diverse groups and regions found that ranges are moving on average 6.1 km per decade towards the poles. In another study, Devictor *et al.* (2008) while evaluating the impacts of climate change on bird communities in France evidenced changes in composition as far as 91 km northward, whilst they found increments in the temperature as far as 273 km northward. This suggests according to the same author that although communities are responding to climate change, their reaction is not immediate and there is a time

lag involved. More recently, Feehan *et al.* (2009) assessing the impacts of climate change on European plants and animals found that plants are expected to shift several hundred kilometres in range and that nearly 60% of mountain species are predicted to become extinct by the year 2100. The same study found that breeding birds are expected to move their ranges about 550 km northeast and nearly 9% of mammals will face extinction. Additionally, Zalakevicius *et al.* (2009) predicting impacts of climate change for the 21st century in Lithuanian birds confirmed a general shift in ranges in a northeastern direction, and established that 17 of 49 species currently protected in Special Protected Areas will likely lose all suitable habitat and become extinct. Consistency in resulting patterns from different studies at local and regional scales, such as those mentioned, suggest a general global tendency (Parmesan, 2006).

On the other hand, climate change has already generated some changes in the synchronisation of different events of plants and animals life cycles. Thus, following increments in accumulated temperatures in mid- and high-latitude regions, spring phenological events are starting earlier in the season and finishing later in the autumn, extending the breeding season in many species (Root & Hughes, 2006). For instance, Parmesan & Yohe (2003) reported spring events are starting on average 2.3 days earlier per decade for a variety of taxa. Root *et al.* (2003, cited in Root & Hughes, 2006), in another global meta-analysis of 64 studies including 694 taxa from diverse groups, determined that phenological events between 1951–2000 started a minimum of 24 days earlier and finished a maximum 6 days later per decade. Additionally, reporting advancement in 5.3 days per decade in average of some phenological events such as blooming and breeding. Moreover, Feehan *et al.* (2009) found evidence that Spring and Summer are starting on average 2.5 days earlier per decade. The same authors argue that animal life cycles are starting earlier, especially in high-latitude regions, including frogs spawning, arrival of migratory birds and butterflies and bird nesting. Extra breeding events due to reported season lengthening may lead either to population explosions or population crashes depending on how synchronised the breeding events and resource availability are in the season (Root & Hughes, 2006; Feehan *et al.*, 2009). Furthermore, greater impacts are expected in high-latitude regions and in high mountains, where it is projected that major variations in temperature and precipitation will occur (Root & Hughes, 2006).

Documented changes on biodiversity due to climate change appear smaller than impacts generated by processes such as deforestation and fragmentation (Parmesan, 2006). In fact Loiselle *et al.* (2010) measured effects of past deforestation and future climate on the spatial distribution of environmental conditions in the “Mata Atlantica” and within the range of 21 bird species confirming this idea. Among their main findings, they evidenced that deforestation resulted in a decrease of 78–93% of suitable habitat for the bird species studied and that, overall, the forest changed to

wetter and less seasonal environmental conditions, whilst they are expected to become drier and less seasonal in future climate conditions. Moreover, results also showed that changes in environmental conditions due to deforestation were larger than shifts in conditions predicted by climate change. Continued climate change can reshape biotic interactions and destabilise communities, inducing major biome replacements (Parmesan, 2006). Furthermore, changes in the future may be even greater than expected due to the synergistic effects between different causes of biodiversity loss (Hannah *et al.*, 2006).

Potential impacts from climate change represent a major challenge *per se* for conservation science and practice. Conservation needs to change its approach from protecting and preserving particular species or portions of biodiversity *in situ* to preserving ecological and evolutionary processes in the long term (Hannah *et al.*, 2006). In expected future environmental conditions that can be secured by a continuous monitoring and coordination between reserve areas, aiming to facilitate incoming changes, while preserving processes (Hannah *et al.*, 2006). Studies investigating potential impacts of climate change on future biodiversity are essential to making the best informed choices for conserving biodiversity and its values. Particularly, studies decoupling past and future disturbances, since they permit a better understanding on the effects of different causes of biodiversity loss (Loiselle *et al.*, 2010).

Ideally, the facilitation of changes may be visualised as a contribution to processes of migration and dispersal, although the consequences from changes in community assemblages are largely uncertain (Parmesan, 2006). According to Hannah *et al.* (2006), conservation science and practice need to focus in two main directions: first in generating conservation strategies to facilitate ecological inter-community processes, and second in limiting greenhouse gas levels in the atmosphere to concentrations that will not trigger changes of such a magnitude eliciting extreme conditions threatening biodiversity survival. Furthermore, according to the same authors, climate change integrated conservation strategies (CCS) include: addition of new protected areas to secure biodiversity protection in current and future conditions, create connectivity between large portions of different types of ecosystems and the different land uses within they are embedded, and coordinating and monitoring management actions taken at regional scales.

Despite the fact that climate change is recognised as an important and direct cause of loss of biodiversity in Colombia, still research on the potential impacts of it is relatively scarce, which indeed constitutes an indirect cause of loss of biodiversity. At the national level in Colombia several direct and indirect causes of biodiversity loss have been identified (Chaves & Arango, 1998). The following are listed as direct cause of biodiversity loss: 1) transformation and fragmentation of natural habitats and ecosystems, 2) exotic species introduction, 3) overexploitation of natural

resources, 4) pollution, and 5) global climate change. The indirect causes include: 1) poor knowledge of potential uses of biodiversity, 2) the land tenancy scheme, 3) low scientific and technical institutional capacity, 4) low governmental capacity to control activities, which cause environmental degradation, and 5) lack of economic valuation systems for biodiversity and finally, the inadequate redistribution of biodiversity use related profits.

Thus, the objectives of this chapter are: 1) to present climate–change driven projected changes in avian diversity in West Colombia, addressing its spatial patterns and evaluating differences to diversity under current conditions overall and in Approximate Equal Surface Interval Bands (AEQSIB) in the elevational gradient of the country; and 2) to project, based on resulting maps, potential refugia for avian diversity, trying to select areas where: a) projected diversity is high, b) the raw difference between the modelled scenarios and current condition maps is minimised (*i.e.* areas that will remain climatically stable), and c) the differences between scenarios and current conditions appear to be most robust between reference and models.

6.2. Methodology

6.2.1. Avian diversity maps

Richness and rarity maps produced during the second generation of habitat modelling exercises (Chapter 5, section 5.2.4) were used in this new chapter as the main input for analyses. Thus, as a reminder, habitat suitability models were generated at family and genus hierarchies using MAXENT version 3.2 and two different datasets filtered from the Darwin–Hernandez Database (BioMap–BasicFilHP_v2³³, BioMap–BasicFilHP_v2_1950³⁴). Bird datasets were prepared as *.cvs files and BioClim variables at 1 km aggregated at 3 km; and averaged, except for precipitation related variables which were summed. Previously to run the models a PCA was performed in ENVI 4.3 for the 19 BioClim variables clipped to northern South America and Panama. Accordingly, those variables explaining most of the variation and exhibiting the lowest correlation within the temperature and rainfall related variables subgroups (BIO1, BIO2, BIO3, BIO12, BIO13 and BIO14; see Table 5.2.4.1.2 for more details) were selected. Models were run for all taxa having at least 5 site localities, using 30% of the observations to evaluate model performance when taxa had at least 12 site

³³ BioMap–BasicFilHP_v2: 141,140 accessions retained. Deleted records with uncertain and non–continental localities, and incomplete taxonomy plus deleted records with localities in areas with average slope > 5% and collection–event horizontal error > 2 km.

³⁴ BioMap–BasicFilHP_v2_1950: 69,059 accessions retained. Same as BioMap–BasicFilHP_v2 plus deleted accessions with incomplete recorded date of collection or collected before 1950.

localities, and not performing any evaluation below that threshold. Duplicate presence records were removed in each run and all other parameters were set to MAXENT default values. Models were produced using a mask for Colombia and projected to north South America and Panama for current climatic conditions and under expected climate conditions generated by the HadCM3 model, scenarios A2A and B2A for the years 2020, 2050 and 2080 (Nakicenovic *et al.*, 2001). For each modelled taxon, 25 replicates were run and all resulting maps were produced at 3 km grain size.

Consensus geographical range were produced using a variation of the “best models subset” methodology (Anderson *et al.*, 2003). Thus, for each taxon a “best models subset” of 10 models from the 25 replicas generated in each case was selected. The subset included models with the highest AUC values, lower intrinsic omission error and with significant probabilities for the Binomial Test of Omission ($p \leq 0.05$). It is important to highlight that not in all cases was it possible to have a subset of 10 models, in those cases the best performing models or model was/were selected. Finally, selected raw MAXENT result maps were imported into PCRaster and processed using batch files to reclassify the maps using the equal test sensitivity and specificity (ETSS) threshold of logistic probability and thus generate presence/absence maps and afterwards sum consensus maps to obtain final richness maps.

Additionally, consensus potential range maps were used as the basis for estimating rarity using the “weighted endemism score” (Crisp *et al.*, 2001). This index was calculated by adding all range maps as was also done for plain richness, but first weighting the value of each cell where each taxon is present by the inverse of the projected geographical range (*i.e.* $1 / \text{range size}$). For this purpose, several batch files and one dynamic PCRaster model were written to produce a map stack for all taxa and report the total number of pixels occupied by each taxon to a text file (*.tss). This information was later used to weight the value of each cell where each taxon was present, dividing in each case its corresponding potential range map by the total number of pixels projected as present in northern South America; the total extent at which MAXENT modelling was performed. Finally, the “weighted endemism score” map was calculated adding through all weighted potential range maps at both family and genus levels.

All resulting diversity maps were masked to Western Colombia (WC) to be used in subsequent analyses. Western Colombia is defined here as the half of the country north and west from the Eastern Cordillera and eastern slope isocline above 500 m of elevation.

6.2.2. Expected changes in avian diversity under climate change scenarios

As was mentioned in the previous section, MAXENT models were generated using two different datasets derived from the Darwin–Hernandez database (BioMap–

BasicFilHP_v2 and BioMap–BasicFilHP_v2_1950). Both consist of accessions with complete taxonomy and locality data with the highest certainty and precision according to estimation of error and the filtering process conducted in this thesis to improve the quality of the information (Chapter 4). They represent two different subsets of information in time. The first one includes late collections from the 19th century and collections from the early 20th century taken by several U.S. natural history museums. Explorations were extensive until the Second World War (WWII) post-war period, with two major peaks in the 1910s and 1940s (Verhelst *et al.*, unpublished data). These contributed greatly to improving the knowledge of the avian diversity of the country, since they were careful in describing with fair detail the localities of collection, something that was in need for the country. The second dataset discarded those collections and only included more recent information of specimens collected post 1950 (inclusive), and thus data volumes plummeted from 141,140 to 69,059 accessions. Nonetheless, this dataset still contains invaluable information of the latest collections taken by U.S. natural history museums and all the collections taken by the national natural history museums (Verhelst *et al.*, unpublished data). Modelling bird diversity using these two datasets aimed to detect any signal regarding impacts of climate change during the period before 1950. However, results from modelling experiments indicated that the second dataset was incomplete in relation to the first (Chapter 5, section 5.4.3.1). Additionally, this suggests that land use change may have been a more significant driver, and therefore it is not possible to be conclusive regarding changes produced in bird diversity during that period, as a result of climate only.

In this context, diversity maps generated in this thesis are representations of the potential bird diversity that may have existed in the country from nearly a century ago, and that still may exist in relatively undisturbed areas in West Colombia. However, it is important to note that climatic changes from pre 1950 may have induced shifts in diversity distribution, as would land use changes, which are suspected have been particularly extensive in the western half of the country (Kattan *et al.*, 1994; Renjifo, 1999). Accordingly, future projections constitute not absolute but possible “potential bird diversity scenarios” in Colombia under climate change, certainly limited by assumptions made during the modelling process (Chapter 1, section 1.6). We believe their value lies in the fact that they are spatially explicit hypotheses of the possible changes it may occur in bird diversity in the country during the next century, and may thus inform conservation planning.

Differences in avian richness and rarity in West Colombia (WC) between future projections and current conditions were assessed in three different ways. First, maps of temporal differences were produced by subtracting from each scenario and year map combination the MAXENT–modelled map based on current conditions. These differential maps were examined visually to reveal the spatial distribution patterns of

potential changes in bird diversity in the country. Second, in PCRaster a cartographic model to select 496 points at random from WC was implemented and values extracted from both MAXENT–modelled maps and from maps generated using the “Western Hemisphere Digital Bird Distribution Database – WHDBD Database” (Ridgely *et al.*, 2007, see Chapter 5, section 5.2.4.5), with values written to a text file in each case (*.txt). Text files were imported into Excel and prepared for analysis in the statistical package SPSS (SPSS, 2007). Temporal differences in richness and rarity maps were investigated using multifactor ANOVAS. Furthermore, as part of these analyses we included the estimation of descriptive statistics, confidence intervals for the means, Homogeneity Tests for the variance and several *Post Hoc* multiple comparisons (Chapter 5, section 5.2.4.5). These are common parametric tests easy to apply and interpret, and for this reason were selected to explore the observed differences in diversity. Moreover, confidence intervals for the means were plotted to explore graphically the differences in diversity between the future scenarios and current conditions. Finally, temporal differences in richness and rarity were explored using “approximately equal surface interval bands” (AEQSIB) to evaluate potential changes in diversity across the elevational gradient of the country (see Chapter 5, section 5.2.4.5). Thus, a simple algorithm was implemented in PCRaster using a series of batch files, cartographic models and all the individual geographical range maps to determine the total number of taxa in AEQSIBs of approximately 10,000 km² with results written to *.txt files. Additionally, averages and total sums for both richness and rarity were produced in bands. Text files were imported into Excel and prepared for analysis in the statistical package SPSS (SPSS, 2007). The altitudinal pattern for the different variables was plotted and differences in richness and rarity in AEQSIB maps were investigated using the non–parametric Test of Wilcoxon.

6.2.3. Potential refugia of bird diversity

Due to differences evidenced between modelled (MAXENT) and reference (WHDBD) maps under current conditions (see Chapter 5, section 5.3.4.4) it was decided to focus on defining potential bird diversity refugia under climate change scenarios, whilst exploring the robustness of temporal changes in avian diversity rather than to focus only on the projections of richness *per se*. For this purpose, for each scenario and year combination an index called the “differential ratio index” was produced. This index indicates the magnitude of the divergence and the direction of the difference between scenario and current condition (baseline) maps, when estimated separately with both modelled and reference maps (see Equation 6.2.3.1). This equation has the disadvantage that when both differences are negative, *i.e.* both numerator and denominator are negative, resulting quotient is positive; reversing the direction of the differences observed. To avoid this caveat the equation was implemented in a cartographic model in PCRaster, and using a simple algorithm

instructed to assign a negative result in cases when both differences were negative. Otherwise, the ratio becomes negative if the difference between the scenario and the baseline, from MAXENT modelled current diversity (numerator) or WHDBD based current diversity (denominator), are negative. Hence, pixels with ratio values closer to one indicate areas where predicted diversity changes under future climatic conditions are more robust since differences between scenarios and the baseline diversity maps are more similar. On the other hand, negative values indicate areas where potentially diversity will decrease, whilst conversely positive values indicate areas where potentially diversity will increase.

$$DRI_{sc} = \frac{MAX_{sc} - MAX_{cu}}{MAX_{sc} - WHM} \quad (\text{Equation 6.2.3.1})$$

Where:

DRI_{sc} = differential ratio index for scenario sc

MAX_{sc} = diversity map, either richness or rarity, for scenario sc generated with MAXENT

MAX_{cu} = diversity map, either richness or rarity, for current conditions generated with MAXENT

WHM = diversity map, either richness or rarity, for current conditions generated with WHDBD Database

Following, a simple algorithm to select all areas that may represent bird diversity refugia in future climatic conditions was implemented in PCRaster. The algorithm was intended to select areas where: 1) the diversity was high, 2) the raw difference between the modelled scenario and current conditions maps was minimised, and 3) the differential ratio index was near optimal (*i.e.* values close to 1 or -1). For this purpose, a first batch file was written to export all A2A and B2A scenarios diversity maps for years 2050 and 2080, as well as maps of the raw difference between each particular scenario and year combination and current conditions as text files (*.txt). These files were imported into Excel and for diversity data the minimum, maximum and each quartile estimated. Similar statistics were calculated for the raw difference, although in this case it was performed separately for negative values (raw difference ≤ 0) and for positive values (raw difference > 0). Once having defined the quartiles, in a further step the following algorithm was implemented (Algorithm 6.2.3.1):

(Algorithm 6.2.3.1)

pcrcalc AvianDivRefugiaScore.map =

if ((Div.map ge "median") and (rawDiff.map ge "negative median" and rawDiff.map le 0) and ((DRI.map ge -1.5 and DRI.map le -0.5) or (DRI.map ge 0.5 and DRI.map le 1.5)))

```
then ((-Div.map/"maximum") - (rawDiff.map/"negative median") + DRI.map)  
else ( if ( (Div.map ge "median") and (rawDiff.map ge "positive minimum" and  
rawDiff.map le "positive median") and ((DRI.map ge -1.5 and DRI.map le -0.5) or  
(DRI.map ge 0.5 and DRI.map le 1.5)) )  
  then ((Div.map/"maximum") + (rawDiff.map/"positive median") + DRI.map)  
  else (0) )
```

Where:

.map = suffix to indicate PCRaster map file type extension

Div = prefix to indicate a particular diversity index, either richness or rarity in a particular scenario and year combination

rawDiff = raw difference between a particular modelled scenario and current conditions

DRI = differential ratio index for the particular diversity index treated

Otherwise, "median", "negative median", "maximum", "positive minimum" and "positive median" refers to the respective quartile of each specified map in the algorithm for which the operation is performed. In addition, are used in the equation the logical statements "if then", "if then else", greater than or equal "ge", lower than or equal "le", "and" and "or".

Thus, the algorithm in the first "if" logical statement evaluates three conditions: 1) which cells in the diversity map have values greater than the observed median³⁵ of the values in the map, 2) which cells of the diversity raw difference map between the scenario and the MAXENT modelled current map are negative and are greater than the median of the negative values in the map but smaller than zero, and 3) which cells of the DRI map have values nearer to the unity (1), either positive or negative (*i.e.* |1.5–0.5|). Once evaluated the logical statement the "refugia scores" map is generated (first "then" logical statement) and cells fulfilling the logical conditions receive as value the sum, as negative values, of the diversity (standardised by the maximum value in the map), the diversity raw difference (standardised by the negative median) and the DRI. Otherwise, the algorithm passes to the second set of logical conditions (first "else" and second "if" logical statements), where it addresses the same set of logical conditions as before but changing the second. Accordingly, it evaluates which cells of the diversity raw difference map between the scenario and the MAXENT modelled current map are positive and are greater than the minimum positive value and smaller than the median of the positive values in the map. Thus, cells fulfilling

³⁵ Medians were calculated separately previously in each case and just used the reported value in the algorithm.

these statements receive in the “refugia scores” map (second “then” logical statement) as new value the sum, as positive values, of the diversity (standardised by maximum value in map), the diversity raw difference (standardised by the positive median) and the DRI. In the final step, cells that did not fulfil any of these conditions received zero as value (second “else” logical statement). This algorithm was applied accordingly for both richness and rarity diversity indices at each taxonomic level (family and genus) and avian subset (all taxa, non–marine, forest and strictly forest) for the A2A and B2A scenarios years 2050 and 2080.

Finally, from the maps produced with the algorithm, those related to the forest avian subset for both taxonomic levels were imported into Arc View and a gap analysis conducted to define to what extent the National System of Protected Areas (SINAP by its acronym in Castellano) captures areas projected as potential bird diversity refugia. Thus, new maps for both richness and rarity were generated at each taxonomic level showing the total union and intersection of areas projected as potential bird diversity refugia (Boolean maps) through all scenario and year combinations. In turn these were overlapped with a SINAP polygon shape files (*.shp) to evaluate the approximate area (in pixels) that reserves capture from the potential bird diversity refugia. This allowed us to evaluate how the SINAP captures projected refugia in two extreme situations. First, when are considered altogether all areas projected and selected using each single scenario, and second, when are considered only the most robust areas, and therefore projected and selected in all scenarios. The SINAP polygon shape file was generated based on data for Colombia compiled by the World Database on Protected Areas – WDPA version 2010 (IUCN–UNEP–WCMC, 2010), excluding indigenous reservations, and adding some few new reserves digitised by Conservation International – Colombia (unpublished data), such as “Yariguies” and “Selva de Florencia”. Independently, a polygon shape file for the Indigenous Reservations System (SRI) was produced based on the WDPA data to perform the same analyses. In addition, to which degree private reserves such as those attached to RESNATUR³⁶ version 2004 (CI–Colombia, unpublished data) and ProAves Foundation version 2010 (ProAves, unpublished data) lie on potential bird diversity refugia areas defined in this study was also addressed. Differently to areas from the SINAP and the SRI, each reserve from RESNATUR and ProAves was represented by a single dot in independent point shape files for each organisation, since it was not available detailed cartographic information for all reserves. Shape files were used to extract values from the union and intersection maps of areas projected as potential bird diversity refugia. Representation in each case was estimated as the proportion of reserves that lie on a potential refugia spot.

³⁶ Civil Society Nature Reserves Colombian Network Association

6.3. Results

6.3.1. Expected changes in avian diversity under climate change scenarios

An overall assessment of the changes in diversity at national level in WC revealed that in average bird richness is expected to decrease, whilst rarity is expected to increase under future climate change scenarios (Table 6.3.1.1). However, there are some slight differences in tendency between avian subsets and scenarios. Richness tended to decrease in projections of more severe climatic change or those more distant in time (sequentially, B2A–2050, B2A–2080, A2A–2050 and A2A–2080). An exception to this pattern was observed in the all taxa avian subset at genus level, for which

Table 6.3.1.1. Map averages for richness and rarity in West Colombia for MAX-ENT–BioMap based modelled maps (model) through all taxonomic levels and avian subsets. Habitat suitability modelling: second generation.

Family richness					
Habitat subgroups	Current	B2A–2050	B2A–2080	A2A–2050	A2A–2080
All Taxa (AT)	46.1	40.7	37.7	37.7	38.1
Non Marine (NM)	44.0	38.2	36.4	36.5	36.1
Forest (F)	29.0	23.4	22.1	22.5	21.3
Family rarity ^{1,2}					
Habitat subgroups	Current	B2A–2050	B2A–2080	A2A–2050	A2A–2080
All Taxa (AT)	2.03	2.57	2.52	2.31	2.77
Non Marine (NM)	1.77	2.09	2.31	2.13	2.46
Forest (F)	1.18	1.51	1.76	1.62	1.86
Genus richness					
Habitat subgroups	Current	B2A–2050	B2A–2080	A2A–2050	A2A–2080
All Taxa (AT)	251.9	247.5	236.1	233.3	236.4
Non Marine (NM)	223.5	217.2	207.2	205.3	205.2
Forest (F)	196.2	193.6	181.1	179.8	179.8
Strictly Forest (SF)	180.6	180.0	167.7	166.5	166.4
Genus rarity ^{1,3}					
Habitat subgroups	Current	B2A–2050	B2A–2080	A2A–2050	A2A–2080
All Taxa (AT)	1.70	2.17	2.07	1.98	2.15
Non Marine (NM)	1.52	1.96	1.92	1.83	1.98
Forest (F)	1.34	1.79	1.76	1.68	1.82
Strictly Forest (SF)	1.25	1.69	1.66	1.58	1.71

¹ Weighted Endemism Score; ² values multiplied by 10⁴; ³ values multiplied by 10³

richness exhibited a slight increment in the harshest and most distant scenario (A2A–2080). Conversely, rarity increased under more severe climatic change projections. However, this increment was not held constant. Thus, initially, it increased for all subsets in the B2A–2050 scenario, following a decline in the B2A–2080 and A2A–2050 scenarios, except for the non–marine and forest subsets at family level. Finally, increasing again in the A2A–2080 scenario and reaching maximum values.

