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Diversity and Biogeography of Ferns and Birds in Bolivia: Applications of GIS Based Modelling Approaches

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Para mis queridos viejos
Gladys Auza-Gutierrez y José 'Berno' Soria-Caballero

Abstract

This dissertation focuses on a wide range of biogeographic and macroecological aspects of bird and fern species from Bolivia. In the first chapter I outlined the general purpose of this dissertation, as well as general concepts and implications of large-scale studies. In the second chapter I used the databank of fern species from Bolivia to evaluate the level to which the geographical incomplete data availability of species occurrence affects the perception of species richness and endemism. I performed, for this purpose, a cumulative temporal analysis of the aforementioned databank in a grid context. The patterns of species richness were temporally consistent. The richest areas were always placed along the humid-montane forests, even though collecting intensity were also higher in this area than in others. Endemism, on the other hand, had a lower degree of correlation with collecting intensity, and the resulting endemism spatial patterns were temporally inconsistent. The ratio between the estimated and recorded values of species richness and endemism suggested that the richest grid cells tended to be undersampled. The inter-temporal correlations showed sharper differences of correlations for endemism than species richness. Consequently, back in 1970 botanist had a correct idea of the spatial distribution of pteridophyte richness, although the absolute values of species richness were strongly underestimated. In contrast, the pattern of endemism remained obscure even for the present period.

From the previous paragraph, it is clear that distributional databanks are useful tools to deduce patterns of diversity (although fragmented), while endemism patterns remain obscure. In chapter three I used a modelling approach to model the geographic distribution of a selected group of bird and fern species of specific habitat requirements. Species distribution models (niche modelling) have been proposed as an alternative method to overcome the limited data availability. Previous studies have already addressed the possible sources of uncertainty in modelling species distributions. However, the quality of the environmental layers used to predict species distributions has been largely overlooked. I compared the geographic climatic predictions of two climate models (SAGA and Worldclim), and the geographical discrepancies of using both climate models for modelling ranges of a selected set of bird and fern species endemic to the humid-montane forest and the seasonally dry tropical forests (SDTF). SAGA and Worldclim predicted roughly similar climate patterns that were significantly correlated, but simultaneously showed important differences for the spatial distribution of the precipitation. SAGA predicted better range estimations for species endemic to the humid-montane forests than Worldclim, which

predicted the occurrence of some species near the lake Titicaca (in the high Andes). Worldclim also over predicted the occurrence of montane species in the lowlands of Chapare. Although it was not possible to find any statistical difference between the range estimations obtained with SAGA and Worldclim for the species endemic to the SDTFs, SAGA was able to better discriminate the distribution of these species in the fragments of SDTF in the north Bolivian Andes. These findings strongly suggest the superiority of SAGA over Worldclim, and simultaneously stress how critical is the quality of Worldclim for tropical countries like Bolivia.

In the fourth chapter we aimed to unravel impact of climate, regional area and geometric constraints in determining the patterns of bird species richness along the latitudinal and elevational gradient of bird species richness in the central Andes (from southern Peru and to southern Bolivia). Climate (precipitation) played the mayor role in explaining the pattern of species richness. However the other factors also played an important role that became evident when the study area was partitioned into regions and elevational belts. Precipitation had strongest impacts at lower elevations, as the strongest reductions of precipitation also occurred there. Elevation (temperature) and habitat heterogeneity gained importance especially when we analyzed the data by regions. Narrow-ranged species on the other hand, showed different geographical patterns. The factors determining their distribution were also mainly precipitation followed by habitat heterogeneity. Diversity-parameter relationships recovered when the entire area is analyzed as a sole unit reflected the overwhelming dominance of the widespread species. These finding show that by dissecting the study area into regions and elevational belts, and the species richness into quartiles let us to recover less frequent relationships that are valid for species of geographically restricted ranges. This also strongly suggests that wide continental analyses of diversity may recover only the patterns of the most common species, while overlooking the geographically restricted species that are of priority for conservation.

In chapter five, I used a modelling approach to determine the biogeographic connections of the fragments of seasonally dry tropical forests from the north Bolivian Andes across the Quaternary. I also modelled the patterns of colonization of these fragments by a selected set of bird and fern species endemic to this type of vegetation across the same span of time. The cold-dry and warm-dry climates of the Quaternary were the periods of maximum distribution of the SDTFs in Bolivia. During these periods, the SDTFs covered most of the Bolivian lowlands, and reached the Andean rain-shadow valleys (warm-dry), where today this vegetation persists isolated from the rest of the SDTFs. The central Andes

prevented the expansion of this vegetation from the southern Andes. Species on the other hand, showed different patterns of expansions and colonization of these fragments. Cold-dry Quaternary climates were favourable for connection through the lowlands, while warm climates favoured range expansions across the central Bolivian Andes. Species that today have a higher elevational range were those that reached the fragments of SDTFs across the central Andes. We found strong evidence supporting that the fragments of SDTFs are remnants of the more extensively distributed SDTFs that occupied the central Bolivian lowlands and Andean valleys during the Quaternary dry climates. The modelled distributions of the species suggest that vicariance may have played an important role in determining the current species distributions across the SDTFs in the Bolivian Andes.

In the last chapter I summarized the main findings, the implications and limitations of this type of macroecological studies. Here I presented important advances in a wide range of macroecological and biogeographic issues that ranged from the study of species richness patterns, methodological issues, parameter-diversity relationships and biogeographic processes across the Quaternary. Although Birds and ferns are probably the best documented taxa in Bolivia, distributional data was persistently a limiting factor for an important proportion of bird and fern species (mostly the ones of restricted range).

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Contents

1	An introduction to relevant concepts and problems that studies at large spatial scales face	1
1.1	Coarse diversity patterns what is already known and which are the limitations	2
1.2	Approaches to study diversity patterns in the light of limiting field data	3
1.3	Ecological niche, niche modelling, the estimation of species ranges and further applications	4
1.4	Research objectives	6
1.5	References	9
2	The Influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia	12
2.1	Introduction	14
2.2	Material and Methods	15
2.2.1	Study area	15
2.2.2	Data	16
2.2.3	Analysis	17
2.3	Results	18
2.4	Discussion	23
2.5	References	28
3	Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia	32
3.1	Introduction	34
3.2	Methods	35
3.2.1	Study area and species data	35
3.2.2	Selection of environmental variables and climate models	37
3.2.3	Comparison of climate models	38
3.2.4	Modelling species distribution	39
3.3	Results	40
3.3.1	Comparison between both climate models	40
3.3.2	Modelling species distributions	41
3.4	Discussion	44
3.3.1	Comparison between both climate models	44
3.3.2	Modelling species distributions and implications for conservation	47
3.5	References	50
4	Linking latitudinal and elevational patterns of bird species richness in the central Andes	55
4.1	Introduction	58
4.2	Methods	61

4.3	Results	65
4.4	Discussion	70
4.4.1	General patterns	70
4.4.2	Explanatory parameters	71
4.4.3	Range size	73
4.5	Conclusions	74
4.6	References	75
5	Modelled Quaternary dispersal and vicariance of habitat-endemic fern and bird species in Seasonally Dry Tropical Forests of the Bolivian Andes	80
5.1	Introduction	82
5.2	Methods	85
5.2.1	Current distribution of the SDTFs in Bolivia	85
5.2.2	Species distributions	85
5.2.3	Modelling the distribution of SDTFs	86
5.2.4	Modelling of species distributions	88
5.3	Results	89
5.3.1	Distribution of SDTFs in the present warm-wet climate	89
5.3.2	Distribution of the SDTF during the past climatic scenarios of the Quaternary	91
5.3.3	Patterns of colonization of the Andean fragments of SDTFs	91
5.4	Discussion	95
5.4.1	The distribution of the SDTFs throughout the Quaternary to the present	95
5.4.2	The distributions of species during the Quaternary	96
5.5	Conclusions	97
5.6	References	99
6	General Conclusions	104
6.1	A Summary of the major Findings	105
6.1.1	The Geographic Bias of the sampling intensity and biodiversity patterns	105
6.1.2	The impact of the quality of climate models and their impacts on niche modelling	106
6.1.3	The latitudinal and elevational gradients of bird species richness in the Central Andes	107
6.1.4	Historical distributions of the seasonally dry tropical forest in the Bolivian Andes	108
6.2	Implications and limitations of these research	109
6.3	References	112
	Appendices	115
A1	Appendix A1 to chapter 4	116
A2	Appendix A2 to chapter 4	118
A3	Appendix A3 to chapter 4	120
A4	Appendix A4 to chapter 5	122
A5	Appendix A5 to chapter 5	123

Chapter 1

An introduction to relevant concepts and problems that
studies at large spatial-scales face

1.1 Coarse diversity patterns what is already known and which are the limitations.

It is well known that species are not homogeneously distributed in the world, the latitudinal decrease of species richness from the equator to the poles, for example, is the oldest recognized pattern (e.g., Rosenzweig, 1995; Gaston & Blackburn, 2000). But diversity is not evenly distributed within the tropics either. Rainforests hold, for example, a higher bird species richness than the seasonally dry forests and savannas (e.g., Kier *et al.*, 2005, Hawkins *et al.*, 2006). In addition to the latitudinal gradient, Elevational gradients imposed by mountains also show gradual changes of diversity. These diversity changes along elevational gradients were initially thought to emulate the latitudinal gradient of diversity, mainly because the climatic conditions also change from warm to cold as elevation increase. However, latter studies showed that birds, ferns and other taxonomic groups show hump-shaped curves of diversity, with a maximum diversity at some point in the middle of the ranges (e.g., Kessler & Kluge, 2008).

General patterns of diversity for most animal and plant taxa are confidently well established at regional scales and low resolutions (e.g., Kier *et al.*, 2005; Rahbek *et al.*, 2007). It is, however, widely recognized that the resolution at which biogeographical studies are performed may influence the perception of patterns, processes, and even the correlative relationship of diversity with the explored factors (e.g., Herzog *et al.*, unpubl.). Studies of patterns and processes at large scales and fine resolutions in the tropics have been prevented by the lack of data from most tropical areas. At difference of temperate zones, accessibility to some vast tropical areas is difficult. Therefore few areas within the tropics have been intensely researched, while others still do not have information at all (e.g., Kier, *et al.*, 2005; Soria-Auza & Kessler, 2008). This is remarkable since the implications of the uneven sampling intensity on the locally recorded species richness (Freitag *et al.*, 1998), the perception of centres of endemism (Ponder *et al.*, 2001) and the selection of areas for conservation (Reddy & Dávalos, 2003; Grand, *et al.*, 2007) are of critical importance for biogeography and therefore the conservation of the biological diversity in the tropics, where most of the biodiversity occurs (Rosenzweig, 1995).

1.2 Approaches to study diversity patterns in the light of limiting field data

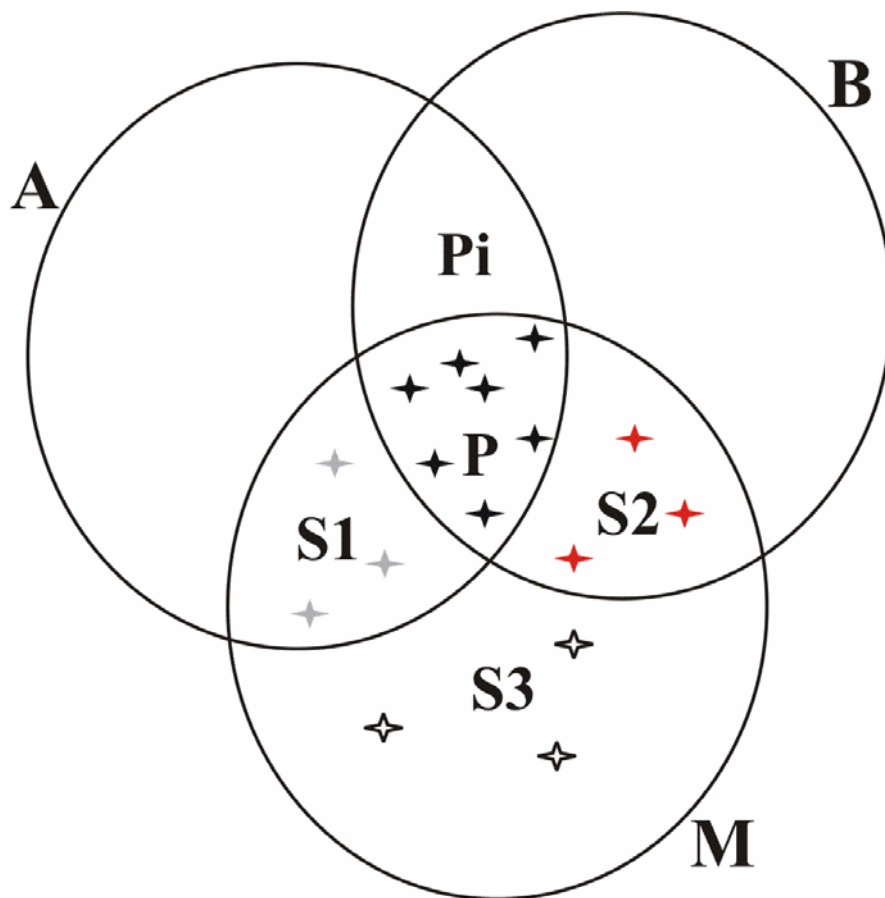


Figure 1.1: The three factors that determine the geographical distribution of a given species: **A** is the geographical projection of the fundamental niche. **B** is the geographical area where the biotic interactions would foster the survival of the species. **M** is the area of the world that is accessible to the species within a time period. **P** is the occupied area of distribution. $A \cap B = P + P_i$ is the geographical projection of the realized niche. P_i is the area that is suitable because both biotic and abiotic conditions co-occur, but is not accessible to the species (e.g., due to geographical barriers). S_1 is the area where sink populations due to competitive exclusion occur. S_2 is the area where sink populations due to negative intrinsic growth rates occur. S_3 is where sink populations due to the combinations of the previous two reasons occur (Modified from Soberón, 2007).

The development of geographic information systems (GIS; e.g., Arcview, Dive GIS, SAGA, etc) together with the increasing availability of climatic and topographic data (e.g., Worldclim and SAGA), as well as specialized software able to analyze data in a spatial context (SAM; spatial analysis in macroecology) have triggered the development of basically two approaches to face the limiting availability of data for biogeographical studies. (1) Extrapolations of species ranges, based on knowledge of the species habitat requirements, and also the geographical distribution of their suitable habitats. (2) Use of niche modelling techniques, also known as species distribution models (e.g., Maxent, Garp, Bioclim, etc.), to estimate species ranges. While the first strategy works well at low ($1^\circ \times 1^\circ$)

to mid (15'x15') resolutions, it fails to reproduce patterns of diversity and verifying hypotheses that take place at finer resolutions and along time spans (e.g., migrations provoked by climate change, among others). Niche modelling techniques, on the other hand, look for the common environmental characteristics from the localities where species have been recorded. Then they project a map that identifies the probable distribution of the species. From this brief explanation, it is implicit that environmental variables are of importance in this process. Therefore, these layers should be of biological significance for predicting the species ranges (e.g., Araujo & Guisan, 2006). Which and how many environmental layers should be used to model species ranges has been a subject of discussion (e.g., Guisan & Zimmermann, 2000). The larger the set of environmental information that is used to predict ranges (e.g., annual rainfall, mean annual temperature, seasonality of both, minimum precipitation, land cover, etc.) the larger will be the probability of excluding non suitable areas. However, if the environmental layers are collinear with each other, then this will cause an overfitting of the predictions. This means that the predictions will concentrate around the points, and leave out other areas where the species may occur (e.g., Araujo & Guisan, 2006; Heikkinen *et al.*, 2006).

1.3 Ecological niche, niche modelling, the estimation of species ranges and further applications

Earlier ecologists perceived the relationship between species ecological requirements and their geographical distribution. This obvious relationship led Grinnell (1917) to coin the concept of ecological niche. Latter, Hutchinson (1957) developed this idea further and defined the fundamental and the realized niches. He defined the first as ‘...all the states of the environment which would permit the species to exist indefinitely’, while the second was defined as a proportion of the fundamental niche that is limited by restrictive factors like inter-specific interactions such as predation, competition, etc. Since niche modelling has profound roots in the niche concepts, discussion around which of this two niche concepts is actually estimated by niche modelling and then projected onto a geographical context is the centre of emotive discussions (e.g., Araujo & Guisan, 2006). Sóberon & Peterson (2005), and Sóberon (2007) approached this issue in an interesting way. These Authors consider that a species would be present at any given point where **(A)** the abiotic conditions have to be favourable for the species (i.e., density independent fitness is positive), **(B)** the appropriate

combination of biotic factors must also occur (e.g., hosts, food plants, pollinators are present, but strong competitors or predators do not occur), and (**M**) regions that are reachable for the species (Fig. 1.1). **A** would be analogue to a geographical projection of the fundamental niche while the intersection between **A** and **B**, the geographical extension of the realized niche ($\mathbf{A} \cap \mathbf{B} = \mathbf{P} + \mathbf{P}_i$; Fig. 1.1). The analogies with Hutchinson's views of species distribution are coupled so far. However, **M**, the third factor that represents space was not accounted by Hutchinson (1957). Dispersal limitations may prevent the colonization of regions that have the favourable combination of abiotic and biotic interactions within a certain time span.

From the above explanation, it is deductible that $\mathbf{A} \cap \mathbf{B} \cap \mathbf{M}$ (**P**; Fig. 1.1) is the occupied area of distribution for any given species where population growth is positive (Gaston, 2003), termed by Jiménez-Valverde *et al.* (2008) as the realized distribution. Now the crucial question is, does niche modelling techniques estimate this area?. The answer is far from straightforward, and depends on several considerations. The specific niche modelling technique used is one of these. Although it is already well established that presence-absence methods outperform presence only methods (e.g., Elith., *et al.*, 2006), and that within the presence only methods, the more complexes outperform simpler ones (Tsoar *et al.*, 2007). A latter study theoretically argued that these differences arise, because presence only methods tend to estimate the potential distribution of the species ($\mathbf{P} + \mathbf{P}_i$), while presence-absence methods estimate the realized distributions (**P**) (Jiménez-Valverde *et al.*, 2008). However, Jiménez-Valverde *et al.* (2008) also show that this distinction is far from dichotomic, but gradual with the more complex presence only methods such Maxent, also tending to estimate the realized niche (or something in between). Unfortunately, absence data is almost non-existent for most species, thereby presence-absence methods are of very limited use, especially in the tropics. However, whether potential distribution ($\mathbf{P} + \mathbf{P}_i$) or the real distribution (\mathbf{P}_i) is being estimated will also depend on the geographical scale at which the range is modelled. Small scales will probably do not include suitable areas where species is not present, while large scales will include such areas (e.g., suitable areas isolated by high mountains that the species can not cross). Another consideration of impact, especially for tropical species with a very limited amount of records, would be the origin of the georeferenced data. Let's imagine that we collected all available records for a rare bird species of restricted range that inhabit the upper part of the humid montane forests in the central Andes. If a considerable percentage of observations come from vagrants recorded in the drier part of the Andes that will not survive in this habitat there long period (**S3**; Fig

1.1), then the estimated range would include this area that do not gather either the biotic or the abiotic conditions. This added area would not significantly modify the range if this percentage of records is significantly low, or the researcher is able to discriminate then before projecting the range. These considerations are discussed in more detail by Soberón & Petterson (2005) and Soberón (2007).

Since their initial development back in the early nineties (e.g., Carpenter *et al.*, 1993), niche modelling has been applied in a wide range of biogeographical research. One of the most prominent applications is predicting the effect of climate change on the distribution of species richness (e.g., Araújo & Rahbek, 2006; Araújo *et al.*, 2006). However, studies focused on the effect of historical processes that led to the current patterns of diversity profited from niche modelling as well (e.g., Graham *et al.*, 2006; Carnaval & Moritz, 2008). Also conservationist initiatives have used niche modelling to find priority areas for threatened species, or species of restricted distribution (e.g., Hernandez, *et al.*, 2008), as well as other macroecological studies.