6.3.1.1. Spatial distribution patterns: areas of high diversity and differences

The two biodiversity indices exhibited relatively well–marked differences in their spatial patterns. Thus, plain richness showed slight differences between avian subsets and taxonomic levels. In general, areas of high richness appeared in all cases on the slopes of the Andean cordilleras and the Sierra Nevada de Santa Marta. At family level, areas with the highest scores tended to shrink slightly as richness was projected into more severe climate change scenarios farther away in time; sequentially, B2A–2050, B2A–2080, A2A–2050 and A2A–2080. This was particularly clear in areas below 1,000 m of elevation in the Sierra Nevada de Santa Marta, in the slopes below 2,000 in the Eastern Cordillera, in the head of the Magdalena valley, the mid and upper Cauca valley and its associated slopes, and some areas in the Pacific region (Figure 6.3.1.1.1). At the genus level this same tendency was maintained, although areas of high richness were even more restricted to the higher slopes and reduced noticeably in the Sierra Nevada de Santa Marta (Figure 6.3.1.1.1). In contrast, spatial distribution patterns for rarity were dissimilar between taxonomic levels and avian subsets, particular at genus level. At family level, very few areas of high rarity emerged in the Andes, with the exception of the B2A–2050 scenario that showed an extensive coverage in the Andes for the forest related avian subsets (Figure 6.3.1.1.2). On the other hand, at genus level, areas with high scores emerged more extensively than at family level in the Andes. Nevertheless, there were some interesting differences between the several scenario–year combinations. Thus, in the B2A–2050 scenario areas with the highest scores appeared extensively in all Andean ranges and the Sierra Nevada de Santa Marta, while they were greatly reduced and mostly confined to the Eastern Cordillera in the B2A–2080 scenario. Otherwise, in the A2A–2050 scenario areas for the non–forest related avian subsets appeared widely in the main mountains ranges above 2,000 m of elevation, whilst for the forest related subsets areas they were more restricted to the central Eastern Cordillera. Conversely, in the A2A–2080 scenario areas for the forest related avian subsets appeared widely in the main mountain ranges above 2,000 m of elevation, and more areas appeared in the Western Cordillera, whilst areas for the non–forest related avian subsets remained restricted to the highest zones of the cordilleras and the Sierra Nevada de Santa Marta (Figure 6.3.1.1.2). Raw maps of family rarity show the highest values in the mountains,

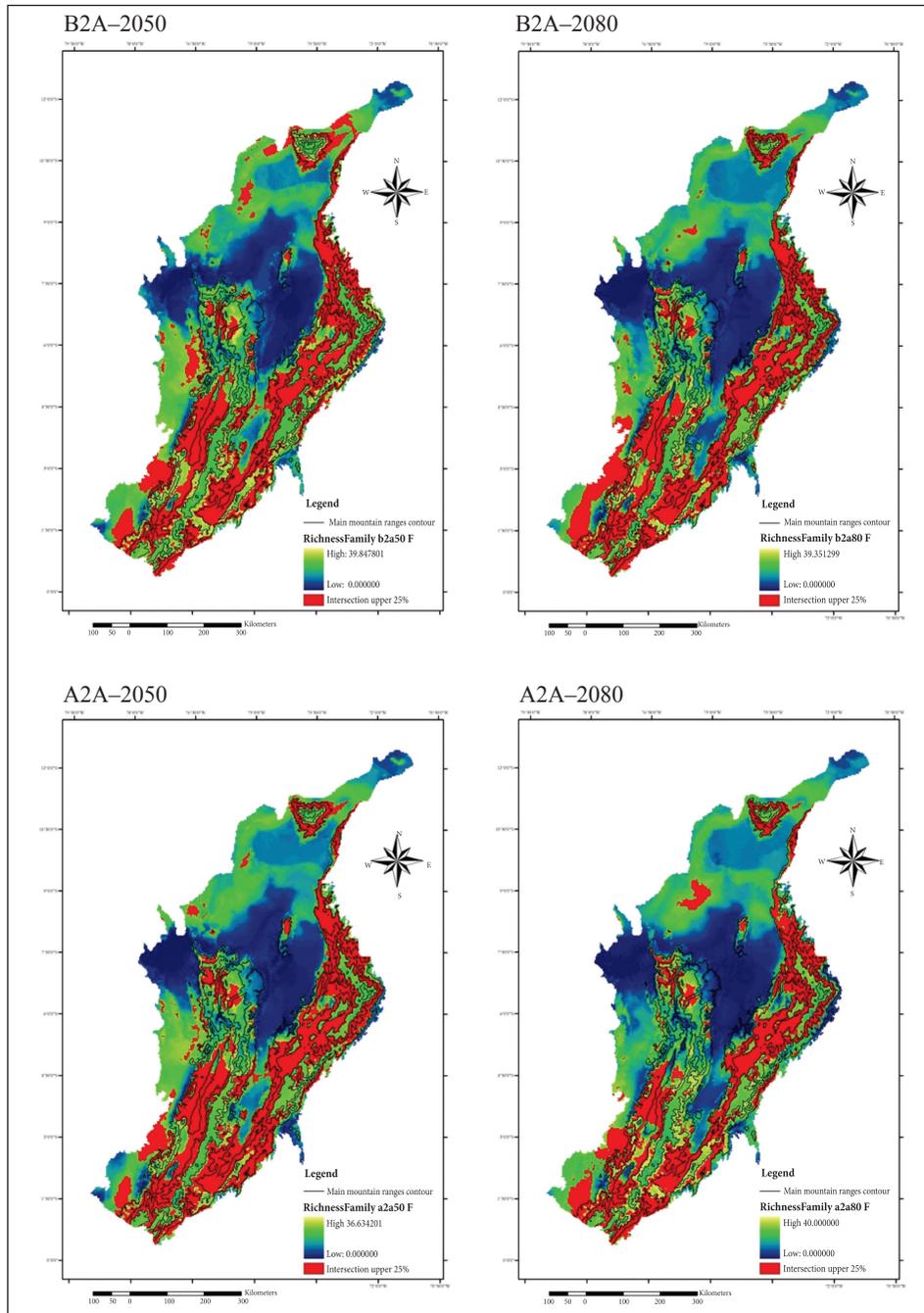


Figure 6.3.1.1a. Family richness projected in WC using MAXENT–BioMap under climate change scenarios. Richness maps for the forest avian subset. In all maps, red represents the intersection of areas within the highest 25% in range values through all avian subsets (all taxa, non-marine and forest).

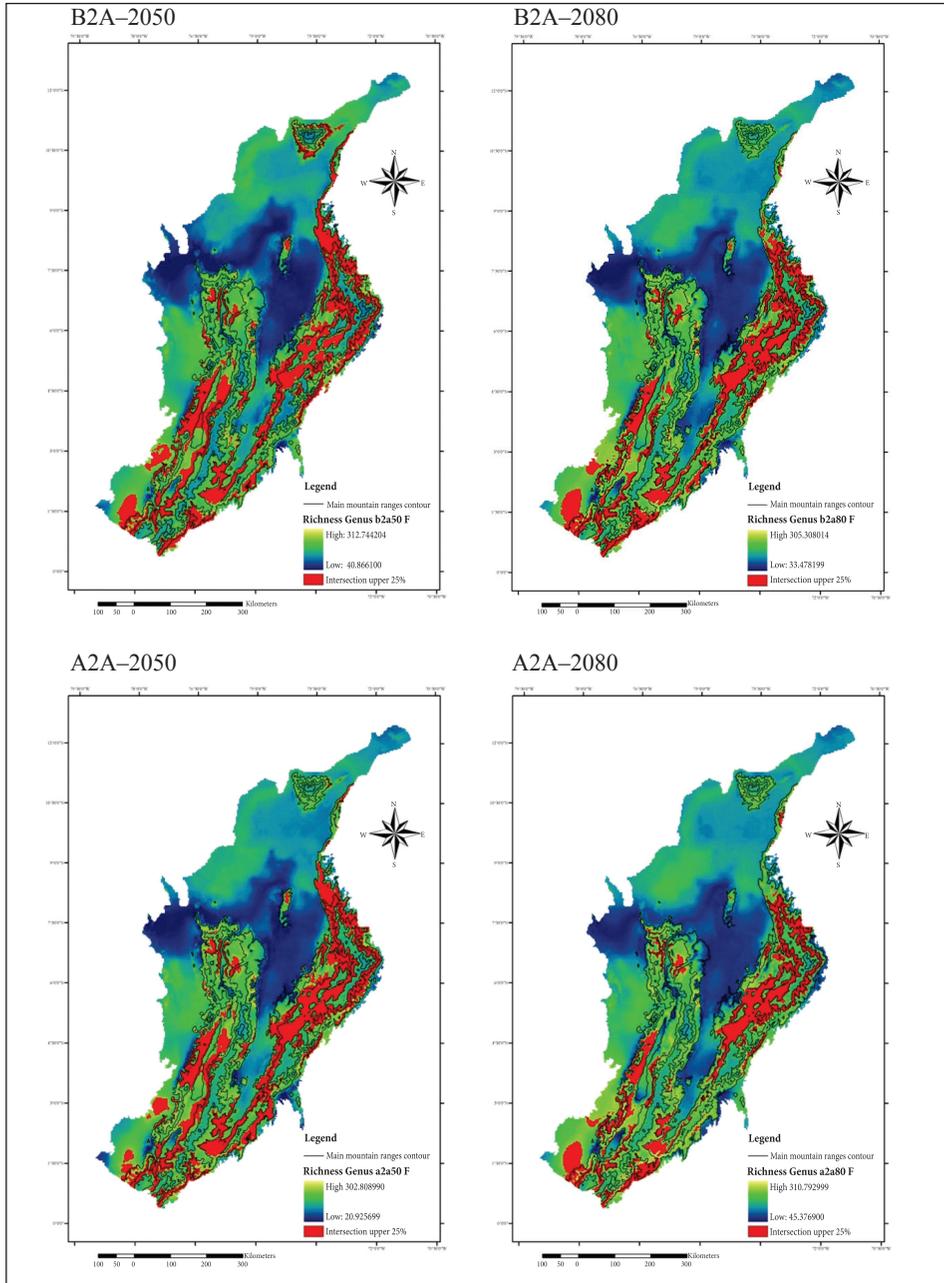


Figure 6.3.1.1.b. Genus richness projected in WC using MAXENT–BioMap under climate change scenarios. Richness maps for the forest avian subset. In all maps, red represents the intersection of areas within the highest 25% in range values through all avian subsets (all taxa, non–marine, forest and strictly forest).

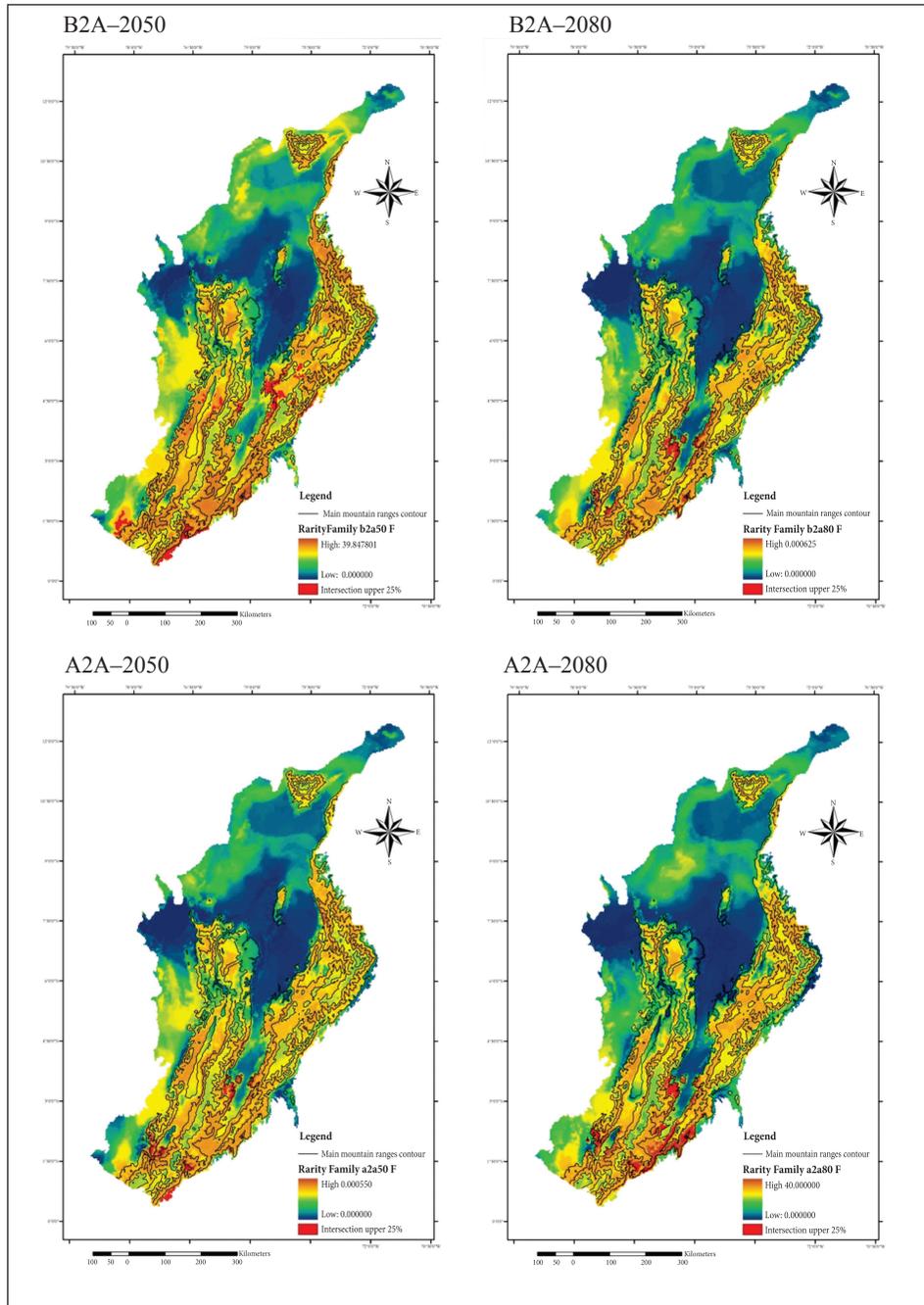


Figure 6.3.1.1.2a. Family rarity projected in WC using MAXENT-BioMap under climate change scenarios. Rarity maps for the forest avian subset. In all maps, red represents the intersection of areas within the highest 25% in range values through all avian subsets (all taxa, non-marine and forest).

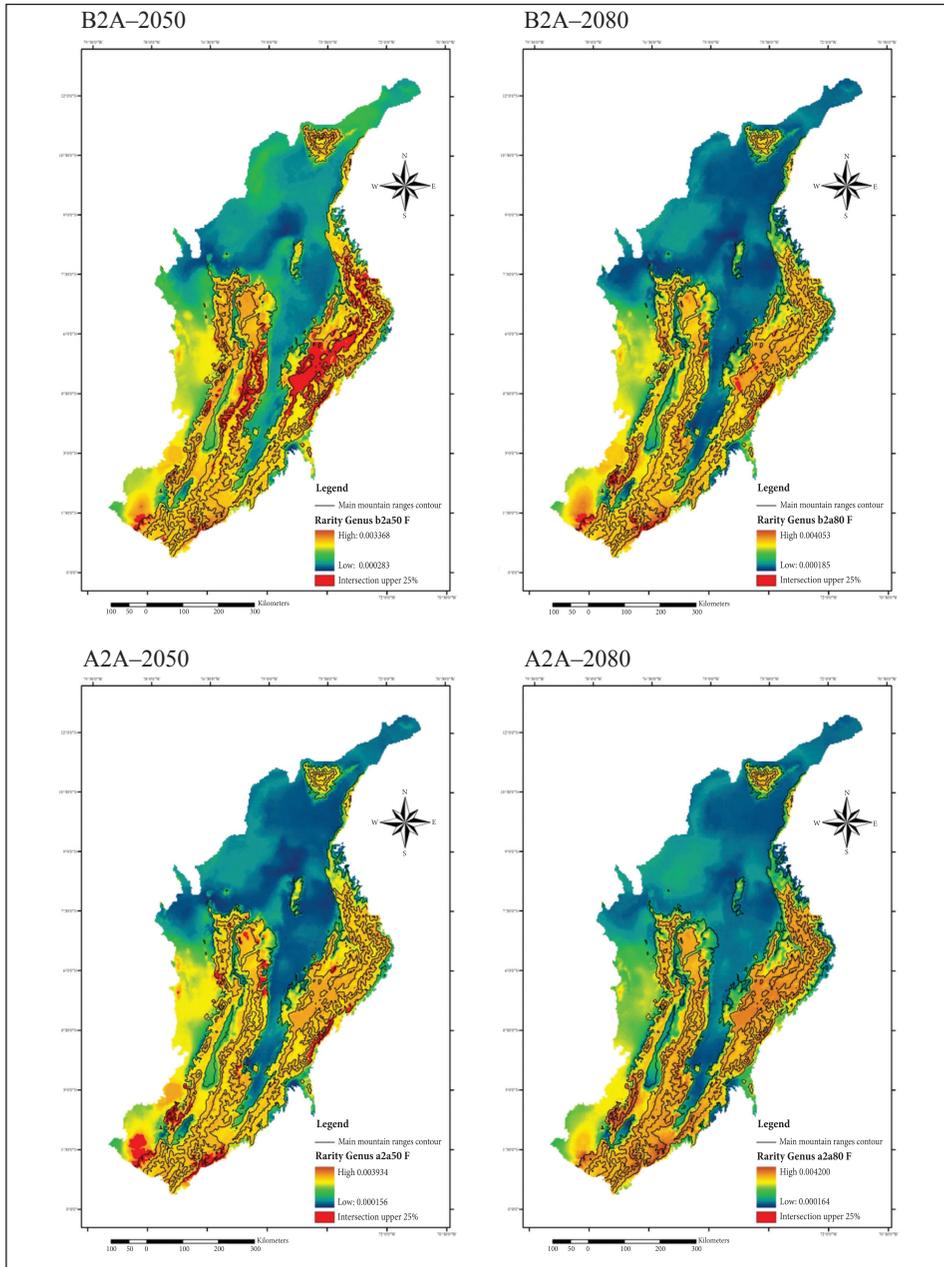


Figure 6.3.1.1.2b. Genus rarity projected in WC using MAXENT–BioMap under climate change scenarios. Rarity maps for the forest avian subset. In all maps, red represents the intersection of areas within the highest 25% in range values through all avian subsets (all taxa, non-marine, forest and strictly forest).

though few areas have scores within the highest 25% for each map. This is especially the case in more severe and/or more distant in–time climate change scenarios, which suggests that although in those scenarios the maximum value in maps increased, a major number of cells had values below the top 25% in the range for each map. Otherwise, at genus level although areas with high scores extended moderately over the Andes, especially over 2,000 m of elevation, areas of coincidence between avian subsets were limited and decreased when the more severe and/or distant in–time climate change scenarios were mapped.

6.3.1.2. Evaluation of differences using extracted points

When maps were sampled and tested statistically, observed differences in diversity were significant at both taxonomic levels (Three Factor ANOVA, $p < 0.05$; one test for each biodiversity index–taxonomic level, four in total). Nonetheless, there are several dissimilarities in the tendencies observed between biodiversity indices and taxonomic levels. In this sense, results at family level showed that estimated mean values of richness were higher in current condition (baseline) maps³⁷ than in future scenario maps through all avian subsets (Figure 6.3.1.2.1). Differently, at genus level the same was true only when comparing richness under current conditions to the most severe and/or distant in–time climate scenarios (B2A–2080, A2A–2050 and A2A–2080) (Figure 6.3.1.2.1). In addition, when used the data subset that retained only accessions collected post 1950, differences between current conditions and future scenario richness maps were significant at family level, and disappeared when comparing at genus level (Figure 6.3.1.2.1). It is important to highlight that in this case average richness estimations became more homogenous between scenarios and differences decreased slightly between avian subsets.

On the other hand, results at the family level showed that estimated mean values of rarity were higher in future scenario maps than in current conditions maps, except in the nearest scenarios (B2A–2020 and A2A–2020), through all avian subsets (Figure 6.3.1.2.2). Contrastingly, at genus level all future scenarios consistently exhibited greater values than current condition maps (Figure 6.3.1.2.2). Furthermore, when the data subset only retaining accessions collected post 1950 was used, the tendencies observed in differences between current conditions and future scenarios richness maps changed (Figure 6.3.1.2.2). Thus, at family level, for both all taxa and non–marine avian subsets, the most severe and distant in–time scenario (A2A–2080) showed average rarity values greater than current conditions. Other scenarios did not exhibit any differences or had even lower values than current conditions. Interestingly, the forest avian subset showed a more consistent pattern, as was observed before when using all accessions. For this

³⁷ In this chapter, referring just to the MAXENT–based modelled maps unless otherwise stated.