1.4 Research objectives

During the development of this dissertation I've been repeatedly asked, about the connection between birds and ferns in my research. Once, I was asked by a random person, whether birds act as pollinators or active dispersers of ferns. Although it is obvious that this 'nette Kerl' had no much knowledge of fern and bird biology (I do not deny the remote possibility that birds could act as passive dispersers of ferns), he had the common sense to ask a question that is directed to find out which is the biological link between these two groups (something that any scientist would also tend to do). However, it is not the goal of this dissertation to put both taxa into a scheme of biological interactions, but to use them in order to answer some biogeographical and macroecological questions. I already mentioned that data availability is a limiting factor in the Neotropics, and so it is the case for Bolivia. However, thanks to the effort of M. Kessler and A. Smith (ferns), and Asociación Armonía-BirdLife International (birds), these two taxonomic groups now count with considerably large data banks of circa 29 000 and 65 000 records respectively. Such large amount of data makes these two groups, the better documented taxa in Bolivia, and consequently the best taxa to prove macroecological and biogeographical hypotheses.

The specific goals I aimed in each chapter are quite heterogeneous, but they are linked by the large-scale approach of diversity aspects that I detail in the next paragraphs.

Chapter 2 provides an assessment of one of the most important confounding factor that influences the perception of the spatial patterns of diversity at large scales, namely the spatial structure of the field data. In this chapter we analyzed the database of ferns in a temporal context to show that the spatially structured bias of fern collections has a differential level of influence in the reception of patterns of species richness and endemism of this group.

Chapter 3 highlights the geographical discrepancies and potential conservationist implications of modelling species ranges with environmental layers that may not represent the real geographical climate pattern. In this chapter we compared SAGA and Worldclim (two climate models, extrapolated from the same field data) as a source of important discordances. Previous studies have focused on the discordances of predictions estimated by different niche modelling techniques (Elith *et al.*, 2006), the spatial structure of the field data (Loiselle *et al.*, 2007), the number of available records (Araújo *et al.*, 2005), the behavioural and mobility characteristics of the species (Pöyry *et al.*, 2008), the geographical extension of the species (Araújo *et al.*, 2006) and the amount of environmental variables to model the ranges (Luoto *et al.*, 2007) as sources of error. However, the spatial structure of the environmental variables has been left behind, so far.

In the chapter 4 we aimed to disentangle the role of climate, geometric constraints and area in determining the elevational and latitudinal gradient of bird species richness in the central Andes (southern Peru and Bolivia). We mapped the distribution of each species at a resolution of 15' x 15' (ca. 27 x 27 km) (the manual interpolation approach detailed above). We analyzed the impact of each environmental variable in determining the species richness pattern of the whole bird species richness for the whole study region. Then we divided the study region into regions and elevational belts, and the bird species richness into four groups (quartiles), from the species with the geographically most restricted distribution to the species with the largest species. We pursued to disentangle the impact of the aforementioned factors in determining the bird species diversity at different scales, and for the different components of the bird community along the latitudinal and elevational gradients in the central Andes of South Peru and Bolivia.

In the chapter 5 we used a modelling approach to reconstruct Quaternary distributions of the seasonally dry tropical forests (SDTF) across the four most contrasting quaternary climates. SDTF is the major biome in the south Andes and the lowlands of

Bolivia. However, in the Northern Bolivian Andes they are fragmented and restricted to the rain-shadow valleys, surrounded by either humid montane forests or other high Andean vegetations (Wood, 2006). We aimed to answer of whether these fragments resulted from a process of large distance dispersal of SDTFs through the Andes during the arid periods of the quaternary, or whether these fragments resulted from a vicariance process of the SDTFs that occurred in the central Bolivian lowlands and reached the north Bolivian Andes during the dry periods of the Quaternary. We also modelled a subset of bird and fern species endemic to the SDTFs to check whether the historical distribution of these species also coincided with the modelled distribution of the SDTFs.

1.5 References

- Araujo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global ecology and Biogeography*, 14, 529-538.
- Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677-1688.
- Araújo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity?. *Science*, 313, 1396-1397.
- Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33, 1712-1728.
- Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian atlantic forest. *Journal of Biogeography*, 35, 1187-1201.
- Carpenter, G., Gillison, A., & Winter, J. (1993) Domain: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity Conservation*, 2, 667-680.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehman, A., Li, K., Lohman, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Shaphire, R.E., Soberon, J., Williams, S., Wisz, M. & Zimmermann, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Freitag, S., Hobson, C., Biggs, H.C. & Van Jaarsfeld, S.A. (1998) Testing for potential survey bias: the effect of roads, urban areas and nature reserves on South African mammal dataset. *Animal Conservation*, 1, 119-127
- Gaston, K.J. & Blackburn, T.M. (2000) Pattern and process in Macroecology. *Blackwell Science*. London, UK.
- Gaston, K.J. (2003) The structure and dynamics of geographic ranges. *Oxford University Press*. Oxford.
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological modelling*, 135, 147-186.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforests fauna. *Proceedings of the Natural Academy of Sciences*, 103, 632-636.

- Grand, J., Cummins, M.P., Rebelo, T.G., Ricketts, T.H. & Neel, M.C. (2007) Biased data reduced efficiency and effectiveness of conservation reserve networks. *Ecology Letters*, 10, 364-374.
- Grinnell, J. (1917) The niche-relationships of the California Thrasher. *Auk*, 34, 427-433.
- Hawkins, B.A., Fields, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J. T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. and Turner, J.R.G (2003) Energy, Water and broad-scale geographic patterns of species richness. *Ecology*, 84, 3105-3117.
- Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Postecocene climate change niche conservatism, and the latitudinal gradient of New World birds. *Journal of Biogeography*, 33, 770-780.
- Hernandez, P.A., Franke, I., Herzog, S.K., Pacheco, V., Paniagua, L., Quintana, H.L., Soto, A., Swenson, J.J., Tovar, C., Valqui, T.H., Vargas, J. & Young, B.E. (2008) Predicting species distributions in poorly-studied landscapes. *Biodiversity and Conservation*, 17, 1353-1366.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harb. Symp. Quant.Biol.* 22, 415-427.
- Kessler, M. & Kluge, J. (2008) Diversity and endemism in tropical mountain forests – from patterns to processes. *The tropical mountain forest-Patterns and processes in a biodiversity Hotspot* (ed. by S.R. Gradstein, J. Homeier and D. Gansert). Pp 35-50. Göttingen Centre for Biodiversity and Ecology. Göttingen, Germany.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*, 32, 1107-1116.
- Loiselle, B.A., Jørgensen, P.,M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G. & Montiel, O.M. (2007) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes?. *Journal of Biogeography*, 35, 105-116.
- Luoto, M., Virkkala, R. & Heikkinen, R. K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global ecology and biogeography*, 16, 34-42.
- Ponder, W.F., Carter, G.A., Flemons, P. & Chapman, R.R. (2001) Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology*, 15, 648-657.

- Pöyry, J., Luoto, M., Heikkinen, R.K., Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, 17, 403-414.
- Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.L.F., & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Philosophical Transactions of the Royal Society of London, Series B*, 274, 165-174.
- Reddy, S. & Dávalos, L.M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, 30, 1719-1727.
- Rosenzweig, M.L. (1995) Species diversity in space and time. *Cambridge University Press*, Cambridge.
- Soria-Auza, R.W., & Kessler, M. (2008) The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, 14, 123-130.
- Soberón, J. (2007) Grimeian and Eltonian niches and geographical distribution of species. *Ecology letters*, 10, 1115-1123.
- Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species distributional areas.
- Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R. (2007) A comparative evaluation of presence only methods for modelling species distribution. *Diversity and Distributions*, 14, 397-405.
- Wood, J.R.I. (2006) Inter-Andean dry forests of Bolivia- Floristic affinities and patterns of endemism: Insights from Acanthaceae, Asclepiaceae and Labiateae. *Neotropical Savannas and seasonally dry forests* (ed. by T. Pennington, G.P. Lewis and J.A. Ratter), pp. 235-256. Taylor and Francis group. United States of America.

Chapter 2

The Influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia

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Abstract

The distribution of tropical plant and animal diversity is still poorly documented, especially at spatial resolutions of practical use for conservation. In the present study we evaluated the level to which geographical incomplete data availability of species occurrence affects the perception of biodiversity patterns (species richness and endemism) among pteridophytes in Bolivia. We used a database of Bolivian pteridophytes (27,501 records), divided it into three time periods (1900-1970, up to 1990 and up to 2006), and created grid-files at 15' -resolution for species-richness and endemism. For each of these biodiversity properties we estimated the species richness (Chao 2) and the index of sampling completeness (C index) per grid. And then all these variables at both species richness and endemism were correlated. Patterns of richness were fairly consistent along all periods; the richest areas were placed along the humid-montane forest, even though they were strongly influenced by collecting intensity. Endemism had a lower degree of correlation with collecting intensity, but varied much more strongly through time than species richness. According to the C index, which gives the ratio between estimated (by Chao 2) and recorded values of species-richness and endemism, both biodiversity properties tended to be undersampled in the richest grid cells. Inter-temporal correlations showed sharper differences of correlations for endemism than species-richness. Consequently, already in 1970 botanist had a correct idea of the spatial distribution of pteridophyte richness in Bolivia (even though the magnitude was grossly underestimated). In contrast, patterns of endemism, which are of high conservation importance, may not even today be reliably known.

Key words: Bolivia, Collecting activity, Conservation, Pattern of species-richness, Pattern of endemism, Pteridophyta.