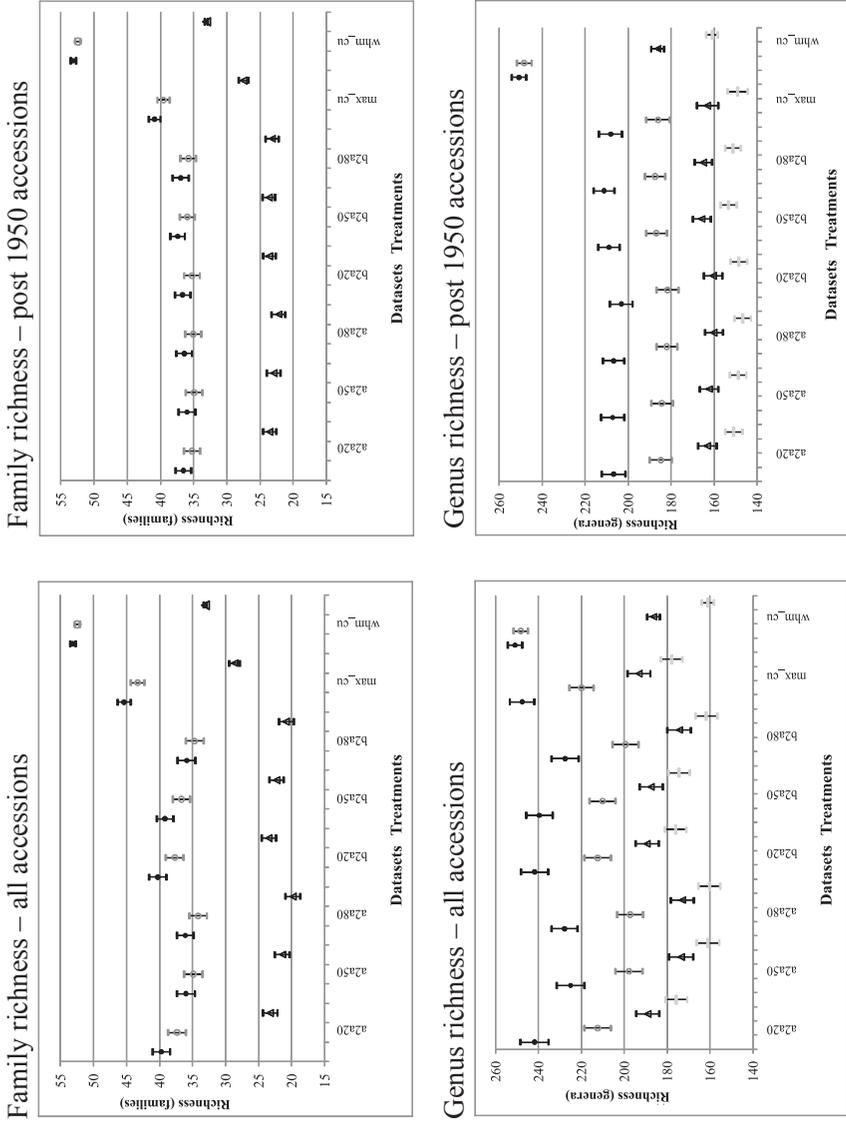


Figure 6.3.1.2.1. Family and genus richness projected in WC using MAXENT–BioMap under climate change scenarios. Confidence intervals for the mean at the 95% probability. Solid black circles (all taxa), open red circles (non-marine), open black triangles (forest), open green rectangles (strictly forest). Current conditions: max_cu (MAXENT), whm_cu (WHDBD). Scenarios: a2a and b2a years 2020, 2050 and 2080.

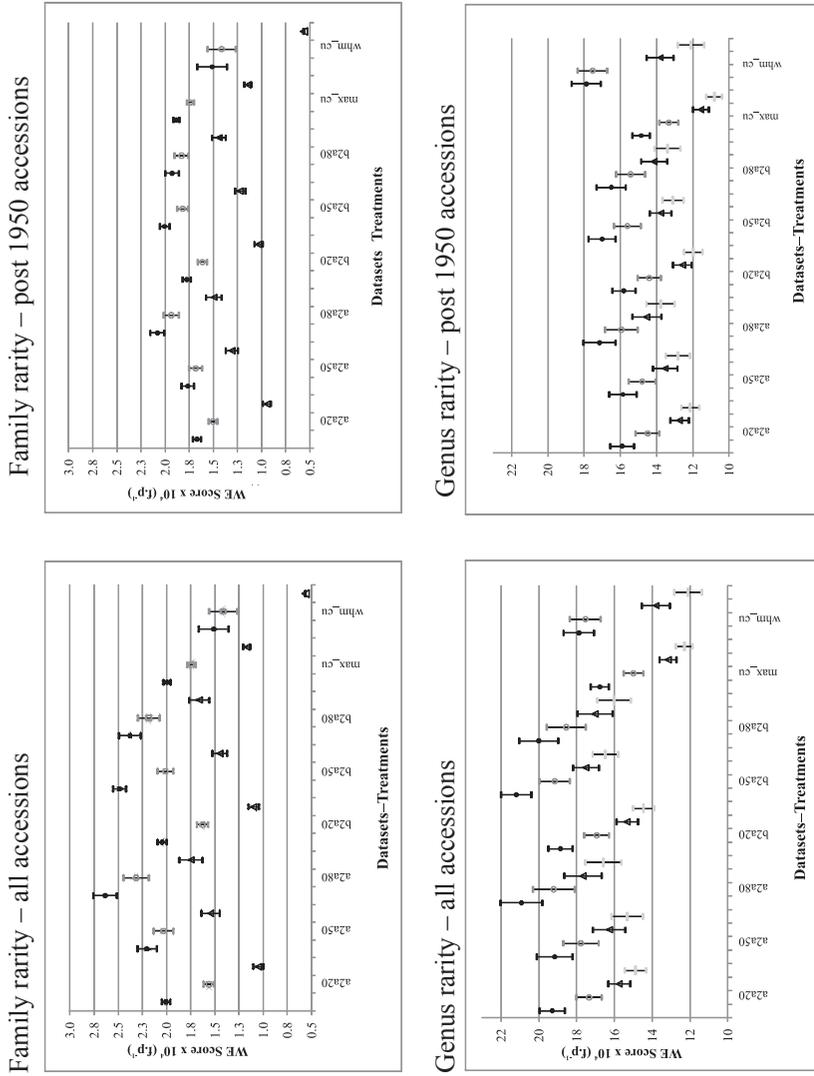


Figure 6.3.1.2.2. Family and genus rarity projected in WC using MAXENT+BioMap under climate change scenarios. Confidence intervals for the mean at the 95% probability. Solid black circles (all taxa), open red circles (non-marine), open black triangles (forest), open green rectangles (strictly forest). Current conditions: max_cu (MAXENT), whm_cu (WHDBD). Scenarios: a2a and b2a years 2020, 2050 and 2080.

last avian subset, the most severe and/or distant in-time scenarios (B2A–2080, A2A–2050 and A2A–2080) exhibited higher average rarity than current conditions maps, which in turn did not show differences in comparison to the B2A–2050 scenario and exhibited higher values than the nearest scenarios (B2A–2020 and A2A–2020). At genus level, tendencies were similar with the main difference that for both all taxa and for non-marine avian subsets average rarity in future scenarios was never lower than current conditions, whilst forest related avian subsets kept consistently the same pattern described in this same paragraph when using all accessions. Again, as noted previously, average rarity estimates became more homogenous between scenarios and differences decrease slightly between avian subsets.

6.3.1.3. Evaluation of differences using AEQSIBs

Plotting of total richness and total rarity in AEQSIBs permitted an insight into the potential elevational tendencies that both biodiversity indices may exhibit under some of the several possible future climate-change scenarios. In this sense, there was a general tendency for total richness at low and mid elevations to exhibit in future climate scenarios lower values of richness than current conditions, while at high elevations the opposite occurred and total richness in current conditions showed values below those observed for future climate scenarios (Figure 6.3.1.3.1). This general pattern varied slightly between avian subsets and taxonomic levels, and in most cases, the shift was observed around 1,500–2,000 m of elevation at family level, whilst it occurred at about 2,000–2,500 m of elevation at genus level (Figure 6.3.1.3.1). Additionally, it is important to highlight that observed differences between current conditions and future climate-change scenarios were easier to perceive at genus than at family level. On the other hand, when tested statistically, observed differences along the elevational gradient in total band richness were not always significant. Accordingly, scenarios A2A–2020, B2A–2020 and B2A–2050 were the most consistent in showing significant differences through all taxonomic levels and avian subsets (Table 6.3.1.3.1).

Contrastingly, total rarity exhibited an elevational distribution that is very different to the one observed for total richness for both current conditions and for future climate change scenarios (Figure 6.3.1.3.2). For the case of the scenarios, slightly decreasing initially and later increasing with elevation describing a humpback-shaped or a logistic curve depending on the taxonomic level and avian subset. However, it is interesting to note that in this case similarly as observed before for richness, total rarity showed a tendency at low elevations to exhibit in future climate scenarios lower values than under current conditions, while at high elevations this pattern was reversed. It is important also to add that the general pattern also varied slightly between avian subsets and taxonomic levels as noted before for richness

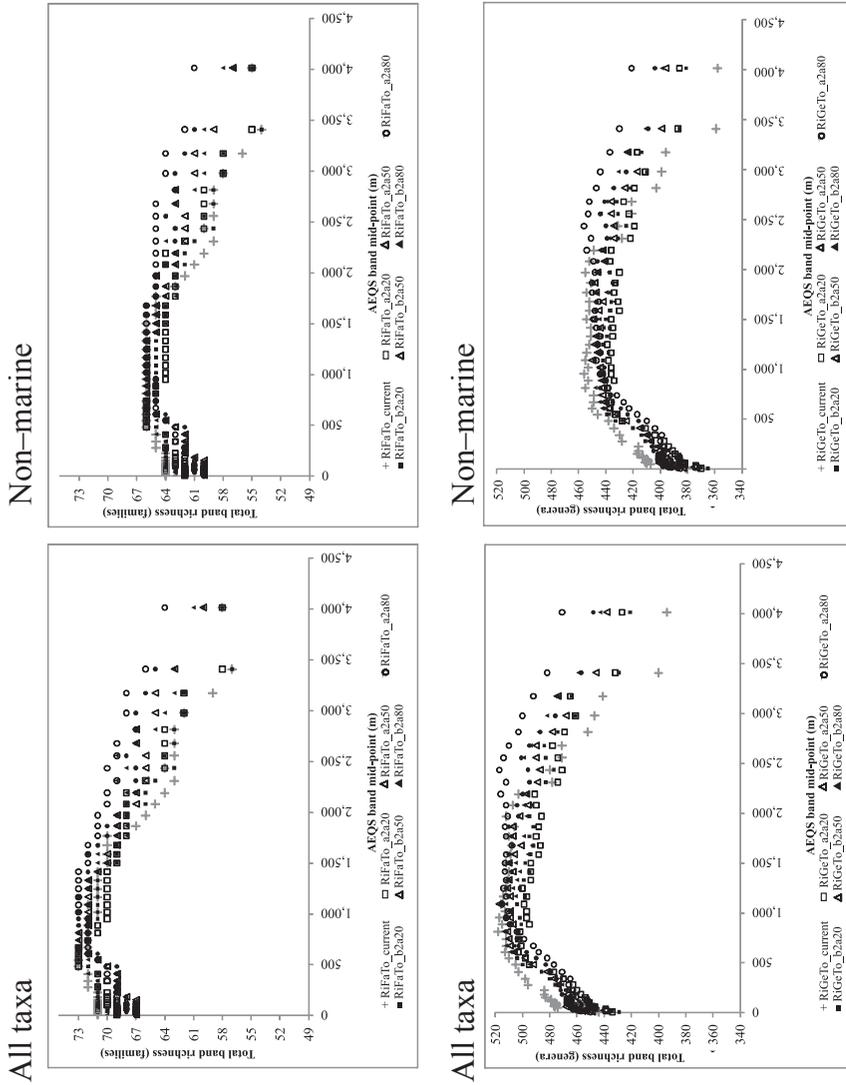


Figure 6.3.1.3.1a. Elevation gradient in estimated total family (RiFaTo) and genus (RiGeTo) richness when used AEQSiB in WC for current conditions maps and future climate change scenarios. Suffixes: _current, MAXENT models in current conditions; scenarios a2a and b2a; years 2020, 2050 and 2080. Models based on all accessions. All taxa and non-marine avian subsets.

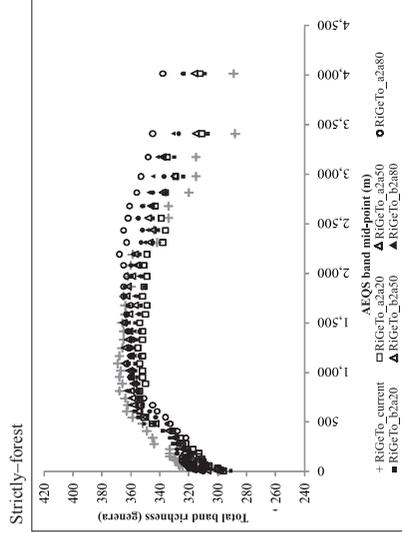
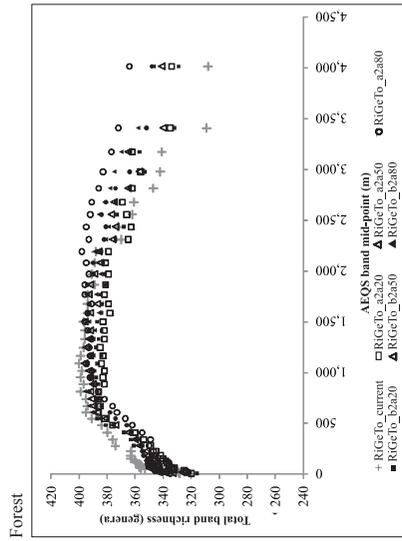
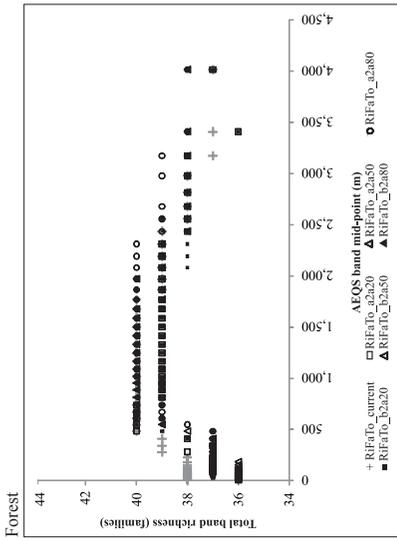


Figure 6.3.1.3.1b. Elevational gradient in estimated total family (RiFaTo) and genus (RiGeTo) richness when used AEOQSIB in WC for current conditions maps and future climate change scenarios. Suffixes: _current, MAXENT models in current conditions; scenarios a2a and b2a; years 2020, 2050 and 2080. Models based on all accessions. Forest and strictly-forest avian subsets.

Table 6.3.1.3.1. List of future climatic scenarios that exhibited significant differences in relation to current conditions MAXENT-based model maps (Wilcoxon Test, $p < 0.05$), both for total richness and total rarity in AEQSIBs through all taxonomic levels, data subsets and avian subsets in the elevational gradient of WC.

Total richness* in bands						
	Scenarios					
	A2A-2020	A2A-2050	A2A-2080	B2A-2020	B2A-2050	B2A-2080
Family – all taxa	X				X	
Family – non-marine	X	X		X		
Family – forest	X	X	X	X	X	X
Family 1950 – all taxa	X		X	X		
Family 1950 – non-marine	X			X		
Family 1950 – forest	X			X	X	
Genus – all taxa	X			X	X	
Genus – non-marine	X	X		X	X	X
Genus – forest	X			X	X	
Genus – strictly forest	X			X	X	
Genus 1950 – all taxa	X			X	X	
Genus 1950 – non-marine	X	X	X	X	X	X
Genus 1950 – forest	X			X	X	
Genus 1950 – strictly forest	X			X	X	
Total rarity** (sum) in bands						
	Scenarios					
	A2A-2020	A2A-2050	A2A-2080	B2A-2020	B2A-2050	B2A-2080
Family – all taxa		X	X	X	X	X
Family – non-marine	X	X	X		X	X
Family – forest	X	X	X		X	X
Family 1950 – all taxa	X		X		X	X
Family 1950 – non-marine	X		X		X	X
Family 1950 – forest	X	X	X	X	X	X
Genus – all taxa	X	X	X	X	X	X
Genus – non-marine	X	X	X	X	X	X
Genus – forest	X	X	X	X	X	X
Genus – strictly forest	X	X	X	X	X	X
Genus 1950 – all taxa	X	X	X	X	X	X
Genus 1950 – non-marine	X	X	X	X	X	X
Genus 1950 – forest	X	X	X	X	X	X
Genus 1950 – strictly forest	X	X	X	X	X	X

* Richness calculated within each band as the total number of taxa implementing an algorithm in a cartographic model in PCRaster (see Chapter 5, section 5.2.4.5).

** Rarity calculated as the total sum in each band implementing the operator areatotal in a cartographic model in PCRaster.

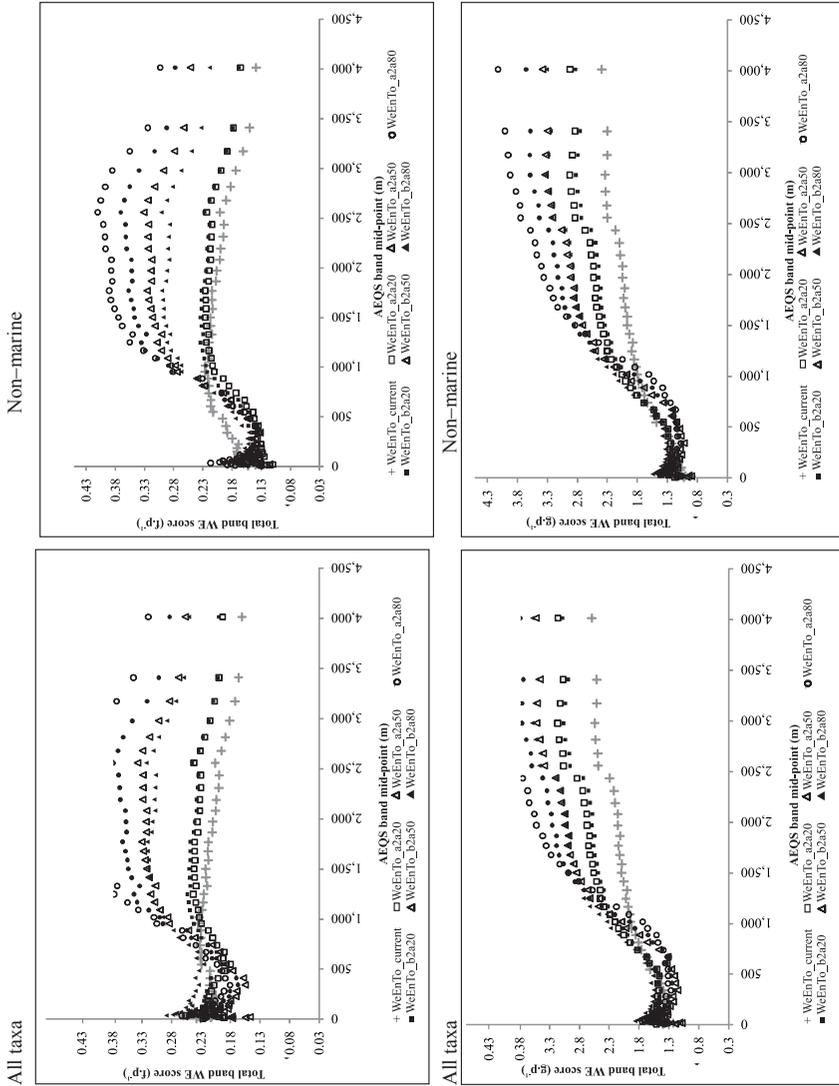


Figure 6.3.1.3.2a. Elevational gradient in estimated total family and genus rarity (Weighted Endemism Score, WeEnTo) when used AEQSIB in WC for current conditions maps and future climate change scenarios. Suffixes: _current, MAXENT models in current conditions; scenarios a2a and b2a; years 2020, 2050 and 2080. Models based on all accessions. All taxa and non-marine avian subsets.

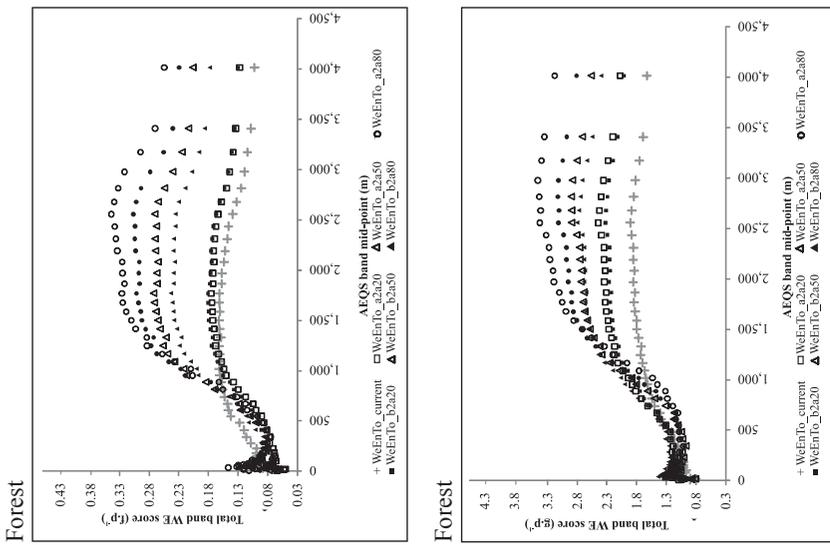


Figure 6.3.1.3.2b. Elevational gradient in estimated total family and genus rarity (Weighted Endemism Score, WeEnTo) when used AEOQSIB in WC for current conditions maps and future climate change scenarios. Suffixes: _current, MAXENT models in current conditions; scenarios a2a and b2a; years 2020, 2050 and 2080. Models based on all accessions. Forest and strictly-forest avian subsets.

(Figure 6.3.1.3.2). For rarity, the point at which future climate–change scenarios had values greater than current conditions was noted at roughly 1,000 m of elevation for both taxonomic levels (Figure 6.3.1.3.2). Furthermore, differences between current conditions and future climate–change scenarios were far clearer in this case than for total richness. Thus, when tested statistically, observed differences in the elevational gradient in total band rarity were significant in most cases through all taxonomic levels and avian subsets (Table 6.3.1.3.1).

6.3.2. Potential refugia of bird diversity

6.3.2.1. Differential Ratio Index (DRI) maps

Prior to generating maps of potential refugia of bird diversity in West Colombia a visual inspection of the Differential Ratio Index (DRI) maps generated through the different avian subsets and future climate–change scenarios at both taxonomic levels was conducted. Results showed that areas where temporal changes in avian diversity are possibly more robust, defined as those areas where the DRI exhibited absolute values close to one ($0.75 < |DRI| < 1.25$), were relatively limited and mostly found in the slopes and foothills of the main mountain ranges. It is important to add that the distribution of these areas showed slight variations between avian subsets, although there was a great deal of variation in their pattern when comparing taxonomic levels. Moreover, spatial distribution of most robust areas showed marked differences between richness and rarity indices.

Thus, for family richness, the most robust areas appeared in the Serrania de La Macarena, in a narrow band in the northeastern slope of the Eastern Cordillera, also in the western slope of the same Cordillera, and in the high Magdalena valley and associated slopes (Figure 6.3.2.1.1). Other areas included the northeastern section of the Central Cordillera and towards Serrania de San Lucas, the northwestern section of the Pacific slope of the Western Cordillera, extending to the lowlands and the Serrania del Baudo, and in the foothills of the Sierra Nevada de Santa Marta and adjacent lowlands, as well as limited extents in some other areas along the three cordilleras (Figure 6.3.2.1.1). This general pattern was kept through the different modelled scenarios, although there was a slight tendency to extend to nearby areas under more severe and/or distant in–time scenarios (Figure 6.3.2.1.1). In this sense, this variation was easier to detect when comparing maps for the years 2050 and 2080 within the same scenario (A2A and B2A). At genus level, robust areas contracted markedly, just remaining in the northern portion of the Serrania de La Macarena and in the northern foothills of the northern Central and Western cordillera, in the Sierra Nevada de Santa Marta, as well as in limited areas in the southeastern slope of the Eastern Cordillera, in the northern portion of Serrania del Baudo and in the Caribbean

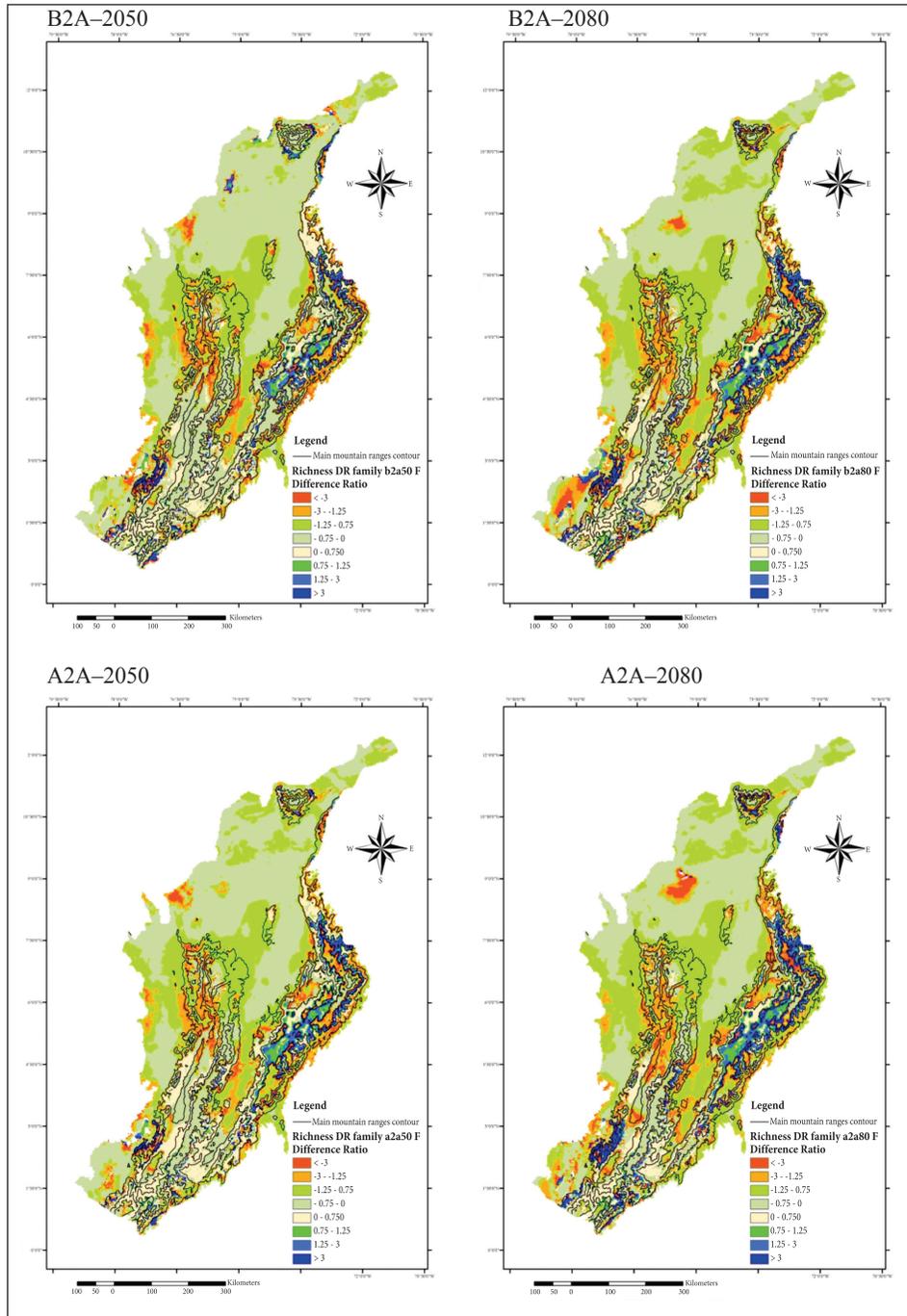


Figure 6.3.2.1.1. Family Differential Ratio Index (DRI) between future climate-change scenarios and current conditions for richness in West Colombia. Forest avian subset.

Region and the Andes (Figure 6.3.2.1.2). Moreover, some more robust areas appeared in the northern portion of the Eastern Cordillera in a semicontinuous band between 2,000–3,000 m of elevation and in the southwestern section of the Pacific slope of the Western Cordillera from northern Nariño to Valle del Cauca (Figure 6.3.2.1.2).

At both taxonomic levels, non-optimal areas with high absolute values tended to expand to neighbouring areas when modelled in more severe and/or distant in-time scenarios, particularly at genus level. These occurred, first, in a broken belt in the Andean slopes and the Sierra Nevada de Santa Marta, mostly below 1,000–2,000 m of elevation, and in the Eastern Cordillera near the Sierra Nevada del Cocuy in some zones between 3,000–4,000 and the Sierra Nevada de Santa Marta at similar elevations, where bird richness is expected to decrease. Second, in a semicontinuous band between 2,000–3,000 m of elevation in the Eastern Cordillera, in the Sierra Nevada de Santa Marta, in the Central Cordillera from the Ruiz–Tolima Volcanic Complex south towards the Colombian Massif, and in the southwestern section of the Pacific slope of the Western Cordillera from north Nariño to Valle del Cauca between 1,000–3,000 m of elevation, where bird richness may increase. Otherwise, most of the lowlands of the country exhibited low non-optimal values where richness is expected to decrease.

On the other hand, the spatial distribution of the most robust areas for rarity showed marked differences in relation to richness and between avian subsets, particularly for the forest related ones. At the family level, robust areas appeared in the three cordilleras and the Sierra Nevada de Santa Marta³⁸, as well as in some more areas in the lowlands in the mid Magdalena valley, the Caribbean and the Pacific regions (Figure 6.3.2.1.3). This pattern was very similar between all avian subsets, extending for the forest avian subset to areas just above 2,000 m in the Eastern Cordillera north of Sierra de La Macarena, and in its southern portion to areas as low as 1,000 m, while shrinking in the other Andean ranges and in the Sierra Nevada de Santa Marta (Figure 6.3.2.1.3). Some additional areas were noted in the southwestern portion of the Western Cordillera and adjacent Pacific lowlands, as well as in the Caribbean region nearby the Sinu River and San Jorge River valleys (Figure 6.3.2.1.3). Similar

³⁸ In the Eastern Cordillera usually above \approx 2,500 m of elevation, in its northeastern portion and further south around the Paramo de Sumapaz, in the Central Cordillera from the zone around the Ruiz–Tolima Volcanic Complex south to the Paramo de Las Hermosas and the high Saldaña River valley and spotily in the Paramo de Las Papas and the Colombian Massif, in the Western Cordillera spotily in its northwestern end, around the Cerro Tatama and south of Farallones de Cali to the border with Ecuador in areas as low as 1,000 m of elevation. Additionally, in the Sierra Nevada de Santa Marta, extending in its northeastern section to areas as low as 1,000 m and some more very few limited areas at the same elevation in its southern and western slopes, as well as in Serrania del Perija extending to areas as low as \approx 1,500 m of elevation.

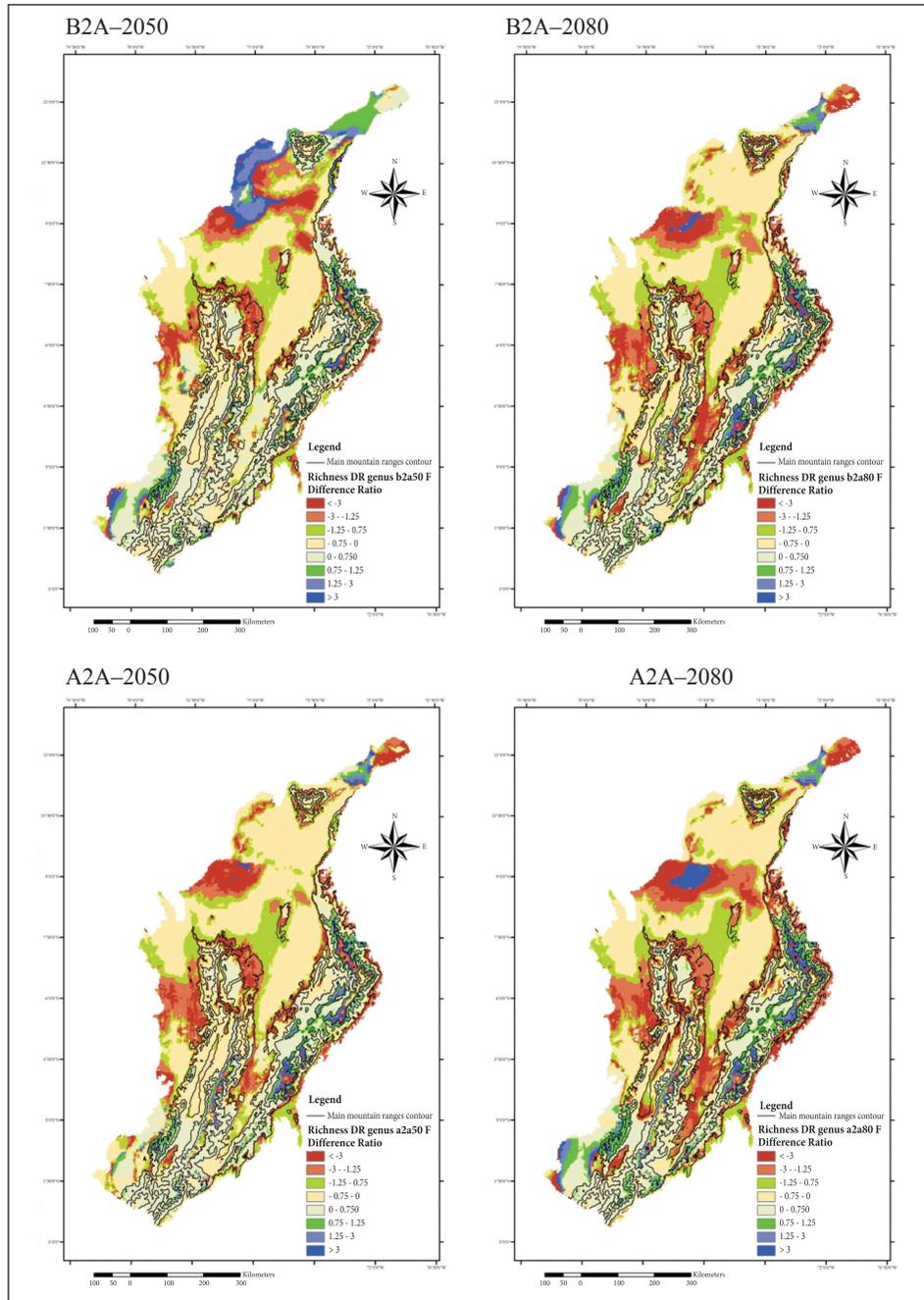


Figure 6.3.2.1.2. Genus Differential Ratio Index (DRI) between future climate–change scenarios and current conditions for richness in West Colombia. Forest avian subset.

as occurred for richness, there was a slight tendency to extend to nearby areas under more severe and/or distant in–time scenarios (Figure 6.3.2.1.3). As noted before, this was easier to see when comparing maps for the years 2050 and 2080 within the same scenario (A2A and B2A). At genus level, robust areas emerged also in the main mountain ranges and adjacent lowlands, although in a more limited manner and exhibiting a slight different spatial distribution^{39**} (Figure 6.3.2.1.4).

Additionally, robust areas appeared in the highest parts of Sierra Nevada de Santa Marta above 3,000 m and sparsely below that, as well as in some few lowland areas in the Caribbean Region (Figure 6.3.2.1.4). As described before, there was a slight tendency to extend to nearby areas under more severe and/or distant in–time scenarios and an increment in robust areas was observed when forest related avian subsets were modelled, particularly in the Eastern Cordillera (Figure 6.3.2.1.4). However, other areas such as some around the Sabana de Bogota, the Ruiz–Tolima Volcanic Complex and the southern portion of the Central and Western Cordillera disappeared (Figure 6.3.2.1.4). Otherwise, areas in the lowlands of the Caribbean region extended and contracted in different scenarios and avian subsets, suggesting an increase in robust areas from the A2A–2050 to A2A–2080 scenarios and a decrease in areas from the B2A–2050 to B2A–2080 scenarios.

Spatial distribution of non–optimal areas with absolute high scores showed slightly different tendencies between taxonomic levels when more severe and/or distant in–time scenarios were simulated. At the family level, most areas of this type were located in the lowlands and they tended to extend in more severe and/or distant in–time scenarios, especially in the high Magdalena valley, although shrinking slightly in the Caribbean Region for the A2A scenario. It is interesting to highlight that most of these areas constitute zones where we expect rarity to decrease. Moreover, some few non–optimal areas where rarity may increase in future climate–change scenarios appeared in the Sierra Nevada de Santa Marta, in the lowlands of the Caribbean Region and in the mid Magdalena valley, which, also tended to shrink. On the other hand, at genus level both types of non–optimal areas were distributed in the mountain ranges and the lowlands. Areas where rarity may increase, are predominant in the

39 ** In the northern half of the Eastern Cordillera in both slopes between $\approx 2,000$ – $3,500$ m and further south in its most southern portion, in the northern and eastern slope of the Central Cordillera in the foothills (below 1,000 m) of its most northeastern third section extending in some areas towards Serranía de San Lucas, also further south in more limited areas around the Ruiz–Tolima Volcanic Complex between $\approx 2,000$ – $3,000$ m, and in the western slope from the high La Vieja River valley south to the head of the Cauca River valley and in more limited areas to the Huaca Massif. As well as in the western slope of the Western Cordillera in the slopes between $\approx 2,000$ – $3,000$ m of its most northwestern third section, and further south in more limited areas along its whole Pacific slope to the border with Ecuador extending in some areas towards the Pacific lowlands, especially in Choco and Nariño.

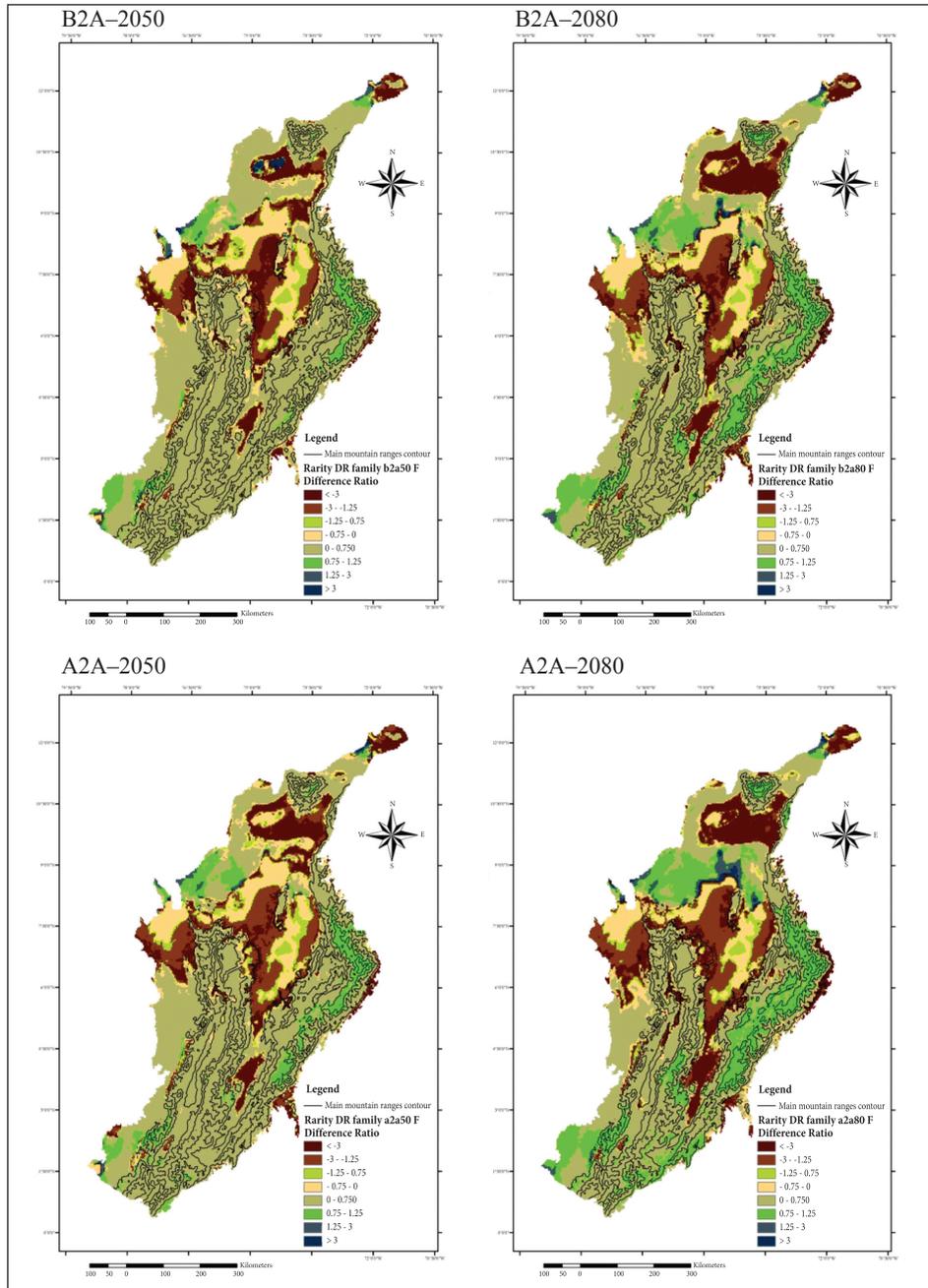


Figure 6.3.2.1.3. Family Differential Ratio Index (DRI) between future climate-change scenarios and current conditions for rarity in West Colombia. Forest avian subset.

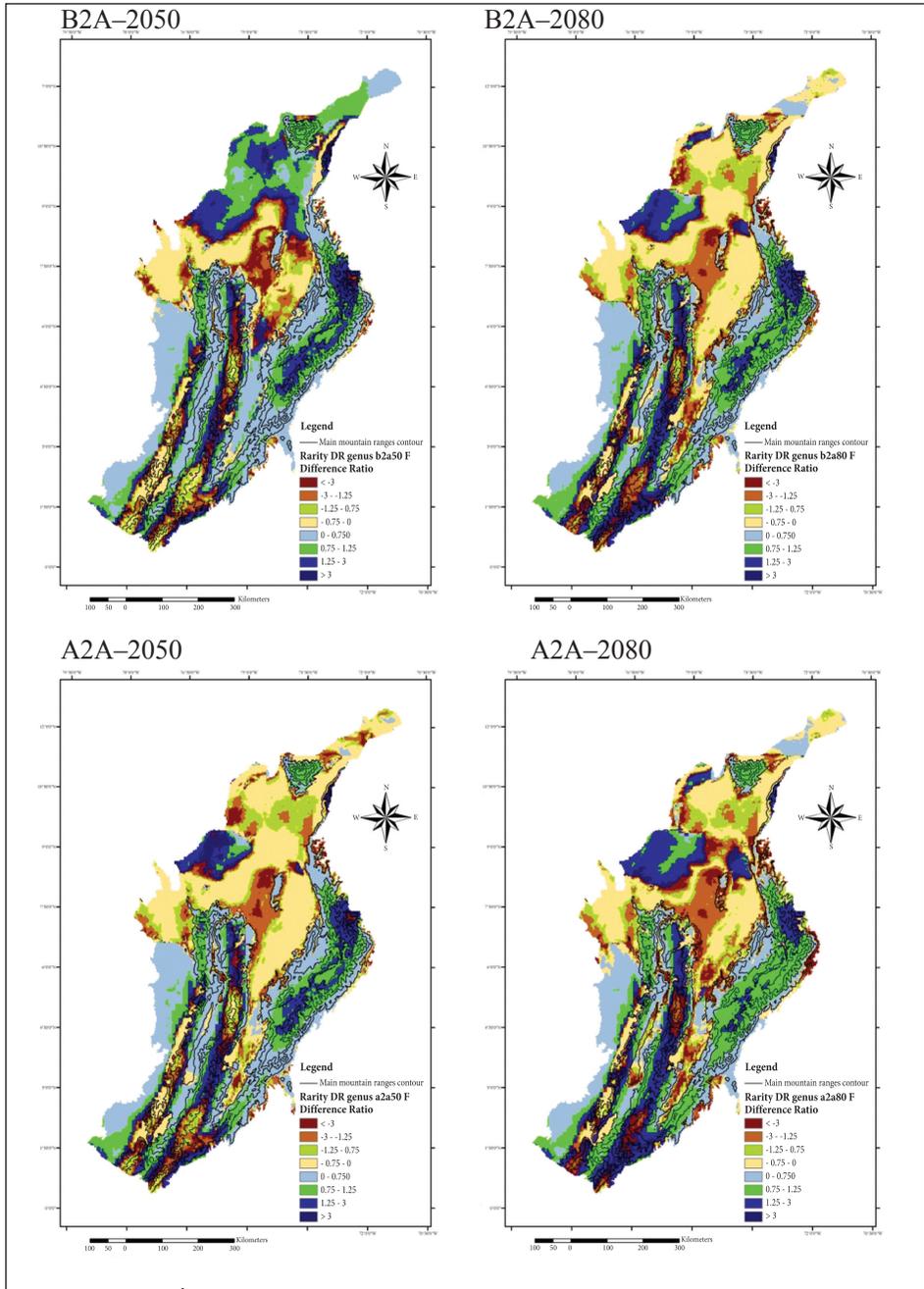


Figure 6.3.2.1.4. Genus Differential Ratio Index (DRI) between future climate-change scenarios and current conditions for rarity in West Colombia. Forest avian subset.

Eastern Cordillera, but located in a narrow band in the northeastern slope and around the Altiplano Cundiboyacense are some areas where rarity is expected to decrease. In the Central and Western Cordillera, areas where rarity is expected to decrease dominate in the highest parts of both ranges, and areas where rarity may increase occur in the slopes below. Areas where rarity may increase also appear in the Sierra Nevada de Santa Marta, and areas where rarity is expected to decrease appear and in the lowlands of the Caribbean, whereas in the lowlands in the Pacific Region appear areas where rarity is expected to increase. Finally, both types of non-optimal areas with high absolute scores became slightly more marked in the Central and Western cordilleras when modelled in more severe and/or distant in-time scenarios, while in the lowlands of the Caribbean Region they extended and contracted in different scenarios and avian subsets. Non-optimal areas with high absolute scores increased from the A2A-2050 to A2A-2080 scenarios and a decreased from the B2A-2050 to B2A-2080 scenarios, although not with a definite clear tendency through all avian subsets.

6.3.2.2. *Potential refugia and gap analysis*

Implementation of the refugia selection algorithm, trying to highlight areas where: 1) the diversity was high, 2) the raw difference between the modelled scenario and current conditions maps was minimised, and 3) the differential ratio index was near optimal (*i.e.* values close to 1 or -1), generated a collection of relatively limited areas, mostly in the mountain ranges. Similarly to results observed previously for the general patterns of diversity change and potential change robustness, the potential refugia areas obtained varied moderately between future climate-change scenarios and avian subsets, and markedly between richness and rarity indices. For simplicity results obtained for the forest avian subset only are shown in this section. Thus, for richness, potential refugia areas were very limited, especially at genus level (Figure 6.3.2.2.1). Moreover, it was possible to detect variations in the spatial distribution of the selected areas where richness is expected to increase and decrease, as well as slight changes in the location of those areas when modelled under different scenarios (Figure 6.3.2.2.1). Despite variability, potential refugia emerged mostly in the upper Tropical, Subtropical and Temperate zones (*sensu* Chapman, 1917) of the Andean ranges and the Sierra Nevada the Santa Marta ($\approx 1,000\text{--}3,000$ m). Additionally, several more areas appeared in the Pacific Region, including Serrania de Baudo, and in the Caribbean lowlands, although these were highly variable between scenarios and taxonomic levels (Figure 6.3.2.2.1). It is interesting to highlight that when projected to future climate-change scenarios, potential refugia areas tended to appear better marked in the upper Tropical and Subtropical zones when selected under more severe and/or distant in-time scenarios, especially at family level (Figure 6.3.2.2.1).