2.1 Introduction

The tropics are well known to harbour a high proportion of global biodiversity. This contrasts with the still imperfect knowledge of the taxonomy and distribution of many tropical taxa. Large regions of the tropics have never been inventoried in detail for many plant and animal groups (Frodin 2001; Kier *et al.*, 2005), and thousands of species continue to be described each year (Sayer & Whitmore, 1991; Reed, 1996; Nichols *et al.*, 1998; Midgley *et al.* 2002). Reliable data on the distribution of tropical biodiversity is of crucial importance both for ecologists seeking to understand how this diversity has evolved and is maintained, and for conservationists struggling to optimize the use of their limited resources. In the last two decades, a number of global prioritization schemes have been proposed, such as the biodiversity hotspots of Myers *et al.* (2000) or the Global 200 approach of WWF (Olson *et al.*, 2001). These schemes attempt to quantify the spatial distribution of biodiversity, among other factors (Reid, 1998; Stattersfield *et al.*, 1998; Myers *et al.*, 2000). As useful as these approaches are, their spatial resolution is very low, e.g., the tropical Andes recognized as a single, high priority region by Myers *et al.* (2000). While the general assessment of the tropical Andes as a biodiversity hotspot in need of conservation action is certainly correct, actual conservation actions usually have to take place at a much finer scale, e.g., involving individual protected areas, and it is at this scale that biological baseline data in the tropics is often inadequate.

The use of large biodiversity databases drawing information from a wide range of sources, such as museum collections and published records, is potentially critical in assessing biodiversity patterns due to the risk of assuming, overlooking, or misunderstanding information, and due to biases in the geographical configuration of data (Kodric-Brown & Brown, 1993; Freitag *et al.*, 1998). Possibly the most important source of spatial bias is the ad hoc spatial arrangement of the samples, i.e. with most of the collected data coming from easy-access localities (Ponder *et al.*, 2001; Reddy & Dávalos, 2003; Grand *et al.*, 2007). Some authors have shown that the unevenness in collecting activity affects the locally recorded species richness (Freitag *et al.*, 1998), the perception of centres of endemism (Ponder *et al.*, 2001), the selection of priority areas for conservation (Reddy & Dávalos, 2003; Grand *et al.* 2007), and even compromise the geographical placement of the postulated Amazonian refuges during the dry-periods of the Pleistocene (Nelson *et al.*, 1990).

The aim of the present study was to assess the degree to which the spatial arrangement of collecting intensity and the resulting imperfect knowledge of the distribution of biodiversity in the tropical Andes affects the perception of biodiversity patterns and resulting potential conservation actions. Using the example of pteridophytes (ferns and fern-like plants), we analyzed two different aspects of biodiversity, namely species richness and endemism. Although both overall richness and levels of endemism tend to be higher in the tropics than in temperate regions, these two aspects tend to show only limited correlation at the spatial level relevant for conservation actions (e.g., Jetz & Rahbek, 2002; Jetz *et al.*, 2004). Our approach was to map the temporal development of the knowledge of the distribution of pteridophyte richness and endemism in Bolivia using three time periods (up to 1970, up to 1990, and up to 2006). We used pteridophytes as a model group because they have been the focus of taxonomic and ecological research by Kessler since 1995 (e.g., Kessler, 2000; Kessler *et al.*, 2001a, b) and are now possibly the best-known major plant group in Bolivia. Pteridophytes contribute considerably to plant diversity in humid tropical forests, especially in montane regions, where they represent up to 19% of the local plant diversity (Young & Leon, 1990). The total known species richness of Bolivian pteridophytes is 1165 species (M. Kessler & A.R. Smith unpubl. data), approximately 10% (123 species) of which have been proposed as threatened (www.fernsofbolivia.uni-goettingen.de).

2.2 Material and Methods

2.2.1 Study area

Bolivia (1'098,581 km²) can be broadly divided into Andean and lowland areas. The Andes are divided in two ranges, the eastern and the western. This configuration causes a contrasting distribution of climatic and ecological conditions. The eastern (outer) slopes of the eastern Andean range are extremely humid, reaching approximately 6000 mm of rain fall per year in central Cochabamba. However, south of the 'Andean elbow' humidity decreases considerably (Fig. 2.1). The main natural vegetation in this area is humid montane forest. Contrastingly this high mountain range produces a rain-shadow effect to the west giving rise to principally drought-adapted vegetation in the inter-Andean valleys and slopes, and westwards across the dry grasslands of the high-Andean plateau (3800-4000 m.).

The lowlands are not homogeneous either. Northern Bolivia is dominated by rain forest whose distribution extends narrowly along the lower eastern Andes to the ‘Andean elbow’, and in eastern Bolivia to the protected Area Noel Kempff Mercado (Fig. 2.1). The area between these two narrow spits of rain forest is mainly dominated by seasonally flooded savannahs with gallery forest along the rivers. Tropical dry forests dominate the southern landscapes (e.g., dry Chaco, Cerrado; Fig. 2.1) apart from a limited section of the Pantanal wetlands that occurs in south easternmost Bolivia (Ibisch & Mérida, 2003).

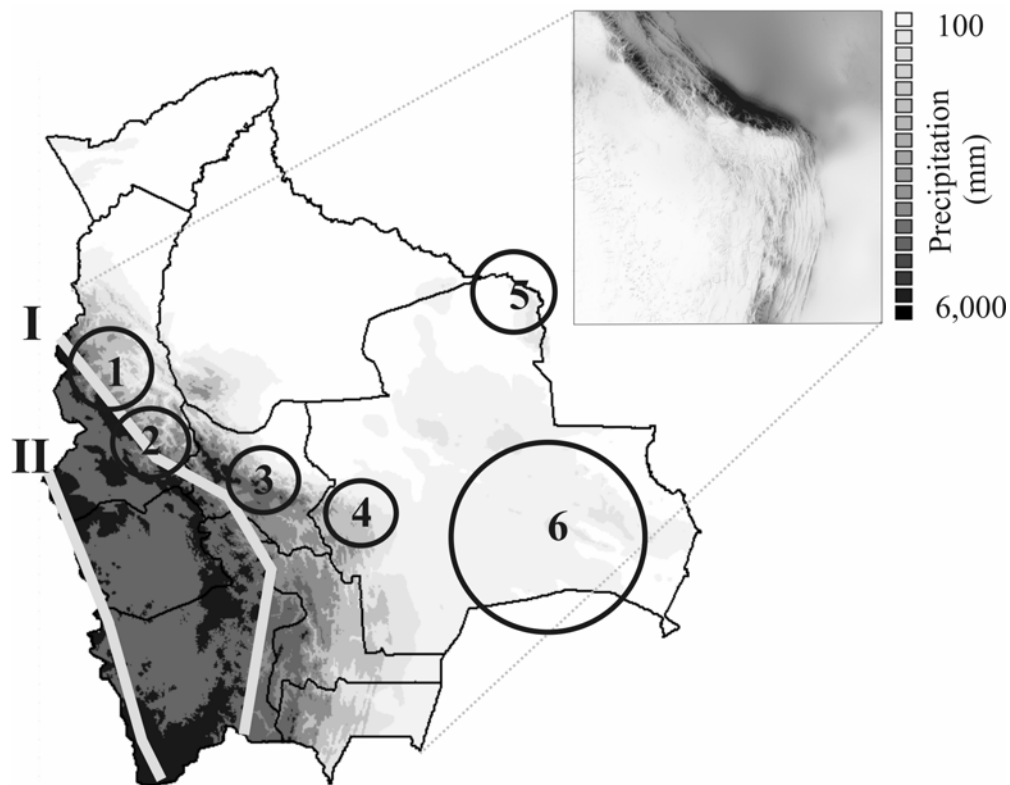


Figure 2.1. Digital altitudinal model of Bolivia (Hijmmans et al.) showing geographical features mentioned in the text: I = eastern Andean range; II = western Andean range; 1 = central La Paz; 2 = south-central La Paz; 3 = central Cochabamba; 4 = ‘Andean Elbow; 5 = Noel Kempff Mercado national park; 6) Cerrado and Dry Chaco. Upper right, the annual rain model developed by Dr. J. Böhner, Goettingen University, Germany (projection: Lambert equal-area azimuthal).

2.2.2 Data

We used a database of Bolivian pteridophyte compiled by M. Kessler and A.R. Smith in the scope of work on a forthcoming field guide to the ferns of Bolivia (www.fernsofbolivia.uni-

goettingen.de). This database contains records from all major herbaria and relevant collections of Bolivian ferns up to December 2006. It contains 27,501 accounting for >95% of all pteridophyte collections made in Bolivia until 2006. Well over 60% of these records are based on determinations made by M. Kessler, A.R. Smith, and researchers collaborating with them on the flora project, ensuring a high quality of species determinations. Prior to the actual analysis we undertook a 'data-cleaning' process according to the following criteria: 1) scientific names were standardized according to M. Kessler and A.R. Smith, 2) records not determined up to species level were removed, and 3) only records with reliable geographical references in the database were taken into account, in this way controlling for all possible sources of error detailed by Chapman (2005). After this process, the databank was reduced to 23,221 records with a mean and median of 20 and 10 records per species, respectively. We treated as endemics all those species restricted to Bolivia. Although this definition of endemism may be problematic in some biogeographic analyses (Gaston, 1994), it is useful in the context of conservation planning and in the case of Bolivia is unproblematic because the low collection density in bordering regions of the neighbouring countries implies that only two range-restricted species occur in Bolivia and just outside of it in Peru; all other shared species are much more widespread. Ultimately, because our aim was to compare spatial patterns of total and endemic species richness over time, and not to, e.g., to conduct biogeographic analyses as such, the actual definition of endemism is not crucial for the scope of this paper.

2.2.3 Analysis

Three time periods were defined for the temporal approach. The first period ranged up to 1970, covering a period of limited collecting activity. During this period, most of the collecting activity was carried out by foreign botanists who deposited their collections in herbaria in Europe and US prior to the establishment of the National Herbarium of Bolivia in La Paz. The second period extends to 1990, i.e., includes the phase during which the National Herbarium was established, while the third period reaches to the end of 2006, i.e., covers the phase of intensive research on Bolivian ferns by Kessler and co-workers (since 1995). For all periods, we used the current species determinations of the records because the database does not include information on the names used for the respective specimens in the past.