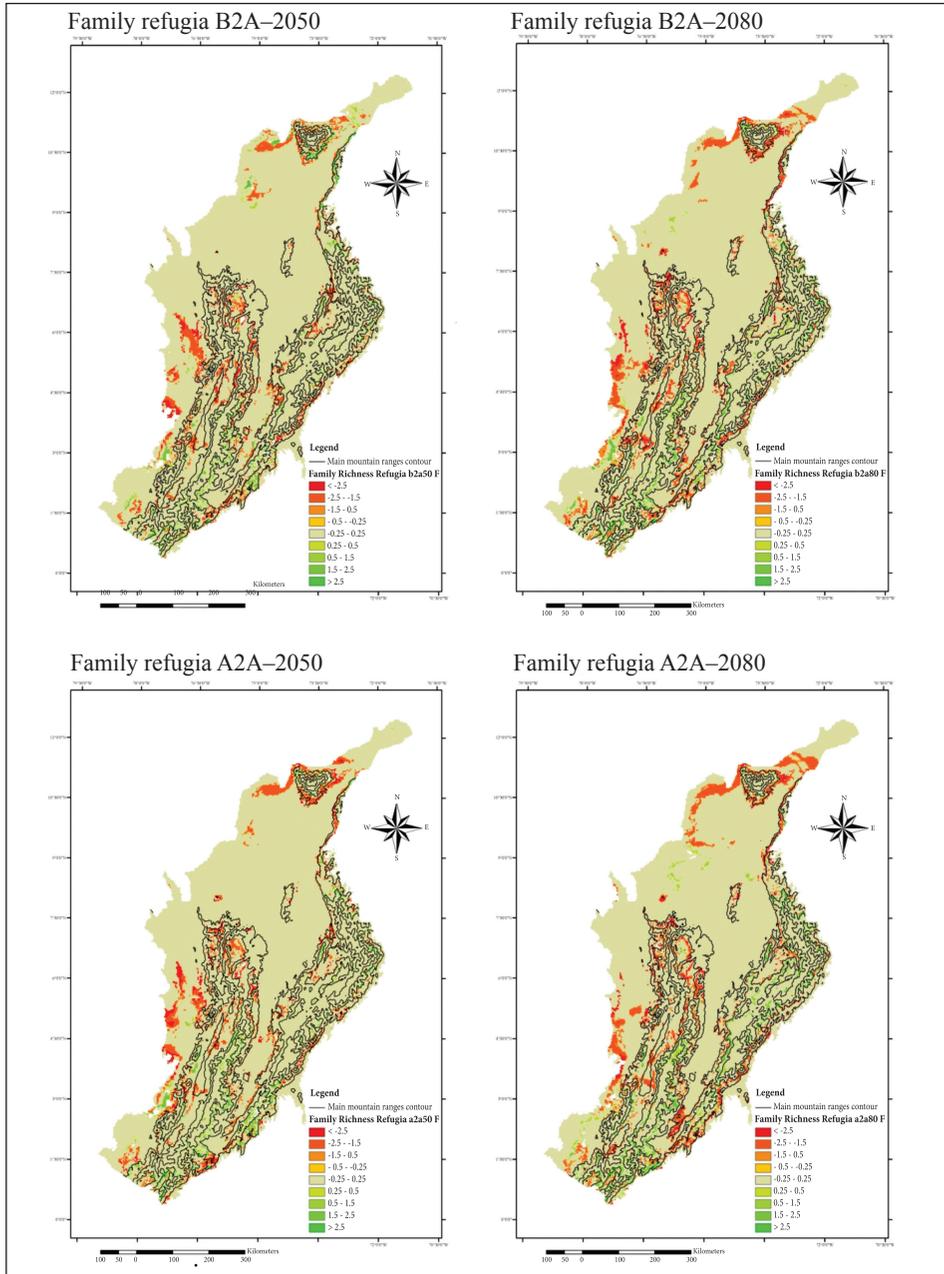


Figure 6.3.2.2.1a. Bird richness potential refugia in future climate-change scenarios in West Colombia at family and genus taxonomic levels. Maps illustrate results obtained for the forest avian subset.

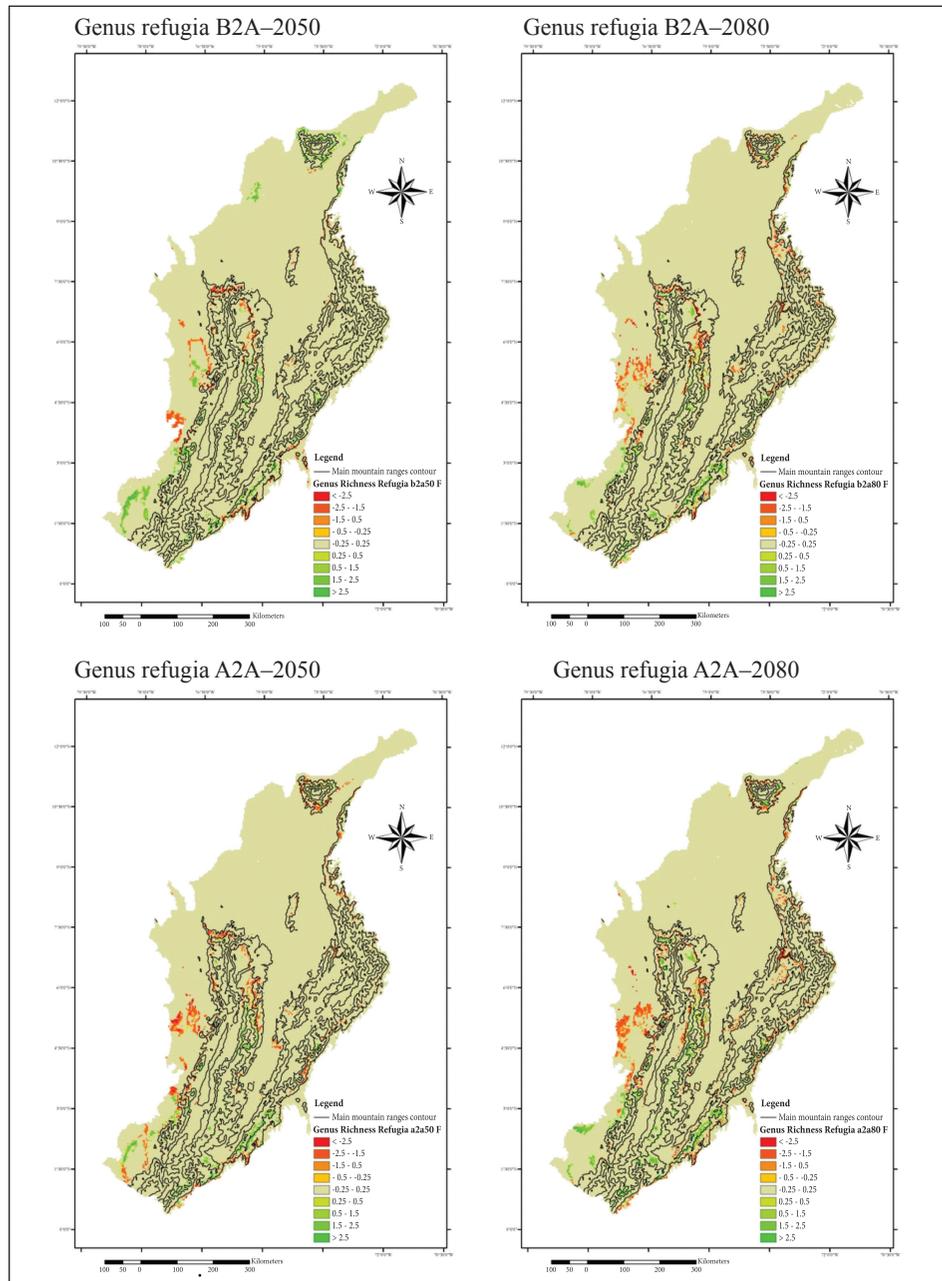


Figure 6.3.2.2.1b. Bird richness potential refugia in future climate–change scenarios in West Colombia at family and genus taxonomic levels. Maps illustrate results obtained for the forest avian subset.

Contrastingly, when rarity patterns are examined, at family level most refugia were located in areas above $\approx 2,500$ m, occupying the Temperate and the Paramo zones (*sensu* Chapman, 1917), particularly exhibiting a higher density in the Central Cordillera and the Sierra Nevada de Santa Marta than in the other ranges (Figure 6.3.2.2.2). Additionally, some areas emerged in the upper Tropical and Subtropical zones of the three cordilleras and the Sierra Nevada de Santa Marta, as well as in the Pacific lowlands in Choco. When rarity was projected in future climate conditions, potential refugia areas tended to extend slightly in the Temperate zone and appear better marked in the upper Tropical and Subtropical zones when selected under more severe and/or distant in-time scenarios (Figure 6.3.2.2.2). At genus level, potential refugia exhibited a different spatial configuration, appearing mainly in the upper Tropical and Subtropical zones of the three cordilleras and the Sierra Nevada de Santa Marta; surprisingly, including very few areas in the Serrania del Perija (Figure 6.3.2.2.2). Selected areas shrank markedly when refugia were selected under more severe conditions for the year 2080 in the scenario A2A, occurring mostly in the belt between 1,000–2,000 m of elevation possibly in the ecotone between the upper Tropical and Subtropical zones. It is interesting to note that in the Sierra Nevada de Santa Marta refugia constituted quite a solid band that descended slightly in elevation towards the upper Tropical zone. This tendency was different for the B2A scenario, which exhibited a higher density of refugia in the upper Tropical and Subtropical zones of the three cordilleras and the Sierra Nevada de Santa Marta under more severe conditions for the year 2080. Otherwise, areas in the Pacific lowlands appeared more markedly at this taxonomic level, apparently extending slightly under more severe and/or distant in-time scenarios (Figure 6.3.2.2.2).

The evaluation of the extent to which potential bird diversity refugia are captured by the National System of Protected Areas (SINAP), Indigenous Reservations System (SRI) and a sample of private nature reserves (RESNATUR and ProAves), showed under all future conditions a very limited inclusion of selected areas within the whole set of conservation areas (Figure 6.3.2.2.3 and Table 6.3.2.2.1). In this sense, at family level the SINAP plus the SRI captured a maximum of 13,059 km² of the potential refugia areas when using richness, whilst overlapping with a maximum of 10,440 km² of the potential refugia areas when using rarity. On the other hand, at genus level the SINAP plus the SRI captured a maximum of 8,487 km² of the potential refugia areas when using richness, whilst overlapping with a maximum of 9,225 km² of the potential refugia areas when using rarity. It is interesting to add that differences observed in both the total number of pixels captured by the two systems and the percentage they represent from the total refugia areas were not significant between taxonomic levels (Wilcoxon Test, $p < 0.05$). Furthermore, in general, both the SINAP and the SRI reserves did not capture more than $\approx 15\%$ of the total areas selected as refugia either when they were summed all together or when intersected

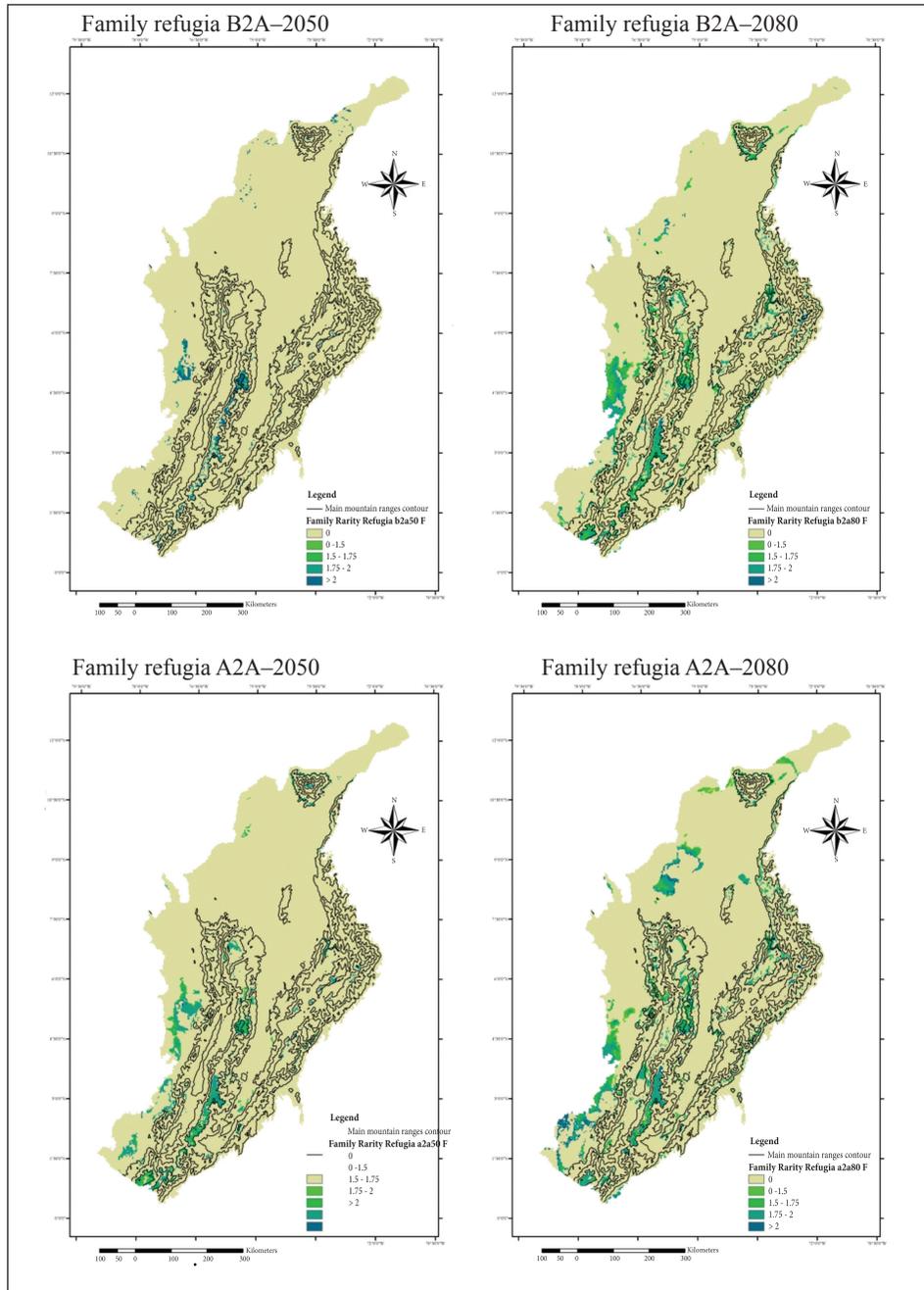


Figure 6.3.2.2.2a. Bird rarity potential refugia in future climate-change scenarios in West Colombia at family and genus taxonomic levels. Maps illustrate results obtained for the forest avian subset.

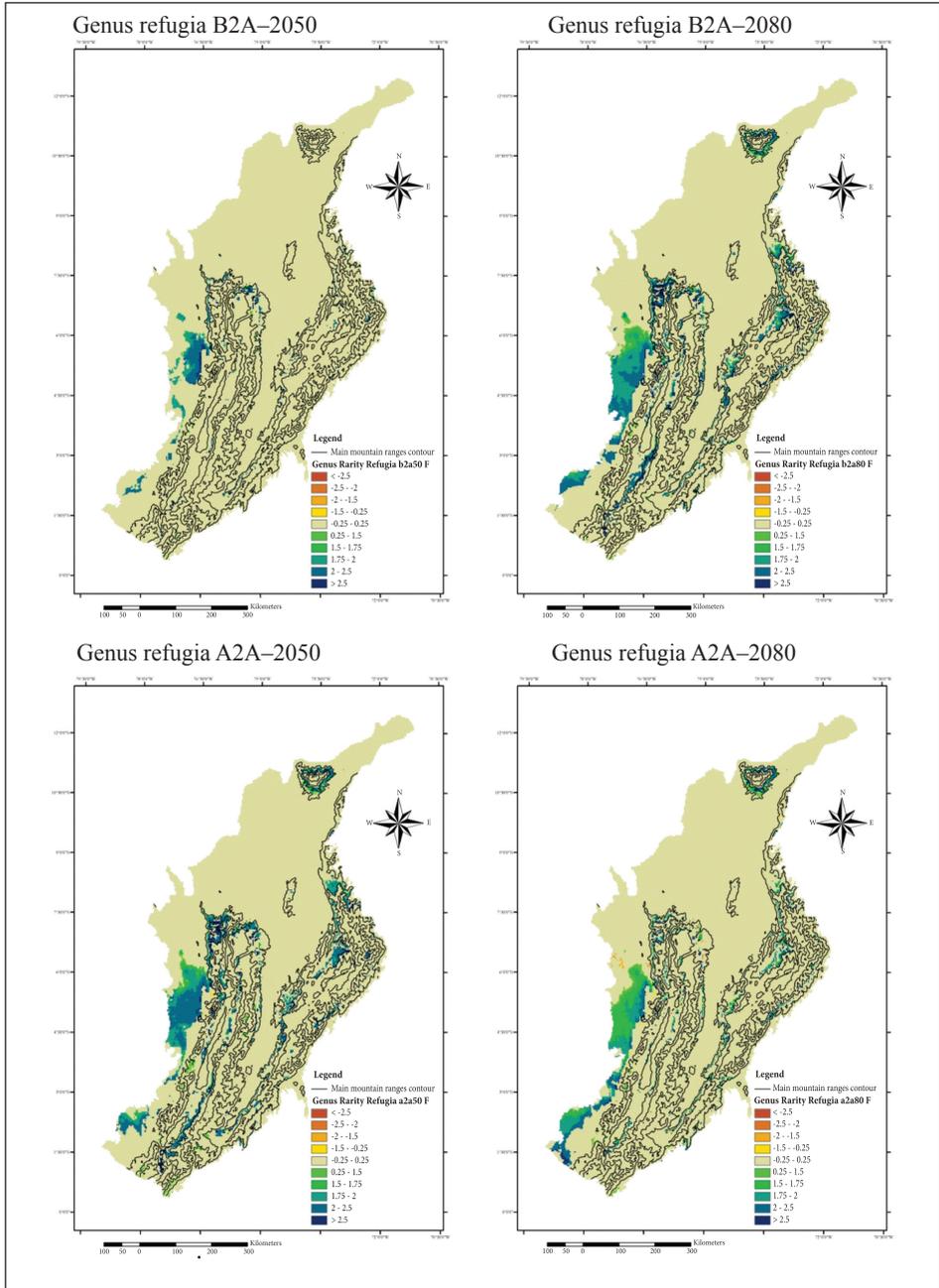


Figure 6.3.2.2b. Bird rarity potential refugia in future climate–change scenarios in West Colombia at family and genus taxonomic levels. Maps illustrate results obtained for the forest avian subset.

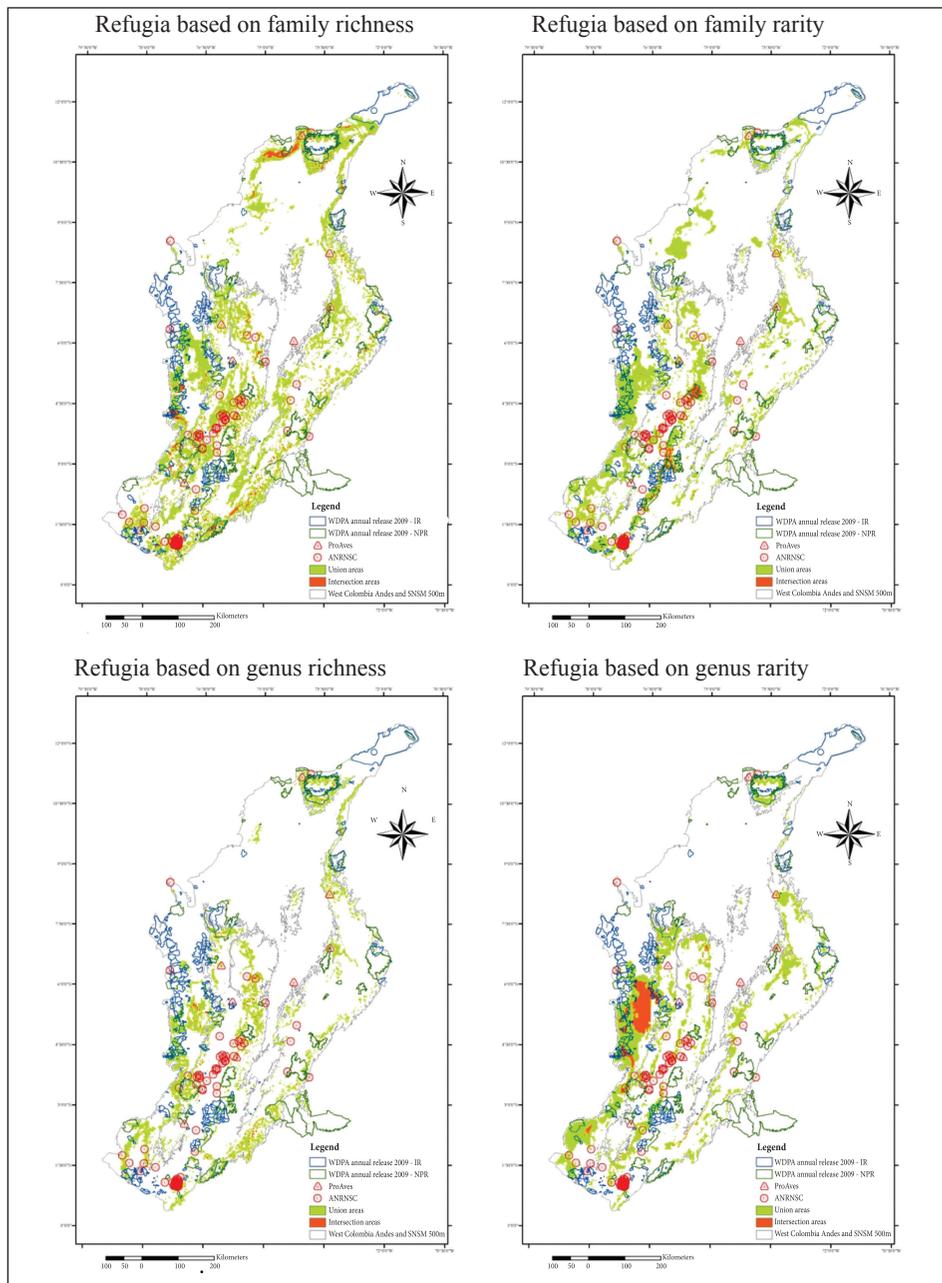


Figure 6.3.2.2.3. Potential avian diversity refugia selected using richness and rarity in West Colombia under all future climate-change scenarios and avian subsets when summed all together (union of areas) and intersected (intersection of areas) and overlapped to the Protected Areas National System (SINAP = WDPA annual release 2009 – NPR), Indigenous Reservations System (SRI = WDPA annual release 2009 – IR) and a sample of private nature reserves; RESNATUR (circles) and PROAVES (triangles).

Table 6.3.2.2.1. Summary of areas captured by the Protected Areas National System (SINAP), Indigenous Reservations System (SRI) and a sample of private nature reserves (RESNATUR and PROAVES) under all future climate-change scenarios when summed all together and intersected the potential refugia selected using richness and rarity in West Colombia. UASA, union of areas selected by algorithm through all avian subsets and scenarios; IASA, intersection of areas selected by algorithm through all avian subsets and scenarios. For areas captured by the SINAP and the SRI, each pixel corresponds to an area of 9 km².

Reserves categories	Family				Genus			
	Total pixels captured	% from total selected by algorithm	Total ¹ reserves overlapped	% from total reserves in category	Total pixels captured	% from total selected by algorithm	Total ¹ reserves overlapped	% from total reserves in category
WDPA ¹ -2009 – parks and reserves (88)	UASA – richness	980	7.59		737	12.31		
	IASA – richness	109	9.41		35	15.42		
	UASA – rarity	880	10.04		569	7.12		
	IASA – rarity	140	45.16		20	1.82		
WDPA ¹ -2009 – indigenous reservations (71)	UASA – richness	471	3.65		206	3.44		
	IASA – richness	54	4.66		12	5.29		
	UASA – rarity	280	3.2		456	5.71		
	IASA – rarity	0	0		67	6.1		
RESNATUR ² -2004 (83)	UASA – richness			34		40.96	8	9.64
	IASA – richness			2		2.41	0	0
	UASA – rarity			13		15.66	17	20.48
	IASA – rarity			0		0	1	1.2
PROAVES ³ -2008 (11)	UASA – richness			1		9.09	1	9.09
	IASA – richness			1		9.09	0	0
	UASA – rarity			2		18.18	1	9.09
	IASA – rarity			0		0	0	0

¹ World Database on Protected Areas; ² Civil Society Nature Reserves Colombian Network Association; ³ Pro-Aves Foundation; ⁴ Represents the number of reserves for which their georeference coincides with areas selected as refugia

(Table 6.3.2.2.1). This is with the exception of the areas captured by the SINAP when overlapped with the intersection of areas selected for rarity at family level, which exhibited a high representation in the system, reaching nearly $\approx 50\%$ from the total selected areas. Despite this, it is important to keep in mind that the captured areas represent less than 2% of the total territory of West Colombia, which constitutes a very limited percentage under any circumstance.

Table 6.3.2.2.2. Most important reserve areas within the Protected Areas National System (SINAP) and the Indigenous Reservations System (SRI) in capturing potential refugia under all future climate-change scenarios when summed all together through all avian subsets and scenarios. Areas captured by the SINAP and the SRI are given in pixels of 9 km².

Name	SINAP			
	Family richness	Family rarity	Genus richness	Genus rarity
Alto Fragua – Indi Wasi	51		35	
Cordillera de Los Picachos	80		97	
El Cocuy	58	49		36
Farallones de Cali	124	53	106	41
Laguna la Cocha – Cerro Patascoy		30		
Las Hermosas	38	57		
Los Nevados		68		
Nevado del Huila	39	115		
Paramillo	103	54	70	114
Purace		70		
Sanquianga		38		65
Sierra de la Macarena			31	
Sierra Nevada de Santa Marta	158	89	174	163
Sumapaz	56	39	37	
Tatama		36		
SRI				
Alta y Media Guajira	87	57		
Arhuaco de la Sierra Nevada	94		97	115
Rios Catru y Dubasa				37
Tahami del Andagueda				30

Finally, it is interesting to note that reserves from the SINAP and the SRI captured differently the potential refugia areas at both taxonomic levels and biodiversity indices (Table 6.3.2.2.2). In this sense, the areas that showed better consistency in capturing selected areas under the SINAP were in descending order: Sierra Nevada de Santa Marta, Paramillo, Farallones de Cali, El Cocuy and Sumapaz. In contrast, under the SRI, just the Arhuaco de la Sierra Nevada showed relatively good coherence through the different biodiversity indices and taxonomic levels.

6.4. Discussion

6.4.1. *Expected changes in avian diversity under climate change scenarios*

Spatial patterns of diversity in West Colombia under climate change conditions were sensitive to taxonomic level, avian subset and scenario used to generate projections. Furthermore, response was different between richness and rarity indices. In this sense, the spatial patterns documented for richness were different to those observed for rarity and spatial tendencies were more similar for richness than for rarity, which exhibited a higher degree of variation. For both indices, areas with the highest scores under future climate conditions were in or adjacent to the main mountain ranges, including the three Andean cordilleras and the Sierra Nevada de Santa Marta.

Observed differences in diversity between future scenarios and current conditions when using random extracted points showed particular sensitivity to the taxonomic level and dataset used to generate individual habitat suitability maps and therefore final diversity maps. Moreover, tendencies between richness and rarity were opposite. Thus, results showed that, in Western Colombia, under future climatic conditions richness is projected on average to decrease, while rarity is expected to increase. This pattern was especially evident when comparing current conditions to the most severe and/or distant in-time scenarios (B2A–2080, A2A–2050 and A2A–2080).

Similarly, results revealed that, in Western Colombia, bird diversity is projected to change asymmetrically in the elevational gradient of the country and that the pattern of potential future bird diversity in the elevational gradient of the country may vary according to the taxonomic level and avian subset. In general, richness in future climatic conditions is expected to be below values observed today at low to mid elevations, while it is projected to go above current values at high elevations. Rarity under future climatic conditions is projected to decrease at low elevations, while it is projected to increase at mid and high elevations. Richness follows a humpback-shaped curve with elevation, whilst rarity describes a slight sigmoidal curve. It is interesting to note that differences to current conditions were far clearer when modelling rarity.

The findings of this study are in agreement with tendencies inferred from cases documented in the literature. In general, within tropical latitudes mountain species have already shifted their ranges to higher elevations and/or are expected to move their ranges uphill in the mountains in the near future due to projected climate change (Hannah *et al.*, 2006; Feehan *et al.*, 2009). In this study, there is no detailed account of how changes will occur for particular taxa in the mountains. However, indirect evidence from changes in the elevational pattern of both richness and rarity in West Colombia suggest agreement with documented tendencies. Results showed a shift in the elevation at which maximum values of bird diversity were observed, this tendency was very mild for richness but particularly evident for rarity when modelled for forest related avian subsets (section 6.3.1.3). In that case, rarity not just increased when projected into future climate conditions, but its values along the elevational gradient peaked roughly at about 2,000–3,000 m instead of 1,000–2,000 m. Suggesting, first that ranges contracted and second that range limits moved at higher elevations. Besides range contractions for some mountain species, also range expansions into the mountains for lowland species may occur. These need further research. Clearly shifts in ranges are expected to affect composition and abundance in bird communities and also migratory movements (La Sorte & Jetz, 2010), especially disrupting the altitudinal zonation of montane communities (Gasner *et al.*, 2010). The fact that models generated in this study are purely correlative and do not include mechanistic elements suggest communities may not keep the compositions projected. Thus, once changes in range occur, biotic interactions may result in completely different outcomes, which possibly render bird diversity scenarios projected here as very optimistic.

In addition, the fact that in Colombia many range-restricted and threatened species occupy the mountains, suggest patterns observed here might indicate that these species may become even more threatened or extinct. However, its confirmation needs a more detailed account at species level, as already conducted by Velasquez-Tibata *et al.* (*in litt.*), whose results are awaiting publication. Other studies in the tropics have shown important changes in diversity due to climate change. Gasner *et al.* (2010) estimated potential changes in abundance and shifts in range due to climate change for 77 forest species in the Tilaran Mountains of Costa Rica. The study found that nearly half of modelled species are expected to decline by the year 2100, from which about 19 species are endemics to Central America and further seven from eight species projected to become locally extinct, are endemics from the mountains of Costa Rica and Panama. Menon *et al.* (2009) studied shifts in range due to climate change for 13 Nuthatch species (family Sittidae) in Asia using GARP ecological niche modelling software. Their results showed range contractions in the southern portion of evaluated ranges, as well as reductions at low elevations along mountain ranges. In their view, results suggest mountain species ranges are more resilient to effects of

climate change on biodiversity than lowlands. Interestingly, another study conducted by Thomassen *et al.* (2010) in Ecuador proved that zones with the highest genetic and phenotypic variation for the Wedge-billed Woodcreeper (*Glyphorynchus snyderi*) were located in the mountains, highlighting the great importance these areas may have in conferring adaptive resilience against climate change impacts. This may be especially true in cases where induced climatic changes are minor and/or affect just a portion of the avian diversity. However, asymmetrical impacts on biodiversity, due to major changes in climate in the mountains, may produce unexpected disruptions of complete communities inhabiting these zones.

Average changes in richness in West Colombia seemed contradictory to tendencies observed in other tropical countries in Africa. Kissling *et al.* (2010) assessed changes in woody plant (1,417 spp.) and bird (1,005 spp.) species richness in Kenya due to climate change using regression models and median climatic forecasts applied through 15 different scenarios, and evaluating projection sensitivity to organism response time. Results from this research showed that – assuming an instantaneous response – as most modelling exercises do, both plant and bird species richness increased in the majority of the country, whilst a strongly lagged plant response triggered an opposite pattern in bird richness. In this sense, the results from this thesis evidenced that on average in West Colombia, richness is expected to decrease. Furthermore, if we assume a lagged response to climatic change, and if a similar tendency such as that found by Kissling *et al.* (2010) apply for all of Colombia, we can then expect even more dramatic reductions in bird richness in the country. Consequence of the time lag expected in tracking suitable conditions by the vegetation, and subsequently by organisms that depend on it such as birds.

Correlative models of diversity such as those built in this research are good as a first approximation to potential impacts of climate change in Colombia. From this point of view it is possible to incorporate more realistic biological assumptions and consider conservation planning focusing on areas where it is expected a major rearrangement of ecological communities (Gasner *et al.*, 2010). However, it is still important to bear in mind that the assumption of unrestricted dispersal capabilities constitutes a main caveat on this study, which according to Thuiller *et al.* (2008) represents the usual limitation of these type of studies. Hence, results constitute a first set of testable hypotheses regarding potential impacts of climate change on bird diversity in the country and might be seen cautiously, particularly if intended to be used in conservation planning. Additionally to the lack of explicit modelling of dispersal, Thuiller *et al.* (2008) identifies also the failure to account for population dynamics on the edges of ranges, biotic interactions and the interaction between the effects of land use and climate change as common pitfalls in climate change impact assessments. However, increasing complexity in models is not necessarily reflected in higher

accuracy, although possibly those reflect better processes occurring at finer scales, novel circumstances and ranges not presently at equilibrium with the environment (Thuiller *et al.*, 2008). Modelling at higher taxonomic levels such as family and genus, as conducted in this thesis, offers an advantage in this respect since at these levels possibly the effects of such processes may be less prevalent than at species level.

Other authors caution against assigning climate change naively as a unique cause of range shifts, while others highlight the importance of validating range models against null models. For instance, Hockey & Midgley (2009) assessing causes of observed southwest range expansions for 18 South African bird species since the 1940's found that – for all species but one – the most parsimonious explanations sustained were related to landscape anthropogenic changes. In this sense, studies decoupling past and future disturbances on biodiversity are of major relevance, since they permit a better understanding on the effects of different causes of loss of biodiversity (Loiselle *et al.*, 2010). On the other hand, Beale *et al.* (2008) evaluated climate change effects in ranges of 100 European bird species, addressing how well climatic envelope models perform in relation to null models. Interestingly, they found evidence that climate model projections were not better than chance for 68 species, suggesting the importance of using critically in conservation planning climatic envelopes models that have not been tested for species sensitivity to climate.

6.4.2. Potential refugia of bird diversity

Implementation of the refugia selection algorithm used in this study generated a collection of limited areas, mostly in the mountain ranges. As noted before, selected potential refugia areas were slightly sensitive to future climate scenarios and very sensitive to the biodiversity index used. In general, both family and genus richness potential refugia appeared in the upper Tropical, Subtropical and Temperate zones between $\approx 1,000$ – $3,000$ m of elevation and in some areas in the Pacific and Caribbean lowlands. In contrast, family rarity areas tended to concentrate in the Temperate and Paramo zones, above $\approx 2,500$ m of elevation, although appeared some below that elevation, whilst at genus level potential refugia occupied mainly the upper Tropical and Subtropical zones and areas in the lowlands, especially in the Pacific Region, where they appeared more extensively than in any other case. Otherwise, selected areas were usually more restricted at genus level, although this pattern varied.

Resulting selected refugia point to areas of high diversity and endemism in the country, noted before by other authors (Renjifo *et al.*, 1995; Stiles, 1998; Salaman *et al.*, 2007b). However, the relatively high degree of uncertainty, particularly in the lowlands, evidenced by the dissimilarity in projections by maps produced using MAXENT and maps generated using the “Western Hemisphere Digital Bird

Distribution Database – WHDBD Database” under current conditions, indicate the use of results in conservation planning must be cautious. These differences are reflected here as high absolute values in the Differential Ratio Index (DRI) maps generated when comparing current and future climate conditions, which suggest refugia are – in this study – strongly limited by the selection of the most robust areas in this aspect; present usually in the mountains or in adjacent areas. In this sense, collection of data of higher accuracy and further advances in more complex and scale refined models is necessary to improve projections, which may help to clarify better the importance of the lowlands.

On the other hand, results showed that current National System of Protected Areas (SINAP), Indigenous Reservations System (SRI) and a sample of private nature reserves (RESNATUR and PROAVES) capture poorly potential refugia under all future climate–change scenarios. Similar situations have been documented in other studies in the Neotropics. For instance, Marini *et al.* (2009) used 8 modelling techniques within the BIOMOD computational framework to project shifts in ranges due to climate change for 38 range restricted bird species in the Cerrado region of Brazil, evaluating changes in the coverage of the Brazilian reserve system for each species. Results revealed that none of the 38 species was covered by the reserve system under any circumstance.

Furthermore, some other studies conducted just in current conditions also point to similar conclusions. Thus, Thomassen *et al.* (2010) in a different study assessing genetic and phenotypic variation in populations of the Wedge–billed Woodcreeper (*Glyphorynchus sphyrapus*) in Ecuador, found that in that country current protected areas capture poorly areas projected as important to maximise adaptive variation, which are mostly present in the mountains. In addition, Verhelst (2004), using earlier versions of the Darwin–Hernandez Database, mapped bird richness at municipality level in the country and evaluated how the richest areas were captured by the SINAP. His findings showed that most municipalities of medium and high species richness were located west of the Andes, in the Subandean belt of the cordilleras, and similarly to that found here, those areas were poorly included in the SINAP of the country.

Finally, results from this study suggest that developments are needed in three main directions. First, a continued advance in model complexity is required, increasing both taxonomic and geographical scale, and integrating intra– and inter–population processes. Second, it is essential to decouple past and future impacts on biodiversity in Colombia trying to understand their potential interactions in future scenarios. This is particularly important since effects such as species local extinctions due to deforestation and fragmentation already are known to be quite widespread in the country (Kattan *et al.*, 1994; Kattan & Alvarez–Lopez, 1996; Renjifo, 1999), especially in the Andean forests where a highly vulnerable avifauna exist (Kattan,

1992). Third, it is vital to use knowledge gained from scientific research in impacts of climate change to plan, implement and feedback integrated conservation strategies (*sensu* Hannah *et al.*, 2006). Accordingly, results from this study suggest efforts must focus predominantly in establishing a network of reserves connecting major types of forest ecosystems in the lowlands and the mountains. This “Trans–Andean Reserves Staircase” may use the main Andean areas from the SINAP as pivotal points from which to delineate new areas to add to the system keeping in mind the need to create connectivity along the cordilleras and through the complete elevational gradient. It is important to highlight that it may be that biodiversity captured and connectivity at this point is even better than what is expected in the SINAP, since there are many reserves owned by the municipalities and regional environmental corporations (ASOCARS) for whom there is no digital cartography and therefore were not included in gap analyses performed here. In this sense, the completion of thorough digital databases of both state and private reserves is fundamental to produce more accurate gap analyses. Ultimately, new potential areas selected and conservation plans must consider keeping very close communication with reserves of the network to facilitate the changes in biodiversity due to climate change (Hannah *et al.*, 2006), incorporating novel approaches in areas already known as impacted heavily by land use (Marini *et al.*, 2009).

Conclusions

The Darwin–Hernandez Database still contains errors and its use in high spatial resolution studies is limited by outstanding georeferencing uncertainty. A new thorough “manual” revision of the whole database record by record is needed to improve georeferencing once more by, for example, checking congruence between the actual locality assigned and the specific locality described in the field “notes”, and addressing georeferencing uncertainty with methodologies such as those used in this thesis.

Differences between reference and modelled bird diversity maps generated were most likely caused by spatial sampling bias, a low number of sample localities for some of the modelled taxa, and a further failure to model several taxa due to a complete lack of data. To generate improved high–resolution bird diversity maps in the country additional field survey effort is necessary in the Orinoco and Amazon regions as well as the lower part of the middle Magdalena valley, the low Cauca valley, and the Atrato, Sinu, San Jorge and Nechi valleys.

Simulations conducted in this thesis showed that under future climate conditions, in West Colombia, richness is predicted on average to decrease, while rarity is expected to increase. Furthermore, along the elevational gradient of the country bird richness is expected to decrease at low and mid elevations, and to increase at high elevations, whilst rarity is projected to decrease at low elevations, and to increase at mid and high elevations.

Potential refugia conserving high family and genus richness may occur in the upper Tropical, Subtropical and Temperate zones between $\approx 1,000$ – $3,000$ m of elevation and in some areas in the Pacific and the Caribbean lowlands. Addressing rarity, potential refugia for families may occur principally in the Temperate and Paramo zones, above $\approx 2,500$ m of elevation, whilst potential refugia for genera may occur mainly in the upper Tropical and Subtropical zones and some areas in the lowlands, particularly in the Pacific region. Moreover, potential refugia were poorly captured by the National system of protected areas (SINAP).

To further advance biodiversity science in Colombia it is necessary to increase model complexity, increasing both taxonomic and geographical resolution, and integrating

intra- and inter-population processes, it is also essential to decouple past and future impacts of climate and land use on bird diversity. It is also vital to use knowledge of the impacts of climate change to inform conservation strategies.

Conservation efforts in Colombia must focus on establishing a network of reserves connecting major types of forest ecosystem in the lowlands and the mountains. This “Trans-Andean Reserves Staircase” may use the main Andean areas from the SINAP as pivotal points from which to delineate new areas to add to the system keeping in mind the need to create connectivity along the cordilleras and throughout the entire elevational gradient.

Future research directions

The comparative study of different means of generating spatial biodiversity measures as conducted here, as well as the continuation of studies refining functional measures of biodiversity represents a unique contribution to biodiversity knowledge in the country and brings the concepts of biodiversity and ecosystems services closer together. Possible directions for further research built on data and results obtained in this thesis may consider five main points. First, to generate under current conditions “hybrid” maps based on both “spatially explicitly-modelled” and “expert-drawn” maps. Second, to model avian ranges assuming limited dispersal from the areas originally occupied. Thus, for instance limiting range projections in final future climate conditions consensus maps only to those areas currently connected and thus representing potential sources from where a taxon may have moved from and sinks to where a taxon may move. Otherwise, dispersal may be allowed within certain distances, permitting the hypothetical colonisation of more isolated areas. Third, it is of interest to refine the ecomorphological measures of avian diversity proposed. In this sense, it would be necessary to gather field data regarding diet, habitat and time budgets to assign more accurately equivalent species within each functional group to each species of hummingbird and tyrant flycatcher. Accordingly, with hybrid maps of higher accuracy it would be possible to obtain more precise maps displaying the spatial distribution of different elements of the biodiversity; and relate them to different ecosystem services. Fourth, we believe it is also of great relevance to clarify past and future impacts of climate and land use on bird diversity. A study intending to focus in this direction may best use a selection of forest taxa with enough data both spatially and temporally and not all avian species. In addition, it may be of convenience to obtain models and maps of deforestation in the country, with which it would be possible to assess better the impact of both factors on avian ranges. Finally, fifth, it would be also relevant to study range filling and patterns of overprediction in tyrant flycatchers using maps generated here, and expand modelling to other families of importance such as tanagers (Thraupidae) and american sparrows (Emberizidae).

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THE STUDY SITE: TOPOGRAPHY, CLIMATE AND VEGETATION

A1.1.1. Topography

In the north, east and southeast, in $\approx 70\%$ of the extension of the continental area, the country is relatively flat, meanwhile the remaining $\approx 30\%$, in the centre, of the country has complex relief due to the presence of the Andes (Hilty & Brown, 2001) (Figure A1.1.1.1). In the south the Andes forms one mountain system that splits soon forming three mountain ranges separated by the Cauca and Magdalena River valleys,

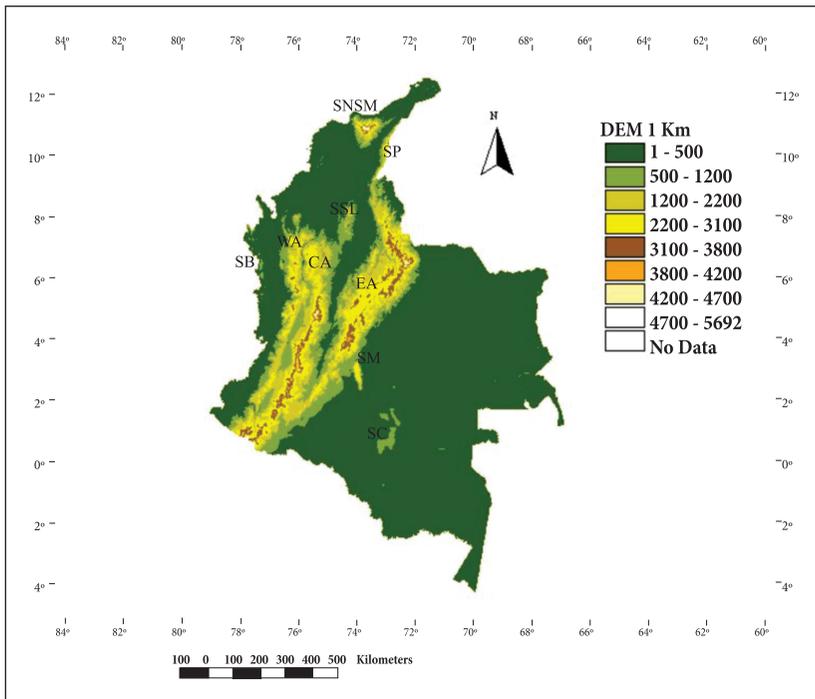


Figure A1.1.1.1. Digital Elevation Model of Colombia. Main mountain ranges: Western Cordillera (WA), Central Cordillera (CA), Eastern Cordillera (EA), Sierra Nevada de Santa Marta Massif (SNSM), Serranía de Perijá (SP), Serranía de La Macarena (SM), Serranía de Chiriquete (SC) and Serranía del Baudo (SB).

to the west and east respectively. In the region known as Huaca Massif or Nudo de Los Pastos, approximately at 1°30' N and 77°30' W, elevation decreases towards the valley of the Patia River. This valley forms a depression that reaches its minimum elevation in the Minama Sickle (400 m). Continuing north–northeast and north is the Western Cordillera, which stretch ≈800 km to about 7°06' N. Otherwise, to the north–northeast and north, and east of the Western Cordillera and the Cauca River valley, runs parallel the Central Cordillera that stretch to the north ≈1,000 km to about 8°30' N in the north end of Serrania de San Lucas (≈200 km). Furthermore, in the south, north of the Huaca Massif, in the area known as the Colombian Massif or Nudo de Almaguer, the Central Cordillera splits near 1°30' N and 76°30' W in a third chain, the Eastern Cordillera, separated from the Central Cordillera by the Magdalena River valley. This last range continues northeast and north ≈1,300 km to about 11°10' N in the north end of Serrania del Perija (≈200 km). Furthermore, in the south, the Eastern Cordillera prolongs southeastward along the Serrania de La Macarena that extends for ≈100 km.