For the spatial analysis we used Diva GIS 5.4, a free geographic information system developed by Hijmans *et al.* (2005). We mapped species richness, number of endemic species, sampling intensity (defined as the number of collections per grid) and subsequent estimates (Chao2 and completeness index), at a grid resolution of 15' X 15' for each time period (ca.735 km²). This resolution results represents a compromise between sampling unevenness and the finest possible resolution that reflect biodiversity patterns (Fjeldså *et al.*, 1999). A parallel analysis analyzing the same data at a resolution of 1° X 1° resulted in very similar patterns (Soria & Kessler, unpubl. data), suggesting a limited influence of spatial resolution. In order to maintain constant the area between grids, we used the Lambert equal-area projection. Chao 2 was calculated using the available application of DIVA of “point to grid” in the menu “analysis”. Since this estimator bases its calculation on the incidence of species per sample (not as a synonym of a record, but a set of records from an area), DIVA divides every grid into several sub-grids (being every sub-grid a sample unit), and applies the following formula: $S_{\text{chao 2}} = S_{\text{obs}} + Q_1^2/2Q_2$, where $S_{\text{chao 2}}$ is the estimated species richness, S_{obs} is the recorded species richness in all throughout all samples, Q_1 is the number of species occurring in one sample and Q_2 the number of species occurring in two samples (Colwell & Coddington, 1994; Magurran, 2004; Hijmans *et al.*, 2005). We chose this estimator because it outperforms other estimators in a wide range of data (Herzog *et al.*, 2002; Walther & Moore, 2005) and because it makes our study comparable to others (e.g., Soberón *et al.*, 2007). The degree of completeness in the recorded species richness and endemism of every cell were calculated by dividing the recorded values (of species richness and endemism, respectively) by the predicted ones (Chao 2). This proportion is known as the index of completeness or C index (Soberón *et al.*, 2007). Finally, in order to assess the degree of congruence in perceived patterns between time periods, we performed analyses of correlation between all variables (species richness, endemism, effort, Chao 2 and C), within and between all periods. Because our data did not fulfil the normal parametric requirements (normal distribution), non parametric spearman correlations were used.

2.3 Results

Our dataset contained 23,221 reliably determined and georeferenced records of pteridophytes from Bolivia, collected between 1900 and 2006. In the first period (1900-1970) the mean number of collections per year was 12.5, increasing to 166.3 (per year) for

the period 1971-1990, and to 959.2 for the period 1991-2006. Up to 1970, the total number of pteridophyte collections from Bolivia was 881, corresponding to 404 species. In 1990, there were 4,207 records representing 743 species. Finally, in 2006, the total number of species was 1,165 species (23,221 records), including 123 endemic species.

Considering the spatial distribution of collections, the most intensely collected area in all periods was the eastern slopes of the Andes; actually, more than the 95 % of the collections during the first period came from this region. At this time, the cell with the highest species richness had 76 species and was placed on the eastern humid Andes in central Cochabamba (Fig. 2.2d). A second centre of species richness was identified for the lower humid montane forest in south-central La Paz (59 spp.; Fig. 2.2d). The extent of collecting activity increased up to 1990, especially southwards along the Andean range and scatteredly in the northern and eastern lowlands. The highest species richness was found in several cells in humid montane forest of south-central La Paz (152, 129, and 127 spp.) and central Cochabamba became the secondary centre of species richness, with two cells holding 104 and 103 spp. (Fig. 2.2e). Finally, up to 2006 about 95 % of the cells on the eastern Andean slopes had been surveyed for ferns (Fig. 2.2c). At this time, the highest species richness was recorded in central Cochabamba (401 spp.), with the second-richest cell in central La Paz (393 spp.; Fig. 2.2f).

Table 2.1. Correlation matrix for species richness. Significant correlations with $p < 0.05$ are in bold. Spp. = Species richness, IC = Intensity of collection, Chao 2 = Estimations by Chao 2 and C = Index of completeness (see text for further explanations).

	Upto 1970 n=84 cells				Upto 1990 n=230 cells				Upto 2006 n=550 cells			
	Spp	IC	Chao2	C	Spp	IC	Chao2	C	Spp	IC	Chao2	C
Spp	1	-	-	-	1	-	-	-	1	-	-	-
IC	0.997	1	-	-	0.995	1	-	-	0.991	1	-	-
Chao2	0.904	0.908	1	-	0.903	0.902	1	-	0.910	0.905	1	-
C	-0.828	-0.807	-0.851	1	-0.765	-0.736	-0.881	1	-0.704	-0.704	-0.801	1

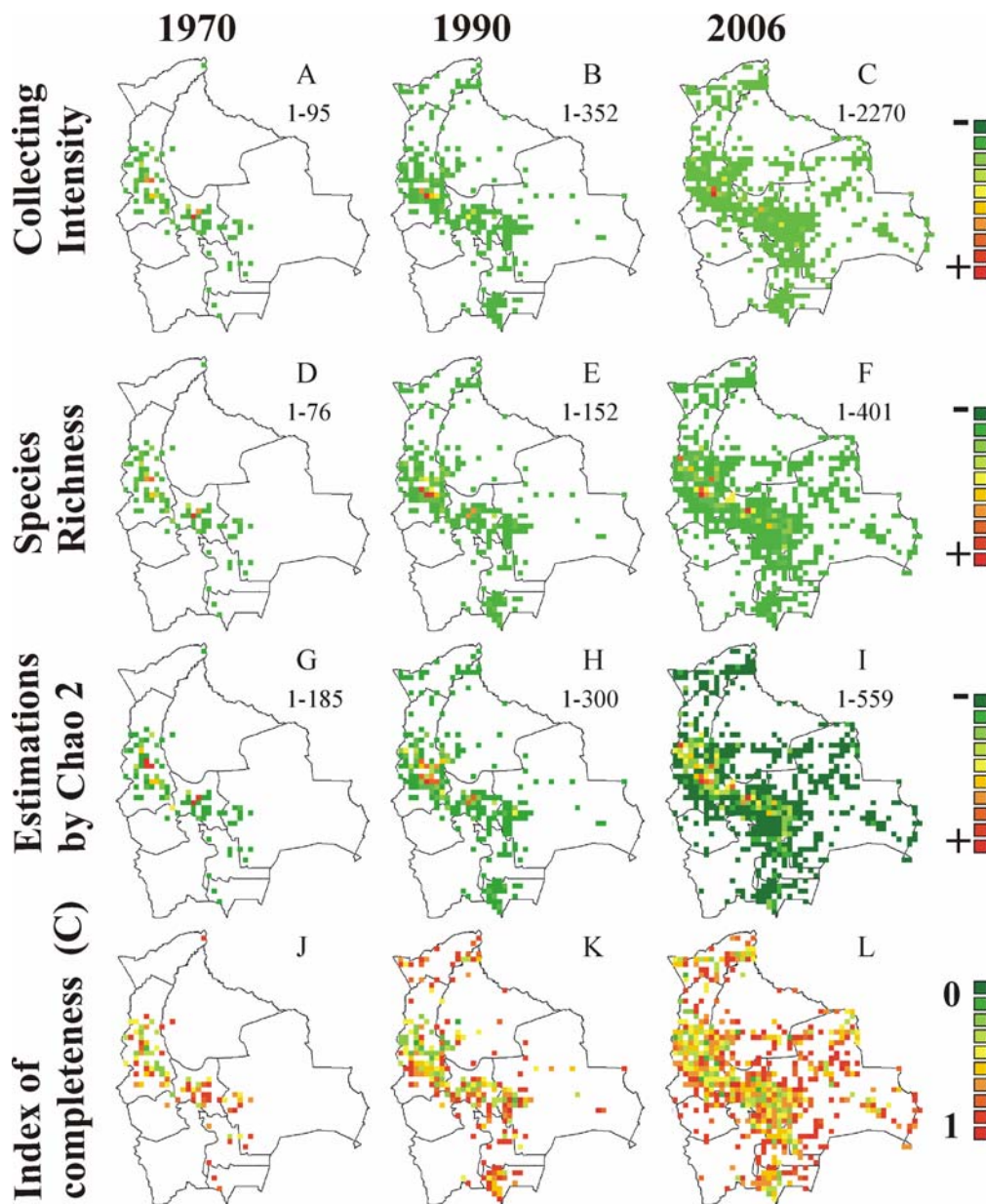


Figure 2.2. *Spatial analysis of species richness. Maps of intensity of collection, recorded species richness, estimated species richness (Chao 2) and completeness for all periods (scale increment in equal intervals). Pixel size is 15' x 15' (ca. 27 x 27 km²), using a Lambert equal-area azimuthal projection.*

Although the location of richest cells shifted between central Cochabamba and south-central La Paz between periods, the general pattern of species richness was relatively constant, showing high richness in the humid montane forest (including transition zones) and lower values in the lowlands and the highlands. These geographical patterns were

highly correlated with the intensity of collection for all time periods (Table 2.1, Fig. 2.2a - f).

A (partial) correction of the influence of collection intensity by the Chao 2 estimator resulted in patterns consistent with those previously depicted by the crude data but with spatially more even patterns (Fig. 2.2d-g, e-h and f-i). Although these patterns were also correlated with the intensity of collection in all periods, the resulting correlation values were lower than for raw species richness (Table 2.1).

The C index reported on average the lowest correlation with other variables for all periods (Table 2.1). As a matter of fact, there was a tendency towards lower sampling completeness in cells with high recorded and estimated richness (Fig. 2.2j, k and l).

The geographical patterns of endemism did not coincide closely with the species richness patterns. The cell with highest endemism up to 1970 (4 spp.) was found in central La Paz, and several other records north-east and east from this cell, whereas in central Cochabamba just two cells held endemic species (Fig. 2.3d). The quantity of cells holding endemic species up to 1990 increased, and almost all of them were placed in the humid Andean forest south to the 'Andean elbow' (Fig. 2.3e). At this time, the highest endemism coincided with the richest cell (Fig. 2.2e, 2.3e). Finally, up to 2006 there were two clearly defined centres of high endemism, the highest coincided with the one identified up to 1990, but at this time the amount of endemic species in this cell reached 29; the second most important cell was placed north-western La Paz (19 spp.).

Although to a lower degree compared with species richness patterns, endemism patterns correlated positively with the intensity of collection for the last two periods (Table 2.2), and it also correlated closely to the estimated endemism by the Chao 2 (Fig. 2.3, Table 2.2).

Finally, considering 2006 scenarios as the most probable estimation of the real patterns of species richness and endemism, between-periods correlations within variables were more stable and higher for species richness than for endemism (Fig. 2.4). And in all cases, patterns in 1990 correlated more closely to patterns in 2006 than patterns in 1970.

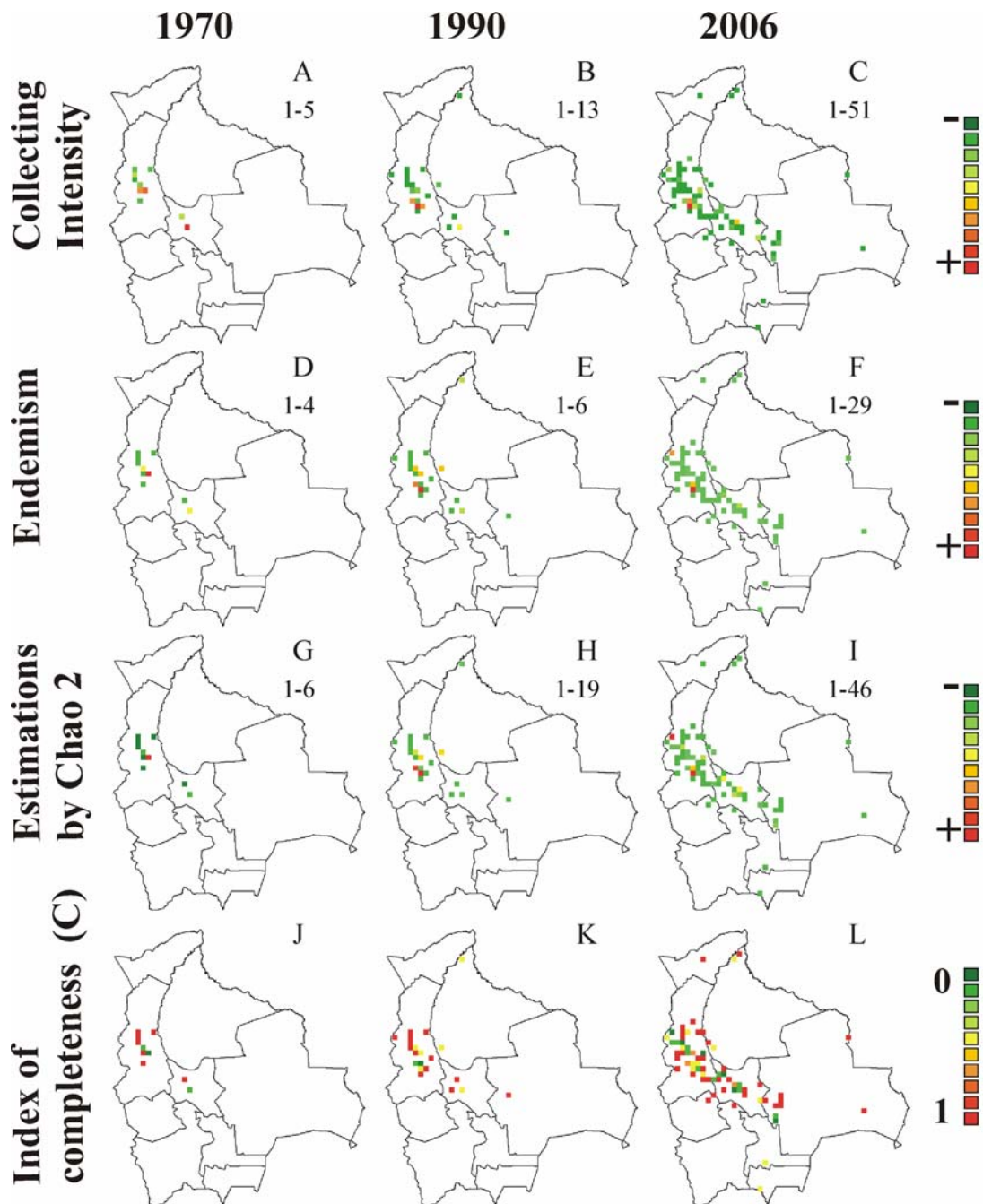


Figure 2.3. *Spatial analysis of species endemism. Maps of intensity of collection of endemic species, recorded endemism, estimated endemism (Chao 2) and completeness for all periods (scale increment in equal intervals). Pixel size is 15' x 15' (ca. 27 x 27 km²), using a Lambert equal-area azimuthal projection.*

Table 2.2. Correlation matrix for endemism. Significant correlations with $p < 0.05$ are in bold. Spp. = number of endemic species (endemism), IC = Intensity of collection, Chao 2 = Estimations by Chao 2 and C = Index of completeness (see text for further explanations).

	Upto 1970 n=11 cells				Upto 1990 n=22 cells				Upto 2006 n=68 cells			
	End	IC	Chao2	C	End	IC	Chao2	C	End	IC	Chao2	C
End	1	-	-	-	1	-	-	-	1	-	-	-
IC	0.584	1	-	-	0.476	1	-	-	0.597	1	-	-
Chao2	0.930	0.584	1	-	0.917	0.577	1	-	0.975	0.563	1	-
C	-0.906	-0.640	-0.911	1	-0.790	-0.538	-0.954	1	-0.791	-0.472	-0.869	1

2.4 Discussion

The aim of this study was to assess the degree to which the history and intensity of field sampling influence the perception of patterns of species richness and endemism in the tropics. Regarding the overall pattern of species richness of ferns in Bolivia (Fig. 2.2d, e and f), the areas with highest species richness were quite consistent across time, with the humid eastern slopes showing the highest values. However, the detailed patterns correlated with the geographically uneven collection intensity (Fig. 2.2a, b and c; Fig. 2.4) and the specific distribution of the cells with the highest recorded richness changed markedly over time as a result of shifts in the geographical distribution of botanical collections. As in many previous studies on this subject (e.g., Freitag *et al.*, 1998; Reddy & Dávalos, 2003), we found a strong positive association between sampling intensity and recorded species richness. However, it does not imply that the cells with the highest recorded richness have such high values only because they are well-collected. After all, cells with few species will have a low number of collections simply because botanists find few ferns to collect. As any field botanist knows, botanists tend to concentrate their efforts in more diverse (and hence “interesting”) areas, avoiding poor species-richness areas.

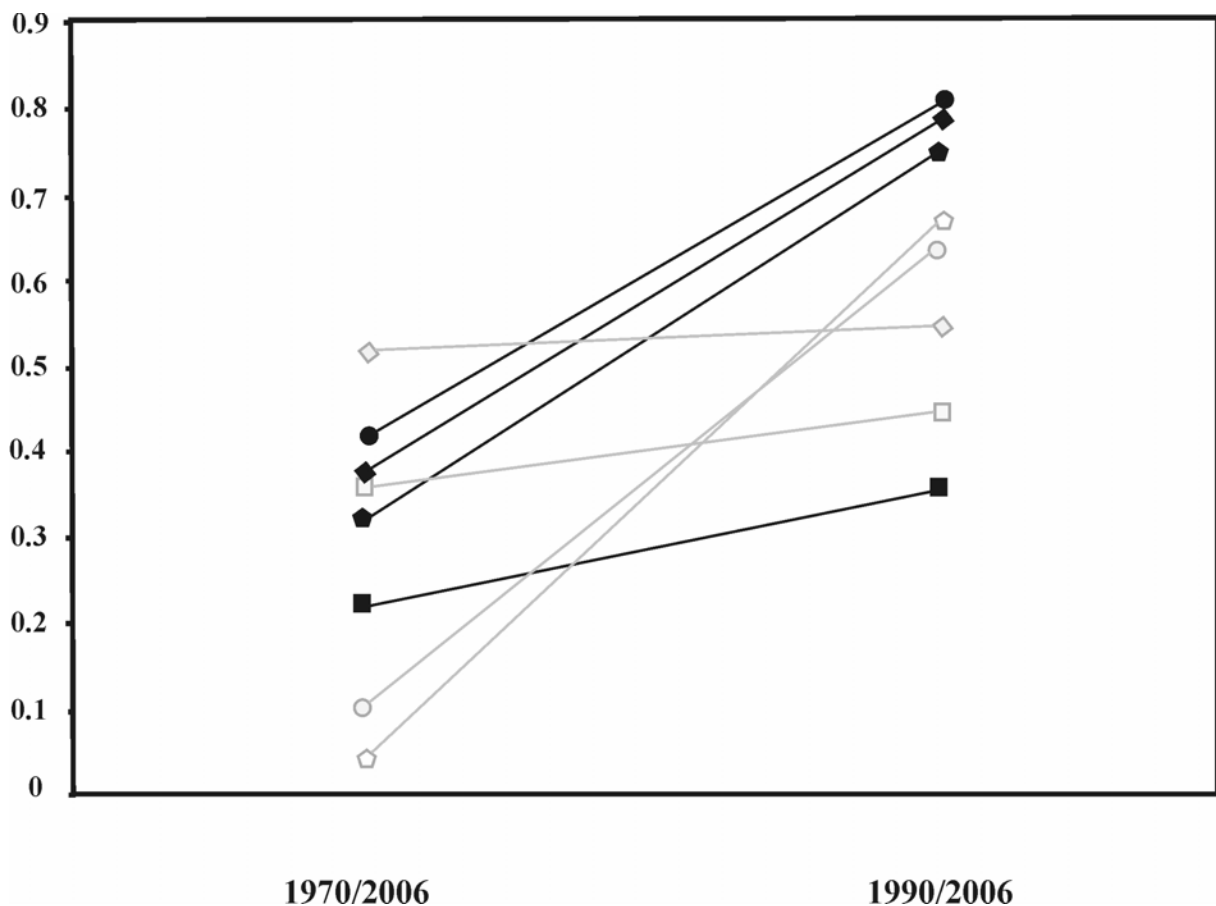


Figure 2.4. Inter-period correlations of collecting intensity (pentagons), observed species numbers (diamonds), estimated species numbers through the Chao2 index (circles), and the C index (squares) for species richness (dark lines, closed symbols) and endemism (gray lines, open symbols) of pteridophytes in Bolivia.