From the three ranges, the Western Cordillera is the narrowest, while the Central is geologically the oldest and has the highest elevations and the Eastern is the widest and geologically the youngest (Hilty & Brown, 2001). The Western Cordillera exhibits an average elevation of ≈2,100 m (CV ≈50%, n = 64,748), and an average width of ≈80 km (CV ≈20%, n = 10) at 500 m of elevation. The maximum elevation (m.e.) of this range occurs in Farallones de Cali (4,400 m), which is below the snowline in Colombia (≈4,700 m) and therefore this range lack snow–capped peaks. Other geographical features of relevance in the Western Cordillera, from south to north, are: Cerro Calima (2,200 m), Cerros de Roldanillo (3,650 m), Cerro Torra (3,670 m), Cerro Tamana (4,200 m), Cerro de Caramanta (3,800 m), Farallones de Citara (3,300 m), Cerro Horqueta (2,800 m), Cerro de Sumbaculo (3,200 m), Cerro de San Jose (3,000), Paramo de Frontino (4,080 m), Alto Yermal (3,100 m) and Paramillo (3,960 m).

The Central Andes Cordillera presents an average elevation of ≈2,700 m (CV ≈55%, n = 128,922), and an average width of ≈130 km (CV ≈40%, n = 10) at 500 m of elevation. This range holds the highest elevations among the three ranges having snow–capped peaks that reach altitudes near 5,600 m. Among the most important geographical features of this range are: Chiles Volcano¹ (4,761 m), Cumbal Volcano (4,850 m), Azufral Volcano (4,070 m), Cerro Patascoy (3,100 m), Bordoncillo Volcano (3,700 m), Doña Juana Volcano (4,250 m), Paramo de Las Papas (4,200 m), Pico Paletara (4,482 m), Sotara Volcano (4,580 m), Nevado del Huila (5,439 m), Paramo

¹ Some authors consider Chiles, Cumbal and Azufral volcanoes as situated on the Western Andes. Nonetheless, this confusion stems from the fact that Chiles Volcano, which is in the border with Ecuador, is certainly in the western range of the Ecuadorian Andes. In despite, in Colombia is part of the Huaca Massif that continues as the Colombian Massif and the Central Andes.

de Las Herosas (3,600 m), Paramo de Barragan (4,500 m), Nevado del Tolima (5,616 m), Nevado del Quindio (5,150 m), Nevado de Santa Isabel (5,110 m), Nevado del Cisne (5,135 m), Nevado del Ruiz (5,300 m), Cerro La Ceja (1,636 m) and Alto de Tamar (2,350 m). The Eastern Cordillera presents an average elevation of $\approx 2,600$ m (CV $\approx 55\%$, $n = 176,067$), and an average width of ≈ 140 km (CV $\approx 50\%$, $n = 11$) at 500 m of elevation. Similarly, to the Central Cordillera, the Eastern Cordillera possesses snow-capped peaks that reach altitudes near 5,500 m. The main geographical features of this range are: Cerro de Miraflores (2,800 m), Cerro Neiva (2,700 m), Alto Las Oseras (3,830 m), Paramo de Sumapaz (3,820 m), Paramo de Chipaque (3,223 m), Paramo de Chingaza (3,950 m), Cerro de Monserrate (3,190 m), Alto El Tablazo (3,285 m), Paramo de Guerrero (3,300 m), Paramo de Pisba (3,900 m), Peña de Saboya (4,003 m), Paramo de Rechimiga (4,650 m), Paramo de Guantiva (4,326 m), Nevado del Cocuy (5,493 m), Paramo del Almorzadero (4,093 m), Paramo de San Turban (4,030 m), Cerro Las Jurisdicciones (3,850 m), Alto del Venado (2,760 m) and Cerro Pintado (3,000 m).

Additionally, to the main ranges there are a series of low mountain ranges and hills in the different regions of the country, which are either a continuation of the main Andean ranges or isolated systems. To the north, in the Caribbean, the Western Cordillera continues as two separated spurs known as Serrania de Abibe and Serrania de San Jeronimo, which presents their maximum elevations in Cerro Carrizal (2,200 m) and Cerro Quimari (2,000 m) in the first case and in Cerro Murrucucu (1,270 m) in the second. On the other hand, extending the Andean region to the north, the Western Andes Cordillera prolongs as Serrania de Ayapel, reaching its maximum elevation in Cerro Oso (600 m). In a similar way, the Central Cordillera projects as the Serrania de San Lucas (m.e. $\approx 2,200$ m), meanwhile the Eastern Cordillera continues as the Serrania de Los Motilones (m.e. $\approx 2,800$ m) and afterwards as the Serrania del Perija (m.e. $\approx 3,500$ m). In the northwest portion of the Caribbean Region is located the most important isolated mountain in the country, the Sierra Nevada the Santa Marta, which according to Haffer (1974) is geologically related to the Central Cordillera. This mountain holds the highest elevations for the country in the peaks Bolivar (5,770 m) and Colon (5,800 m). Other isolated hill ranges of relevance in the region are: Serrania de San Jacinto or Montes de Maria (m.e. ≈ 800 m), Cerro El Caballo (475 m), Serrania del Piojo (m.e. ≈ 500 m), Serrania de Santa Rosa (m.e. ≈ 500 m), Serrania de Cosinas (m.e. ≈ 600 m) and Serrania de Macuira (m.e. ≈ 800 m). In the southwest corner of the Orinoco region, the Eastern Cordillera projects southeast as a spur known as Serrania de La Macarena (m.e. $\approx 2,500$ m) that according to some authors is geologically related to the isolated hills and peaks spread to the east and the Guyanan Shield tepuis (Hilty & Brown, 2001). However, according to the Geology and Mining National Institute (INGEOMINAS), the lithology of La Macarena exhibits elements associated mainly to the Eastern Cordillera and the Amazon and not the Guyana

Shield (IGAC, 1989; Gomez–Tapias *et al.*, 2006). About 150 km southeast from La Macarena there are several plateaus and hills in between the Caqueta and the Apaporis rivers that reach elevations near 700–900 m (Hilty & Brown, 2001). Among those the most important are: Serrania de Chiribiquete (m.e. \approx 800 m), Mesas de Iguaje (m.e. \approx 600 m) and Cerro Campana (\approx 550 m). In the Pacific Region, running along the border with Panama lies a mountain range that continues further south into the Pacific lowlands as a system of low peaks and hills (Hilty & Brown, 2001). In the north portion of this mountain range is located the Serrania del Darien, which presents its maximum elevation in Cerro Tacarcuna (1,900 m). Approximately 70 km southwest from Serrania del Darien is located Cerro Quia (\approx 1,700 m) and further south is placed the Serrania del Baudo that exhibits its maximum elevation in its southern portion in Alto de Buey (1,810 m).

A1.1.2. Climate

Colombia is situated in the tropical zone between the tropics of Cancer and Capricorn. Because of this, by definition warm temperatures predominate in the country, the monthly variation in temperature is lower than the daily variation, and the variation in day length does not exceed one hour. However, temperature changes with elevation in the main mountain ranges of the country (Hilty & Brown, 2001). In this sense, the dry adiabatic lapse rate, which is the decrease in air temperature with increasing elevation, changes by 6.5 °C each 1,000 m (Briggs & Smithson, 1997). Thus, the country exhibits a wide variation in air temperature along the altitudinal gradient, presenting average monthly temperatures that oscillate between 0–10 °C in areas above the 3,000 m to 24–30 °C in the lowlands below 1,000 m (IGAC, 1989). Otherwise, precipitation exhibits a high seasonal variation, caused mainly by processes related to the general circulation of the atmosphere in the tropics (Henriquez–Daza *et al.*, 2001; Hilty & Brown, 2001). Nonetheless, the proximity to the coastline, the mountains and the vegetation play an important role in regional and local variations in both temperature and precipitation (Hilty & Brown, 2001).

The tropics absorb most of the solar energy, which later is transferred to the atmosphere and is the main factor that determines the movement of air masses between the tropics and the poles by means of a meridional circulation (Henriquez–Daza *et al.*, 2001). In this sense, due to the Coriolis Effect, in the tropics wind currents near the surface flow northeast–southwest and southeast–northwest, and are known as the northeast and the southeast trade winds respectively. Then, when both currents meet near the equator, the warm equatorial air ascends, cooling off by expansion and favouring condensation of the air moisture and the formation of clouds. At higher levels in the atmosphere, these currents continue towards northern latitudes, and again due to the Coriolis Effect the winds are deviated flowing southwest–northeast and northwest–

southeast this time. In subtropical regions, at about 30° latitude, this cold air descends heating up by compression and reducing cloud formation. Thus, in each hemisphere a convective meridional air movement circuit is formed in a wide belt known as the Hadley Cell.

Furthermore, the northeast and the southeast trade winds come into contact in a relatively narrow belt known as the Intertropical Convergence Zone (ITCZ) (Henriquez–Daza *et al.*, 2001). Thus, the northeast trades, originated in the high–pressure systems of the north Atlantic, meet the southeast trades, originated in the high–pressure systems of the south Atlantic and Pacific. It is interesting to note that the south Pacific currents cross the Equator and curve to the east, entering to the Colombian Pacific from the southwest as the west equatorials. Due to the continuous and high degree of wind convergence, in the ITCZ occur strong convection processes leading to the formation of cumulus clouds systems continuously, which make the zone the cloudiest and rainiest inside the tropics.

On the other hand, the orbit movement of the earth around the sun and the declination angle of the sun incidence varies through the year north–south, producing a strengthening and weakening of high–pressure zones in the Hadley cells north and south of the equator both in the Atlantic and the Pacific oceans (Hilty & Brown, 2001). This movement of high–pressure zones would theoretically produce two high–precipitation and two low–precipitation alternating periods during the year. Nonetheless, this expected pattern varies greatly in the different areas of the country due to regional and local factors. Moreover, the change in strength of the high–pressure systems leads also to the movement of the ITCZ, which determines the rainiest periods in different areas of the country (Henriquez–Daza *et al.*, 2001).

Regionally, the main mountain ranges and the vegetation exert a strong influence on climate, while locally fluxes associated to the physical behaviour of the air as well as the topography and water masses may have an important role in the predominant conditions. In the Andean Region the three main ranges modify general circulation, acting as elevated sources and sinks of heat through the elevational gradient (Hilty & Brown, 2001), and catalysing orographic precipitation processes (Barry & Chorley, 2003). Thus, the Andean ranges constitute a barrier to the warm and humid winds forcing their upward movement and subsequent cooling off by expansion. The moisture contained condenses and forms clouds that finally precipitate primarily as rainfall in the windward side of Andean foothills and slopes. Moreover, the continued flux of air that reaches the top of the mountains and passes over them then descends creating the so–called rain shadow effect in the leeward side, creating interior dry valleys. In the Amazon and in the Pacific lowlands the extensive masses of forests produce by evapotranspiration a cooling cycle, which plays an important role in the generation of evening rainfalls daily (Hilty & Brown, 2001). In this sense, the warm

air charged of humidity due to the evapotranspiration process, ascends to higher levels in the atmosphere where it is cooled off by expansion and condenses, forming clouds that usually in the late afternoon and evening descend and precipitate as rainfall.

In the different natural regions of the country, the climate varies extraordinarily, each area exhibiting its own characteristic conditions. In the Caribbean, the temperature exhibits the highest values in the country. With a monthly average temperature between 28–32 °C in the medium and high Guajira, central Cesar and Bolivar, and south Magdalena, Atlantico and Bolivar (Henriquez–Daza *et al.*, 2001), and a variation lower than 2 °C between the warmest and the coldest month during the year (Hilty & Brown, 2001). Otherwise, the average monthly temperature ranges between 24–28 °C in the region (Henriquez–Daza *et al.*, 2001). The region shows the lowest values of precipitation in the country and a well–marked seasonality. In general, the average total annual rainfall presents values between 500–2,000 mm, and it shows a well–defined gradient north–south (Henriquez–Daza *et al.*, 2001). From mid December to mid April, during the northern hemisphere winter, the movement to the south of the north trade wind belt induces strong winds over the region that produces a severe drought (Hilty & Brown, 2001). Thus, in most of the region the precipitation exhibits a monomodal pattern. Evolutionarily the dry forest has adapted to these conditions and consequently, many of its trees loss their leaves seasonally, as well as in savannah areas grasses dry completely (Hilty & Brown, 2001). From December to April less than 4 days of rain per month are usually registered, while the rainiest period during the year is observed in May–November, registering a maximum of 15 days with rain in October (Henriquez–Daza *et al.*, 2001). In some areas, a clearly bimodal pattern is observed such as for example in the central Guajira, the slopes of the Sierra Nevada de Santa Marta and to the interior of the region near the Andes. In this sense, in July there is a reduction of rainfall, usually recording between 5–10 days of rain (Henriquez–Daza *et al.*, 2001). The Sierra Nevada de Santa Marta constitutes an exceptional case regarding the amount of precipitation it receives annually. In this case, the mountain traps good part of the humidity of the north trades producing abundant orographic rain on its slopes (Hilty & Brown, 2001). The highest values of precipitation are exhibited in the northwestern slopes in the Guachaca, Buritaca, Don Diego and Palomino watersheds, where have been reported values higher than 4,000 mm of rain per year at elevations between 1,400–2,000 m (IGAC, 1993; Hilty & Brown, 2001).

The Andean region is characterised by a high variability in both temperature and precipitation. Due to the temperature gradient in the Andes, caused by the adiabatic lapse rate, the Andes may be classified in a series of thermal belts in which different temperature conditions predominate. In this sense, according to IGAC (1989) there are six different thermal belts present in the country. At elevations below 1,000 m is the warm belt, which exhibits average monthly temperatures above 24 °C. From

1,000–2,000 m is the temperate belt that presents average monthly temperatures between 16–24 °C. Continuing, ascending in the mountains, from 2,000–3,000 m is the cold belt, which is characterised by average monthly temperatures that oscillate between 10–16 °C. From 3,000–4,000 m is located the paramo belt, where are predominant average monthly temperatures between 0–10 °C. Above the paramo, from 4,000–4,700 m is the superparamo belt, in which average monthly temperatures are usually around 0 °C. Finally, on the top of the Colombian Andes is the snow belt, where permanent glaciers are present and the average monthly temperatures usually are below 0 °C.

The region presents a high variation in precipitation due to its complex relief (Hilty & Brown, 2001). In this sense, the average total annual rainfall ranges between 2,000–5,000 mm per year, showing its lowest values in the Eastern Cordillera and in the high Cauca and Magdalena valleys and its maximum values in the northern middle Cauca and Magdalena valleys (Henriquez–Daza *et al.*, 2001). In general, the precipitation regime in the region is bimodal, presenting two periods of high rainfall and two periods of low rainfall (Hilty & Brown, 2001). Thus, in the northern half of the region, in the departments of Antioquia, Norte de Santander, Santander, Boyaca, Cundinamarca, Caldas, Risaralda and Quindio, the low rainfall periods are observed in January–February and July–August, when usually about 10–15 and 15–20 days of rain per month are recorded respectively (Henriquez–Daza *et al.*, 2001). Otherwise, during the rest of the year more than 20 days of rain per month are registered, especially in the departments of Antioquia, Caldas, Risaralda and Quindio (Henriquez–Daza *et al.*, 2001). In the southern half, in the departments of Tolima, Huila, Valle del Cauca, Cauca and Nariño, a similar pattern in the distribution of rainfall during the year is observed. Nonetheless, contrary to what was described for the northern portion, in the south the period July–August exhibits fewer days of rain than the period January–February (Henriquez–Daza *et al.*, 2001). It is interesting to note that in several areas of the inter–Andean valleys there is an important rain shadow effect, which plays an important role in making them, in general, relatively dry zones; *e.g.* the mid and high Cauca and Magdalena valleys (Hilty & Brown, 2001). The high Cauca valley is the driest, exhibiting an average total annual rainfall of 1,500 mm and 2,000 mm in the adjacent slopes, meanwhile in the high Magdalena valley respective values are 1,700 mm and 3,000 mm (Hilty & Brown, 2001). In the Western Cordillera, the high Sucio, Dagua and Patia valleys form dry valleys immersed in cloud and covered by montane forests (Hilty & Brown, 2001). Similarly, in the Eastern Cordillera in the departments of Norte de Santander, Santander, Cundinamarca and Boyaca, the Zulia, Lebrija, Sogamoso, Suarez and Chicamocha valleys form valleys with very dry conditions in which precipitation ranges from 500–1,000 mm (IGAC, 1989). Similar conditions are observed in the south in Nariño in the Gaitara and Carchi valleys (Hilty & Brown, 2001).

In the Pacific region, climatic conditions are relatively homogeneous, and a warm and humid climate dominates the zone (Hilty & Brown, 2001). The average monthly temperatures range between 24–28 °C, although in the coastline temperatures are slightly lower than in the coastal plains to the east (Henriquez–Daza *et al.*, 2001). The region is one of the rainiest in Colombia and in the world. In the Pacific slopes of the Western Cordillera the rain is mainly orographic, and it is caused by the encounter between the west equatorials and the Western Cordillera, although in the coastal plains the massive extension of forests cause a cooling cycle due to the evapotranspiration process that induce evening rainfalls daily. Thus, average total annual rainfall oscillates between 2,000–12,000 mm per year (IGAC, 1989; Henriquez–Daza *et al.*, 2001). In the coastline in the north of Choco, in the Golfo de Uraba, and in southwest Nariño, in Bahia de Tumaco and north and south of it, the average total annual precipitation ranges between 2,000–3,000 mm per year. The highest values are observed in the centre of the region in the areas around the headwaters of the Atrato and San Juan rivers, with average values above 13,000 mm per year, and historic records above 19,000 mm (Hilty & Brown, 2001 and references therein). Furthermore, in the north and central parts of the region the precipitation does not show marked differences during the year, exhibiting on average 20–25 days with rain per month (Henriquez–Daza *et al.*, 2001). In contrast, to the south the variability in the distribution of rainfall during the year increases, showing maximum variability near Tumaco (Henriquez–Daza *et al.*, 2001). In Tumaco, a monomodal pattern in rainfall exists, with a high rainfall period during January–June when about 14–19 days with rain per month are registered, and a low rainfall period between July–December when rainfall decreases gradually, and 7–13 days with rain per month are recorded, with a minimum in November (Henriquez–Daza *et al.*, 2001).

To the east, the Orinoco region is characterised by a relatively flat relief, which promotes a very homogeneous spatial distribution of the temperatures (Henriquez–Daza *et al.*, 2001). Thus, average monthly temperatures in the region are between 24–28 °C, showing a maximum variability in the Andean foothills with values between 8–20 °C (Henriquez–Daza *et al.*, 2001). In contrast, precipitation shows certain variation ranging between 1,500–6,000 mm of rain per year (Henriquez–Daza *et al.*, 2001). In this sense, the highest values are observed in the Andean foothills where average values of total annual rainfall exceed 3,000 mm of rain per year. Rainfall decreases gradually to the east of the Andes exhibiting values around 2,000–2,500 mm per year in the central part of the region and values close to 1,500 mm of rain per year in the north–centre in Arauca (IGAC, 1989). Rainfall distribution during the year shows a monomodal pattern, exhibiting a high rainfall period in May–October when around 20 days of rain per month are recorded, and a low rainfall period between November–April when about 1–4 days of rain per month are registered (Henriquez–Daza *et al.*, 2001).

To the southeast, the Amazon region presents very similar conditions to the Orinoco. Thus, average temperatures in the Amazon range between 24–28 °C and show a maximum variation in the Andean foothills where temperatures fluctuate in the elevational gradient between 12–20 °C (Henriquez–Daza *et al.*, 2001). Precipitation is relatively high and varies between 3,000–4,500 mm of rain per year. It presents its highest values in the Andean foothills where the average total annual rainfall values may exceed 4,000 mm of rain per year (Henriquez–Daza *et al.*, 2001). To the east most of the region values average 2,500–3,500 mm of rain per year, although there are sparse pockets where values are as low as 2,000 and as high as 4,000 mm of rain per year (Mulligan, 2006). The distribution of precipitation during the year follows a monomodal pattern that is different between regions positioned north and south of the Equator (Henriquez–Daza *et al.*, 2001). In both cases, during the high rainfall period rainfall events usually occur as frequently as 15 days per month or more, north of the Equator around July, while south of it around January. Moreover, the low rainfall period for each hemisphere occurs roughly in the month that coincides with the period of high rainfall in the opposite hemisphere (Henriquez–Daza *et al.*, 2001).

A1.1.3. Vegetation

Vegetation distribution in Colombia is principally determined by regional and local climatic conditions (Hilty & Brown, 2001). In this context, the wide variation in climate in the country results in a high diversity of vegetation formations and ecosystems. Several climatic classification systems used world-wide have been applied to assess the diversity of terrestrial ecosystems or the ecological and vegetation units present in the country (Marquez–Calle, 2003). Most of these classifications are based on the predominant climate conditions and use the average behaviour of variables such as precipitation and temperature to differentiate among units (Henriquez–Daza *et al.*, 2001). Thus, the classifications of Köppen, Thornthwaite, Caldas, Lang, Martonne and Holdridge, among others have been applied in the country (Henriquez–Daza *et al.*, 2001 and references therein). It is interesting to notice that since all of these are based in similar criteria, in general, they present similarities, although they differ in the detail and level of specificity of the different classified units (Table A1.1.3.1). Furthermore, other factors of importance such as for instance soil, winds, proximity to water masses and other local factors, may play an important role in the predominant local conditions and therefore in the ecosystems or ecological and vegetation units present in particular areas (Henriquez–Daza *et al.*, 2001; Hilty & Brown, 2001). In this sense, the most detailed classification to date is the one proposed by Etter (1998), based on Holdridge life zones criteria but integrating soil and biogeographical information (Table A1.1.3.1).

Table A1.1.3.1. Climatic/ecological classification systems applied in Colombia.