Therefore, the challenge at hand is to quantify the degree to which the high number of records (and hence species) in some cells are a result of the highly diverse fern flora or of high sampling intensity. This assessment depends on having fairly complete samples for at least some cells. However, our calculations of expected total species numbers with the Chao 2 estimator and of the C index of sampling completeness revealed that sampling in Bolivia is still far from complete. Indeed, there was a tendency towards less complete sampling in cells with high richness and high number of collections, suggesting that despite the extra effort spent by botanists in species-rich habitats, these are still less completely sampled than many of the species-poor cells.

An alternative approach to assess the reliability of the detected richness patterns is to compare our analysis with field data from local surveys. Bolivia has been subject to

intensive studies of fern diversity using over 1000 standardized plots of 400 m² (Kessler, 2000; 2001; Kessler *et al.*, 2001a, b). While the spatial scale of the two approaches differs by over six orders of magnitude and hence precludes a meaningful quantitative statistical comparison of the spatial patterns of species richness, there is an overall agreement between both approaches. Both our study and the field data document highest fern richness at mid-elevations in the northern Andes, and a general decline of richness from north to south. These patterns suggest a strong dependence of fern diversity with humidity and are in accordance with patterns found elsewhere (e.g., Rey Benayas & Scheiner, 2002; Guo *et al.*, 2003; Aldasoro *et al.*, 2004; Bhattarai *et al.*, 2004; Karst & Lechowicz, 2005; Bickford & Laffan, 2006; Kluge *et al.*, 2006).

Thus, by 1970 biologists already had a correct, even if rough idea of the overall spatial distribution of fern diversity in Bolivia. The magnitude of the richness, however, was strongly underestimated. The richest cell had only 76 recorded species and while the application of the Chao 2 estimator corrected this value to 185, this is still far less than the highest cell-count of 401 known today. Clearly, and as also shown in previous studies (e.g., Herzog & Kessler, 2002; Walter & Moore, 2005) the Chao 2 estimator can only partly correct for incomplete sampling. Soberón *et al.* (2007) have recently shown that estimators do not work accurately on ‘degenerated cells’ with low sampling intensity. Several authors (Colwell & Coddington, 1994; Colwell *et al.*, 2004; Colwell, 2005) have recommended estimating the error of the estimated values, but this cannot be applied to Chao 2. We selected the Chao 2 estimator because it is considered to outperform other estimators (Walter & Moore, 2005) and because it has been used in similar studies (e.g., Soberón *et al.*, 2007), allowing direct comparison. Other estimators suffer from the same general limitations (Herzog & Kessler, 2002; Walter & Moore, 2005). Thus, the use of estimators clearly has limitations and it may be more realistic to use them to assess the degree of sampling completeness than to try to calculate “true” species numbers.

Turning towards patterns of endemism, patterns changed more strongly with time than patterns of species richness (Fig. 2.4). Importantly, patterns of endemism were less influenced by collection intensity (Tables 2.1, 2.2). Although the highest numbers of endemic ferns in Bolivia are also found on the humid eastern Andean slope, their distribution within this region is much more irregular than that of species richness. Again, this is confirmed by field surveys. For example, 514 collections made in a cell in northern La Paz, close the Peruvian border, since 2002 have revealed no less than 19 endemic species (Kessler *et al.*, unpubl.). In contrast, a collection of 303 ferns made by M. Kessler and co-

workers on the Cordillera Mosetenes in northern Cochabamba in 2004 recorded a single endemic species, despite specific searches for unusual ferns. The spatially uneven and less predictable distribution of endemic species compared to overall species richness has previously been documented, e.g., for birds in Africa (Jetz & Rahbek, 2002; Jetz *et al.*, 2004) and palms in the Neotropics (Kreft *et al.*, 2006). Recently, Küper *et al.* (2006) scanned for data-deficiency for vascular plants at a sub continental scale in Africa, finding that geographical patterns of data-deficiency show a reduced geographical overlap when range size of species is incorporated (compare figures 2 a, b and c in Küper *et al.*, 2006). This outcome also supports our findings, and presumably reflects the stronger influence of historical factors in determining the evolution and distribution of species with restricted ranges.

Several general conclusions can be drawn from this study. First, general patterns of species richness can be deduced from fairly incomplete data. However, and second, despite ferns being one of the better-known major plant groups in Bolivia, the absolute number of species per cell and the distribution of endemics are still very incompletely known. If we consider that the sampling intensity of many plant taxa in Bolivia today is roughly comparable to that of ferns in 1990, we can conclude that for these taxa any conclusion about total species numbers and levels of endemism have to be drawn with extreme care. For example, quantitative analyses of the distribution of the diversity and endemism of orchids in Bolivia have been carried by Vásquez & Ibisch (2004) based on a mean of 3.58 collections per species, which is still less than the 5.7 fern collections per species in 1990. Clearly, conservation and research based on such incomplete data can potentially be misleading. Indeed, one of the problems in understanding patterns of endemism in tropical taxa may be our limited knowledge of the distribution of endemic taxa. Since endemism is an important characteristic of biodiversity, and the fact that ferns are one of the best known plant-groups of Bolivia, we must encourage the increase of field data, especially in those places poorly explored. This will offer a better support to those governmental and non-governmental offices in charge of conservation initiatives.

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2.5 References

- Aldasoro, J. J., Cabezas, F. & Aedo, C. (2004) Diversity and distribution of ferns in sub-Saharan Africa, Madagascar and some islands of the South Atlantic. *Journal of Biogeography*, 32, 1579-1604.
- Barrington, D. S. (1993) Ecological and historical factors in fern biogeography. *Journal of Biogeography*, 20, 275-280.
- Bhattarai, K.R., Vetaas, O. R. & Grytnes, J. A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31, 389-400.
- Bickford, S. A & Laffan, S. W. (2006) Multi-extent analysis of the relationship between pteridophyte species richness and climate. *Global Ecology and Biogeography*, 15, 588-601.
- Chapman, A.D. (2005) Principles and methods of data cleaning – Primary species and species occurrence data, Version 1.0. Report for the global biodiversity Information facility, Copenhagen. Available at: <http://www//gbif.org>
- Colwell, R. K. & Coddington, J. A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London, Series B*, 345, 101-118.
- Colwell, R. K., Xuan Mao, C. & Chang J. (2004) Interpolating, extrapolating and comparing incidence-based species accumulation curves. *Ecology*, 85, 2717-2727.
- Colwell, R. K. (2005) Estimate S: statistical estimation of species richness and shared species from samples. Version 7.5. Available at: <http://www.purl.oclc.org/estimates>.
- Ferrer-Castan, D. & Vetaas, O. R. (2005) Pteridophyte richness climate and topography in the Iberian Peninsula: Comparing spatial and non-spatial models of richness patterns. *Global Ecology and Biogeography*, 14, 155-165.
- Fjeldså, J., Lambin, E. & Mertens, B. (1999). Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, 22, 63-78.
- Freitag, S., Hobson, C., Biggs, H. C. & Van Jaarsveld, A. S. (1998) Testing for potential survey bias: the effect of roads urban areas and nature reserves on Southern African mammal data set. *Animal Conservation*, 1, 119-127.
- Frodin, D. G. 2001. Floras in retrospect and for the future. *Plants talk*, 25, 23-29.
- Gaston, K. J. (1994) *Rarity*. Chapman & Hall. London UK.

- Grand, J., Cummins, M. P., Rebelo, T. G., Ricketts, T. H. and Neel, M. C. (2007) Biased data reduce efficiency and effectiveness of conservation reserve networks. *Ecology Letters*, 10, 364-374.
- Guo, Q., Kato, M. M. & Ricklefs, R. E. (2003) Life history, diversity and distribution: a study of Japanese pteridophytes. *Ecography*, 26, 129-138.
- Herzog, S. K., Kessler, M. & Cahill, T. M. (2002) Estimating species richness of tropical bird communities from rapid assessment data. *The Auk*, 119, 749-769.
- Hijmans, R. J., Guarino, L., Jarvis, A., O'Brien, R., Marthur, P., Bussink, C, Cruz, M, Barrantes, I. & Rojas, E. (2005) DIVA GIS V. 5.4. Free GIS for biodiversity research. Available at: <http://www.diva-gis.org>
- Ibisch, P. L. & Mérida, G. (eds.). (2003) Biodiversidad: La riqueza de Bolivia, estado de conocimiento y conservación. Ministerio de desarrollo sostenible. *Editorial FAN*, Santa Cruz de la Sierra – Bolivia.
- Jacobsen, W. B. C & Jacobsen, N. H. G. (1989) Comparison of the pteridophyte floras of southern and eastern Africa, with special reference to high-altitude species. *Bulletin Jardin Botanique Belgique*, 59, 261-317.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and the determinants of avian species richness. *Science*, 297, 1548-1551.
- Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, 7, 1180-1191.
- Jones, M. M., Tuomisto, H., Black, D. B. & Olivas, P. (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *Journal of ecology*, 94, 181-195.
- Karst, J., Gilbert, B. & Lechowicz, M. J. (2005) Fern community assembly: the role of chance and the environment at local and intermediate scales. *Ecology*, 86, 2473-2486.
- Kessler, M. (2000) Elevational gradients in species richness and endemism of selected plant groups in central Bolivian Andes. *Plant ecology*, 149, 181-193.
- Kessler M. (2001) Pteridophyte species richness in Andean forest in Bolivia. *Biodiversity and Conservation*, 10, 1473-1495.
- Kessler M., Parris, B.S. & Kessler, E. (2001a) A comparison of the tropical montane Pteridophyte floras of mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography*, 28, 611-622.