Name	Classified units	Units for Colombia	Remarks
Caldas	Thermal belts	5	Based on temperature.
Lang	Climate classes	6	Based on temperature and precipitation.
Caldas–Lang	Climate types	25	Combine Caldas and Lang criteria.
Martonne	Climate types	6	Based on temperature and precipitation, including information of the driest month.
Köppen	Climate types	12	Based on temperature and precipitation, including information of variation range in values and period of the year when maximum values occur.
Thornthwaite	Climate types	8	Based on water balance, estimated as the difference between precipitation and potential evapotranspiration (PET).
Holdridge	Climate	26	Based on temperature, precipitation and PET.
	Vegetation formation	34	
Hilty–Brown	Vegetation formation	9	Variation of Holdridge classification (Hilty & Brown, 2001).
	Habitat types	22	
Etter	Biome general types	9	Integrate Holdridge life zones with soil and biogeographical information (Etter, 1998).
	Biomes	21	
	Ecosystems	81	
Marquez	Main ecosystem types	5	Variation of Dinerstein et al. (1995) ecoregions classification (Marquez–Calle, 2003).
	Main habitat types	15	

Otherwise the most widely used classification in the country has been the one based on Holdridge life zones (Holdridge *et al.*, 1971; Espinal, 1990). According to Hilty & Brown (2001), who used a variation of Holdridge’s criteria, there are 13 main vegetation formation subdivisions present in the country. Thus, in the Caribbean lowlands are present the tropical desert scrub, tropical thorn woodland and tropical dry forest. In the lowlands of the Pacific, Amazon, and southern Orinoco regions, exist the tropical moist forest. Moreover, tropical wet and rain forest in the central Pacific region and in some pockets in the Amazon and the Andean foothills. In the Andes and the main mountain ranges, is present the dry, moist and wet premontane, and moist and wet montane forest; and at higher elevations, in the cordilleras and in Sierra Nevada de Santa Marta, the Paramo (equivalent to alpine rain tundra). Finally, to the east, most of the Orinoco region is occupied by the tropical savannah.

In the Caribbean the tropical desert scrub is present in areas with an average total annual precipitation lower than 250 mm, a PET ratio equal or higher than 8 and average monthly temperature higher than 24 °C (Holdridge *et al.*, 1971). It is located in the high Guajira, from Riohacha and to the north. In more humid areas with average total annual rainfall between 250–500 mm and PET ratio between 4–8 (Holdridge *et al.*, 1971), is present the tropical thorn woodland. This formation occurs mainly in coastal areas around Cartagena, between Barranquilla and Santa Marta and east and south of Riohacha. Finally, in areas with average total annual rainfall between 500–2,000 mm and PET ratio between 1–4 (Holdridge *et al.*, 1971), is present the tropical dry forest (including the very dry forest). This formation is potentially distributed in the rest of the lowlands of the Caribbean, the mid and high Cauca and Magdalena valleys and in small interior dry valleys of the Andes such as for instance the high Sucio, Dagua and Patia river valleys in the Western Cordillera, and the Zulia, Lebrija, Sogamoso, Suarez and Chicamocha river valleys in the Eastern Cordillera (Hilty & Brown, 2001). In general, these three formations are composed mainly of xerophytic scrub, low bushes and columnar cactuses, and in the driest areas terrestrial bromeliads from the genus *Bromelia* (Hilty & Brown, 2001). However, in the driest regions, the vegetation is shorter and more open, a feature that changes gradually as moisture increases (Hilty & Brown, 2001). The most common bushes genera include *Acacia*, *Calotropis*, *Mimosa* and *Prosopis*, while the most common cactus genera are *Lemaireocereus*, *Pereskia* and *Opuntia* (Hilty & Brown, 2001).

The tropical moist forest is the most widely distributed vegetation formation in the lowlands of Colombia. It is potentially present in areas with an average total annual rainfall of 2,000–4,000 mm of rain and PET ratio between 0.5–1 (Holdridge *et al.*, 1971). Its distribution in Colombia extends from Golfo de Uraba to the east to the mid–low Cauca and Magdalena valleys and the mid Magdalena valley, and to the east of the Andes in the forested areas of the Orinoco and the Amazon region. Major part of the forests found from the eastern half of Vaupes to Vichada and along the Orinoco river grow in “poor” white–sand soils, where usually forests canopy height is shorter and diversity is lower than in other Amazonian forests (Hilty & Brown, 2001). Tree diversity in moist lowland forests in the Neotropics is outstanding, about 300 different species of trees in a single plot of one hectare being found (Gentry, 1988). In this sense, Colombia is not the exception and lowland forests in the country exhibit a high diversity of trees, palms and vines, and although there is no clear dominance in those forests of any particular species or groups there are many species of legumes (family Leguminosae) that are common (Hilty & Brown, 2001). Among the emergent trees are common genera such as *Cedrela*, *Ceiba*, *Lecythis* and *Terminalia*, which usually have an average height of about 40–50 m. Other important genera in the canopy and borders are *Cecropia*, *Erythrina*, *Ficus*, *Hura*, *Inga*, *Jacaranda*, *Nectandra*, *Ochroma*, *Pentaclethra*, *Spondias*, *Tabebuia* and *Virola*, plus *Calophyllum*, *Ficus* and *Ogcodela* in the varzea forests.

The tropical wet and rain forests are present in regions where the average total annual rainfall oscillates between 4,000–8,000 mm and 8,000–16,000 mm, and the PET is around 0.25–0.5 and 0.125–0.25, respectively (Holdridge *et al.*, 1971). These formations represent the dominant formations west of the Western Cordillera in the Pacific region, although the rain forest is restricted to a few pockets in the lowlands adjacent to the Pacific slope (Hilty & Brown, 2001). The wet forest, which is more widely distributed, is present as well in narrow bands in the foothills north of the Central Cordillera in the Serrania de San Lucas, in the eastern slope foothills of the Eastern Cordillera between Yopal and Villavicencio and between Florencia and the border with Ecuador, as well as in northeast Amazon in the border with Vaupes. Similarly, to the moist forest, tree diversity is very high and among the most important genera are: *Ardisia*, *Brosimum*, *Cecropia*, *Cedrela*, *Cespedesia*, *Calophyllum*, *Dussia*, *Gustavia*, *Guateria*, *Hieronyma*, *Hirtella*, *Inga*, *Isertia*, *Jacaranda*, *Miconia*, *Nectandra*, *Parkia*, *Tapirira*, *Virola*, *Vismia* and *Vochysia* (Hilty & Brown, 2001).

The premontane and montane forests are present in mountainous regions of the country. In general, the conditions of rainfall and PET are the same as those mentioned for the respective tropical forest types. However, in this case differently to tropical areas, which average monthly temperatures above 24 °C, in premontane areas temperature averages 18–24 °C, while in montane areas it is between 6–18 °C (Holdridge *et al.*, 1971). In the mountains of Colombia the wide range of climatic conditions promote the existence of different types of forest with very different moisture conditions that vary from dry to very wet, and though humidity is not a limiting factor the height of the canopy decreases in an altitudinal gradient (Hilty & Brown, 2001). In dry valleys, vegetation is predominantly composed of bushes and cacti. Among the most common genera that may be found in those areas are *Agave*, *Euphorbia*, *Spartium*, and *Opuntia* (Hilty & Brown, 2001). In wetter areas, where average total annual rainfall is above 1,000 mm of rain per year, premontane forest trees are usually covered by bromeliads, ferns, mosses and other epiphytes such as for instance orchids of many different genera, as well as are very common arborescent ferns of the genus *Cyanthea* and *Dicksonia* (Hilty & Brown, 2001). Between the dominant families in this formation are: Lauraceae, Moraceae and Myrtaceae, and the most common genera are: *Quercus*, *Cassia*, *Cecropia*, *Clusia*, *Croton*, *Coussapoa*, *Erythrina*, *Ficus*, *Inga*, *Isertia*, *Juglans*, *Miconia*, *Myrcia*, *Ochroma*, *Persea*, *Tecoma*, *Trema*, *Vismia* and *Weinmannia* (Hilty & Brown, 2001). At higher elevations in the lower montane forest average temperatures range between 12–18 °C, trees are shorter and the understory is very dense and usually dominated by small bamboos of the genus *Chusquea* (Hilty & Brown, 2001). In the upper montane forest average temperatures range between 6–12 °C, trees become even shorter and in its upper limit small trees and bushes are predominant, forming more open mosaics in the forest–paramo ecotone. The most common genera in this formation are *Baccharis*,

Escallonia, *Hesperomeles*, *Vallea*, *Gynoxys*, *Hedyosmum*, *Podocarpus*, *Polylepis*, *Rubus*, *Senecio*, *Vaccinium*, *Viburnum* and *Weinmannia* (Hilty & Brown, 2001).

At elevations from 3,100 m to the upper limit for vegetation, it is possible to find the paramo (Hilty & Brown, 2001). However, its upper and lower limits are highly dependent on moisture conditions, which are highly variable between the different Andean ranges and the Sierra Nevada de Santa Marta. Thus, for example in very wet slopes such as in the Central Cordillera the paramo appears above $\approx 3,700$ m, meanwhile in relatively less humid slopes such as in the Eastern Cordillera the paramo starts above $\approx 3,300$ m (Van Der Hammen, 1998). The paramo is mainly a matrix of grasses (*Agrostis* and *Calamagrostis*) with sparse patches of Frailejon (*Espeletia* and *Espeletiopsis*). In this formation is possible to find patches of *Polylepis* sp. woodlands, which usually are present below 3,900 m of elevation (Hilty & Brown, 2001). Moreover, near or surrounding creeks, streams and lagoons it is usual to find bushes from the Asteraceae and Ericaceae families. Hence, the most common genera are *Hypericum*, *Alchemilla*, *Buddleia*, *Escallonia*, *Gynoxys*, *Libonathamus* and *Senecio* (Hilty & Brown, 2001). In the upper limit of the paramo ($\approx 4,500$ – $4,700$ m) bushes disappear and vegetation is composed mainly by *Agrostis*, *Calamagrostis*, *Carex*, *Festuca*, *Valeriana*, etc. mixed with Frailejon and mosses that disappear gradually before the upper paramo limit (Hilty & Brown, 2001). Furthermore, in wetland areas are common *Carex*, *Werneria*, *Distichia*, *Plantago*, *Equisetum*, *Lycopodium*, *Sphagnum*, etc. (Hilty & Brown, 2001).

Finally, the tropical savannah is the vegetation formation that covers most of the Orinoco region. It develops in areas with an average total annual precipitation between 1,700–4,000 mm of rain per year, although this formation is the result of different environmental factors such as soils and seasonal fires that limit the development of forest in those zones (Hilty & Brown, 2001). The savannah is constituted by a matrix of grasses with sparsely distributed trees and riparian forests along watercourses. Grasses vary in size, from the short *Axonopus*, *Leptocoryphirum*, *Paspalum*, *Trachypogon* in the driest areas to the long *Andropogon* and *Mesosetum* in the wettest areas (Hilty & Brown, 2001). In the foothills of the Eastern Cordillera the savannah intergrades with the forests as well as it occurs along the rivers to the east, where grow gallery forests or “Morichales”, where the palm *Mauritia* is dominant (Hilty & Brown, 2001). In the driest areas, the most common tree species are *Byrsonima*, *Curatella*, *Palicourea*, *Pavonia*, *Psidium* and *Mauritia*, while in the gallery forests are frequently found genera as *Jacaranda*, *Miconia* and the palm *Acrocomia* (Hilty & Brown, 2001). Otherwise, in the wettest areas where usually there are present seasonally-flooded plains or “Esteros” is also common to find stands of the tree *Caraipa* (Hilty & Brown, 2001).

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APPENDIX 2
BIOCLIM PRINCIPAL COMPONENTS ANALYSES

Table A2.1. WorldClim bioclimatic variables list.

BioClim code	BioClim variable name
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (* 100)
BIO4	Temperature Seasonality (standard deviation *100)
BIO5	Max. Temperature of Warmest Month
BIO6	Min. Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Table A2.2. PCA eigenvalues table for BioClim variables obtained during the first modelling generation. Analysis was performed for Colombia using a grain of 1km.

Basic Stats	Min.	Max.	Mean	S.D.	Num.	Eigenvalue
Bio1	-4.6	29.2	24.579	4.512	1	8.01644
Bio2	4.6	13.3	9.521	0.861	2	6.61421
Bio3	6.6	9.6	8.110	0.615	3	1.77888
Bio4	9.9	124.5	56.524	23.218	4	1.39868
Bio5	0.5	36.4	30.812	4.901	5	0.62276
Bio6	-11.3	23.9	19.084	4.555	6	0.30027
Bio7	5.7	17.0	11.728	1.264	7	0.09849
Bio8	-4.2	29.2	24.139	4.378	8	0.08015
Bio9	-5.7	30.0	24.842	4.683	9	0.05260
Bio10	-3.8	30.3	25.239	4.670	10	0.01559
Bio11	-5.8	28.5	23.785	4.383	11	0.00825
Bio12	261	11,314	2,671.035	1,076.353	12	0.00525
Bio13	72	1,325	352.782	116.886	13	0.00384
Bio14	0	752	84.744	81.049	14	0.00192
Bio15	10	118	42.273	16.230	15	0.00158
Bio16	169	3,794	967.038	334.815	16	0.00079
Bio17	0	2,495	322.772	252.604	17	0.00015
Bio18	22	2,751	459.036	294.714	18	0.00007
Bio19	0	3,132	853.456	367.068	19	0

Non-shaded cells represent temperature related variables, while shaded cells indicate rainfall related variables.

Table A2.2. PCA correlation matrix for BioClim variables obtained during the first modelling generation. Analysis was performed for Colombia using a grain of 1km.

Co- rrela- tion	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	
Bio1	1																			
Bio2	0.038	1																		
Bio3	-0.309	0.106	1																	
Bio4	0.447	-0.107	-0.902	1																
Bio5	0.985	0.130	-0.412	0.538	1															
Bio6	0.992	-0.060	-0.275	0.428	0.967	1														
Bio7	0.246	0.722	-0.608	0.544	0.393	0.145	1													
Bio8	0.996	0.033	-0.260	0.397	0.972	0.988	0.207	1												
Bio9	0.996	0.031	-0.347	0.488	0.989	0.990	0.267	0.988	1											
Bio10	0.998	0.031	-0.363	0.502	0.991	0.989	0.279	0.990	0.998	1										
Bio11	0.998	0.048	-0.256	0.390	0.977	0.991	0.218	0.997	0.992	0.992	1									
Bio12	0.232	-0.266	0.266	-0.147	0.167	0.288	-0.389	0.238	0.239	0.215	0.248	1								
Bio13	0.299	-0.166	0.112	-0.001	0.268	0.344	-0.199	0.289	0.310	0.292	0.309	0.924	1							
Bio14	0.009	-0.284	0.569	-0.456	-0.099	0.065	-0.617	0.045	-0.009	-0.027	0.037	0.799	0.570	1						
Bio15	0.196	0.255	-0.556	0.477	0.291	0.148	0.596	0.161	0.196	0.229	0.174	-0.495	-0.200	-0.777	1					
Bio16	0.319	-0.202	0.083	0.035	0.287	0.367	-0.208	0.307	0.334	0.314	0.326	0.946	0.985	0.597	-0.248	1				
Bio17	0.035	-0.308	0.517	-0.401	-0.069	0.093	-0.600	0.067	0.022	0.002	0.060	0.840	0.620	0.990	-0.782	0.649	1			
Bio18	-0.115	-0.233	0.605	-0.549	-0.219	-0.070	-0.597	-0.079	-0.141	-0.152	-0.083	0.773	0.601	0.899	-0.645	0.599	0.893	1		
Bio19	0.347	-0.168	-0.036	0.157	0.343	0.396	-0.100	0.316	0.381	0.351	0.347	0.847	0.894	0.460	-0.198	0.918	0.522	0.401	1	

Non-shaded cells immediately left from the diagonal represent temperature related variables, while shaded cells immediately left from the diagonal indicate rainfall related variables.

Table A2.2. PCA eigenvalues table for BioClim variables obtained during the second modelling generation. Analysis was performed for northern South America using a grain of 1km.

Basic Stats	Min.	Max.	Mean	S.D.	Num.	Eigenvalue
Bio1	-6.5	29.2	24.882	3.803	1	7.09303
Bio2	4.5	15.9	10.049	1.204	2	2.45642
Bio3	4.7	9.6	8.120	0.598	3	1.06530
Bio4	8.5	251.6	52.421	24.345	4	0.34467
Bio5	0	36.4	31.183	3.830	5	0.03190
Bio6	-16.7	24.0	18.803	4.277	6	0.00353
Bio7	5.6	20.6	12.379	1.835	7	0.00342
Bio8	-5.3	29.2	24.683	3.663	8	0.00126
Bio9	-8.0	29.9	24.758	3.991	9	0.00029
Bio10	-5.3	30.3	25.465	3.835	10	0.00014
Bio11	-8.0	28.5	24.151	3.827	11	0
Bio12	1	11,158	2,287.909	866.558	1	5.27842
Bio13	1	1,281	311.520	100.540	2	1.63426
Bio14	0	739	77.627	66.800	3	0.64001
Bio15	7	259	46.352	23.581	4	0.28669
Bio16	1	3,684	862.866	285.502	5	0.11690
Bio17	0	2,457	274.812	209.936	6	0.02771
Bio18	0	2,713	462.665	226.034	7	0.0108
Bio19	0	3,094	602.926	386.307	8	0.00518

Non-shaded cells represent temperature related variables, while shaded cells indicate rainfall related variables.

Table A2.2. PCA correlation matrix for BioClim variables obtained during the second modelling generation. Analysis was performed for northern South America using a grain of 1km.

Co- rrela- tion	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	
Bio1	1																			
Bio2	-0.349	1																		
Bio3	-0.105	-0.075	1																	
Bio4	-0.003	0.136	-0.675	1																
Bio5	0.972	-0.188	-0.262	0.135	1															
Bio6	0.970	-0.533	0.015	-0.080	0.903	1														
Bio7	-0.232	0.851	-0.582	0.469	-0.018	-0.445	1													
Bio8	0.991	-0.326	-0.120	0.041	0.964	0.950	-0.203	1												
Bio9	0.992	-0.388	-0.082	-0.023	0.962	0.980	-0.276	0.970	1											
Bio10	0.996	-0.340	-0.168	0.084	0.981	0.961	-0.191	0.990	0.987	1										
Bio11	0.997	-0.361	-0.057	-0.081	0.959	0.974	-0.267	0.984	0.991	0.986	1									
Bio12												1								
Bio13												0.868	1							
Bio14												0.743	0.396	1						
Bio15												-0.572	-0.210	-0.761	1					
Bio16												0.887	0.988	0.415	-0.236	1				
Bio17												0.788	0.445	0.991	-0.776	0.463	1			
Bio18												0.696	0.474	0.727	-0.542	0.489	0.735	1		
Bio19												0.718	0.725	0.473	-0.308	0.723	0.517	0.197	1	

Non-shaded cells immediately left from the diagonal represent temperature related variables, while shaded cells immediately left from the diagonal indicate rainfall related variables.

APPENDIX 3

RECLASSIFICATION OF WEST COLOMBIA ELEVATIONAL GRADIENT
IN APROXIMATELY EQUAL SURFACE AREA BANDS

Table A3.1. Parameters used to reclassify DEM of West Colombia using Approximately Equal Surface Area Bands. New bands were created aggregating estimations of total surface area in 1m bands along West Colombia.

New_Band_Value	New_Band_Label	Sum of Surface ($10^3 \times \text{km}^2$)	Absolute difference from 10 ($10^3 \times \text{km}^2$)	New_Lower_Limit (m)	New_Upper_Limit (m)
0		4.328591438	5.671408562		
1	4.5–12.5	10.49987859	0.499878592	4.5	12.5
2	12.5–18.5	10.4203351	0.420335104	12.5	18.5
3	18.5–24.5	10.29725594	0.297255936	18.5	24.5
4	24.5–31.5	9.77899136	0.22100864	24.5	31.5
5	31.5–39.5	10.66627571	0.666275712	31.5	39.5
6	39.5–47.5	10.62442547	0.624425472	39.5	47.5
7	47.5–55.5	10.36128576	0.36128576	47.5	55.5
8	55.5–64.5	10.44310234	0.443102336	55.5	64.5
9	64.5–73.5	10.2786016	0.2786016	64.5	73.5
10	73.5–83.5	9.810011456	0.189988544	73.5	83.5
11	83.5–94.5	9.930785088	0.069214912	83.5	94.5
12	94.5–106.5	9.65196096	0.34803904	94.5	106.5
13	106.5–121.5	10.1947375	0.194737504	106.5	121.5
14	121.5–141.5	10.00210483	0.002104832	121.5	141.5
15	141.5–165.5	10.13780806	0.137808064	141.5	165.5
16	165.5–201.5	10.12491357	0.124913568	165.5	201.5
17	201.5–251.5	10.04083314	0.040833136	201.5	251.5
18	251.5–309.5	9.977611792	0.022388208	251.5	309.5
19	309.5–373.5	10.0438472	0.0438472	309.5	373.5
20	373.5–447.5	10.06654194	0.066541936	373.5	447.5
21	447.5–518.5	9.935921136	0.064078864	447.5	518.5
22	518.5–577.5	9.973784056	0.026215944	518.5	577.5

Table A3.1. Continued.

New_Band_Value	New_Band_Label	Sum of Surface (10 ³ × km ²)	Absolute difference from 10 (10 ³ × km ²)	New_Lower_Limit	New_Upper_Limit
23	577.5–638.5	10.03370386	0.033703864	577.5	638.5
24	638.5–703.5	9.94516616	0.05483384	638.5	703.5
25	703.5–777.5	10.02967695	0.029676952	703.5	777.5
26	777.5–849.5	9.974191952	0.025808048	777.5	849.5
27	849.5–922.5	9.935551456	0.064448544	849.5	922.5
28	922.5–983.5	9.96804756	0.03195244	922.5	983.5
29	983.5–1051.5	9.992018904	0.007981096	983.5	1051.5
30	1051.5–1127.5	9.939625976	0.060374024	1051.5	1127.5
31	1127.5–1206.5	10.02025867	0.020258672	1127.5	1206.5
32	1206.5–1289.5	10.01398321	0.013983208	1206.5	1289.5
33	1289.5–1371.5	9.907576212	0.092423788	1289.5	1371.5
34	1371.5–1457.5	9.991077824	0.008922176	1371.5	1457.5
35	1457.5–1544.5	10.0765462	0.076546196	1457.5	1544.5
36	1544.5–1631.5	10.01002181	0.010021812	1544.5	1631.5
37	1631.5–1721.5	10.02646792	0.026467924	1631.5	1721.5
38	1721.5–1817.5	10.05571672	0.05571672	1721.5	1817.5
39	1817.5–1914.5	9.965662672	0.034337328	1817.5	1914.5
40	1914.5–2026.5	10.04941777	0.049417768	1914.5	2026.5
41	2026.5–2135.5	9.968999688	0.031000312	2026.5	2135.5
42	2135.5–2248.5	9.989251096	0.010748904	2135.5	2248.5
43	2248.5–2373.5	9.958723894	0.041276106	2248.5	2373.5
44	2373.5–2498.5	10.05537977	0.055379774	2373.5	2498.5
45	2498.5–2616.5	10.00148515	0.001485154	2498.5	2616.5
46	2616.5–2741.5	10.00072971	0.000729712	2616.5	2741.5
47	2741.5–2889.5	9.982585886	0.017414114	2741.5	2889.5
48	2889.5–3067.5	10.03408629	0.034086292	2889.5	3067.5
49	3067.5–3279.5	9.965663242	0.034336758	3067.5	3279.5
50	3279.5–3539.5	9.980424858	0.019575142	3279.5	3539.5
51	3539.5–4490.5	9.989691706	0.010308294	3539.5	4490.5



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