- Kessler, M. Herzog, S. K., Fjeldså, J. & Bach, K. (2001b) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and distributions*, 7, 61-77.
- Kier, G., Mutke, J., Dinerstein, E., Ricketts, T. H., Küper, W., Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography*, 32, 1107-1116.
- Kluge, J. & Kessler, M. (2006) Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. *Diversity and Distributions*, 12, 535-545.
- Kodric-Brown, A. & Brown, J. H. (1993) Incomplete data sets in community ecology and biogeography: a cautionary tale. *Ecological Applications*, 3, 736-742.
- Kreft, H., Sommer J. H. & Barthlott, W. (2006) The significance of geographic range for spatial diversity patterns in Neotropical palms. *Ecography*, 29, 21-30.
- Küper, W., Sommer, J. H., Lovett, J. C. & Barthlott, W. (2006) Deficiency in African distribution data – missing pieces of the puzzle. *Botanical Journal of the Linnean Society*, 150, 355-368.
- Magurran, A. E. 2004. Measuring biological diversity. *Blackwell Publishing*. UK.
- Midgley, G. F., Hannah, L., Millar, D., Rutherford, M. C. & Powrie, L. W. (2002) Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biodiversity*, 11, 445-451.
- Myers, N., Mittermeier, R. A., Mittermeier C. C., Da Fonseca, G. A. B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853-858.
- Nelson, W. N., Ferrera, C. A., Da Silva, M. F. & Kawasaki, M. L. (1990) Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature*, 345, 714-716.
- Nichols, J. D., Boulmier, T., Hines, J. E., Pollock, K. H. & Sauer J. R. (1998) Estimating rates of local species extinction, colonization, and turnover in animal communities. *Ecological Applications*, 8, 1213-1225.
- Olson, D. M., Dinerstein E., Wikramanayake, E. D., Burgess, D. N., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allmutt, T. F., Ricketts, T.H., Kura, Y., Lamoreaux, J. F., Wettengel, W. W., Hedao, P. & Kassen, K. R. (2001) Terrestrial ecoregions of the world: a new map of the life on Earth. *BioScience*, 51, 933-938.

- Ponder, W. F., Carter, G. A., Flemons, P. & Chapman, R. R. (2001) Evaluation of museum collection data for use in biodiversity assessment. *Conservation Biology*, 15, 648-657.
- Reed, J. M. (1996) Using Statistical probability to increase confidence of inferring species extinction. *Conservation Biology*, 10, 1283-1285.
- Reid, W. V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, 13, 275-280.
- Rey Benayas, J. M. & Scheiner, S. M. (2002) Plant diversity, biogeography and environment in Iberia: Patterns and possible causal factors. *Journal of Vegetation Science*, 13, 245-258.
- Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, 30, 1719-1727.
- Sayer, J. A. & Whitmore, T. C. (1991) Tropical moist forest: Destruction and species extinction. *Biological conservation*, 55, 199-213.
- Soberón, J., Jiménez, R., Golubov, J. & Koleff, P. (2007) Assessing completeness of biodiversity databases at different spatial scales. *Ecography*, 30, 152-160.
- Stattersfield, A. J., Crosby, M. J., Long, A. J. & Wedge, D. C. (1998) Endemic Bird Areas of the world, priorities for biodiversity conservation. *Cambridge. BirdLife International. Conservation Series No. 7.*
- Vásquez, Ch. R. & Ibisch, P. L. (2004) Ochids of Bolivia, diversity and conservation status Vol. II. Laeliinae-Polystachyinae, with update and complementation of Pleurothallidinae. *FAN ed.* Santa Cruz de la Sierra, Bolivia.
- Walther, B. A. And Moore, J. (2005) The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. *Ecography*, 28, 453-470.
- Young, K. & Leon, B. (1990) Catálogo de plantas de la zona alta del parque nacional Río Abiseo, Perú. *Publicaciones del museo de historia natural UNMSM*, Lima B34, 1-37.

Chapter 3

Impact of the quality of climate models for modelling species occurrences in countries with poor climatic documentation: a case study from Bolivia

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Submitted to Ecological modelling

Abstract

Increasingly, modelled species distributions are used as a basis for conservation planning, especially in the face of climate change and associated range shifts. However, the quality of climate models has largely been overlooked as a possible source of uncertainty that may affect the outcomes of species distribution models, especially in the tropics, where comparatively few climatic stations are available. We compared the geographical discrepancies and potential conservation implications of using two different climate models (Worldclim, SAGA) in combination with the species modelling approach Maxent in Bolivia. We estimated ranges of selected bird and fern species biogeographically restricted to either humid montane forest of the northern Bolivian Andes or seasonal dry forests (in the Andes and southern lowlands). Worldclim and SAGA predicted roughly similar climate patterns that were significantly correlated, but that showed important differences for the spatial distribution of precipitation. Species ranges estimated with Worldclim and SAGA likewise produced distinct results. Ranges of species endemic to humid montane forests estimated with SAGA had higher AUC values than those estimated with Worldclim, which for example predicted the occurrence of humid montane forest bird species near Lake Titicaca, an area that is clearly unsuitable for these species. Likewise, it over predicted the occurrence of fern and bird species in the lowlands of the Chapare region and well south of the Andean elbow, where more seasonal biomes occur. By contrast, SAGA predictions were coherent with the known distribution of humid montane forests in the northern Bolivian Andes. Estimated ranges of species endemic to seasonal dry forests predicted with SAGA and Worldclim were not statistically different in most cases. However, detailed comparisons revealed that SAGA was able to distinguish fragments of seasonal dry forests in rain-shadow valleys of the northern Bolivian Andes, whereas Worldclim was not. These differences highlight the neglected influence of climate layers on modelling results and the importance of using the most accurate climate data available when modelling species distributions. Although most species modelled were of low conservation priority, many species of conservation concern in Bolivia are restricted to humid montane or seasonal dry forests, and we expect our conclusions to apply to threatened and restricted-range species as well.

Keywords: Birds, Ecological niche modelling, Ferns, Maxent, SAGA, Worldclim

3.1 Introduction

Species distribution models (SDM) are probably one of the most promising tools biogeographers have to improve the understanding of biodiversity patterns and their relationship with climate and topography (Cumming, 2000; Bahn & McGill, 2007). The use of modelling techniques implies predicting the distribution of species, and therefore, these techniques inherently have some level of uncertainty that researchers must consider. Discordant predictions rendered by different modelling techniques using the same data have revealed different levels of uncertainty. One of the most relevant outcomes comparing different species distribution models is that presence-absence models offer more accurate estimates than presence-only models (Elith *et al.*, 2006). However, absence data is non-existent for most taxa, and consequently, the applicability of presence-absence models is limited especially in highly diverse but under-surveyed tropical areas.

The species distribution model chosen, however, is not the only source of uncertainty (Araújo & New, 2007). Other sources include the spatial structure of the field data that may be collinear with environmental variables (Araujo & Guisan, 2006; Loiselle *et al.*, 2007). For example, most of the species presence records come from localities that are easily accessible and that are clustered in areas near the centre of the range of climatic conditions under which a species occurs. Hence, records often do not cover the complete range of environmental variability that a species of interest inhabits. The number of available records also has an inverse impact on the quality of the prediction (Araujo *et al.*, 2005). Pöyry *et al.* (2008) showed that inherent behavioural and mobility characteristics of the species under study may also have an effect on the predictive power of species distribution models. Additionally, Araujo *et al.* (2006) found that models tend to predict the distribution of range-restricted species better than those of widespread species. Moreover, the choice of environmental variables used to model species distributions may result in different distribution maps for the same species (Luoto *et al.*, 2007).

One of the least studied sources of uncertainty in species distribution modelling comes from the environmental data used to run the models, particularly the climate data. Climatic layers are raster layers that result from extra- and interpolating data collected from climatic field stations (hereafter called field stations). Therefore, different spatial patterns may arise for a given environmental variable depending on the extra- or interpolation procedures used. Temperate regions have several climate models constructed from very robust networks of field stations, whereas tropical countries lack such robust systems.

Notwithstanding this limitation, considerable advances in constructing reliable climatic layers at a global scale have been made in the last few years. Worldclim (Hijmans *et al.*, 2005) is perhaps the most outstanding global climate data set. It was reported to accurately represent climate in North America and Europe (Hijmans *et al.*, 2005), and consequently has been used repeatedly in a wide range of biogeographic studies, including testing the potential effects of climate change on species ranges (Araújo & Rahbek, 2006; Araújo *et al.*, 2006; Graham *et al.*, 2006; Killeen *et al.*, 2007; Bauermann *et al.*, 2008; Carnaval & Moritz 2008; Hernandez *et al.*, 2008). However, the accuracy of the model in tropical areas remains to be evaluated, although Killeen *et al.* (2007) have pointed out some obvious biases of Worldclim for the Bolivian Andes and adjacent lowlands.

In the present study we aim to highlight the geographical discrepancies and conservation implications of using two different climate data sets to estimate patterns of species richness of a set of bird and fern species characteristic of humid montane and seasonally dry forests in Bolivia. The climate data sets used were Worldclim and the alternative model SAGA (hereafter called climate models). SAGA has been used for climate models in Europe (Böhner, 2005) and Bolivia (Kessler *et al.*, 2007), whereas Worldclim has a global coverage (Hijmans *et al.*, 2005). Although both climate models use the same raw data to produce environmental raster-layers, they apply distinct mathematical processes to construct the models. To assess the impact of climate model choice on species distribution models, we first compared the predictions of the two climate models. Then we used the species distribution model Maxent (Phillips *et al.*, 2006; Phillips and Dudík, 2008), in combination with each climate model, to model the ranges of the selected species and compared the resulting species range maps.

3.2 Methods

3.2.1 Study area and species data

Bolivia covers slightly more than one million square kilometres in south-central South America, with about one third of the country in the Andes and the remainder in the lowlands. Humid montane forests range from approximately 500 m to ca. 4000 m. This type of forest is the dominant vegetation on the east Andean slopes north-west of the Andean

elbow (ca. 18° S, Fig. 3.1a). According to SENAMHI (Servicio Nacional de Meteorología e Hidrología), precipitation reaches its maximum in Bolivia on the slopes of the Chapare region in Cocha-

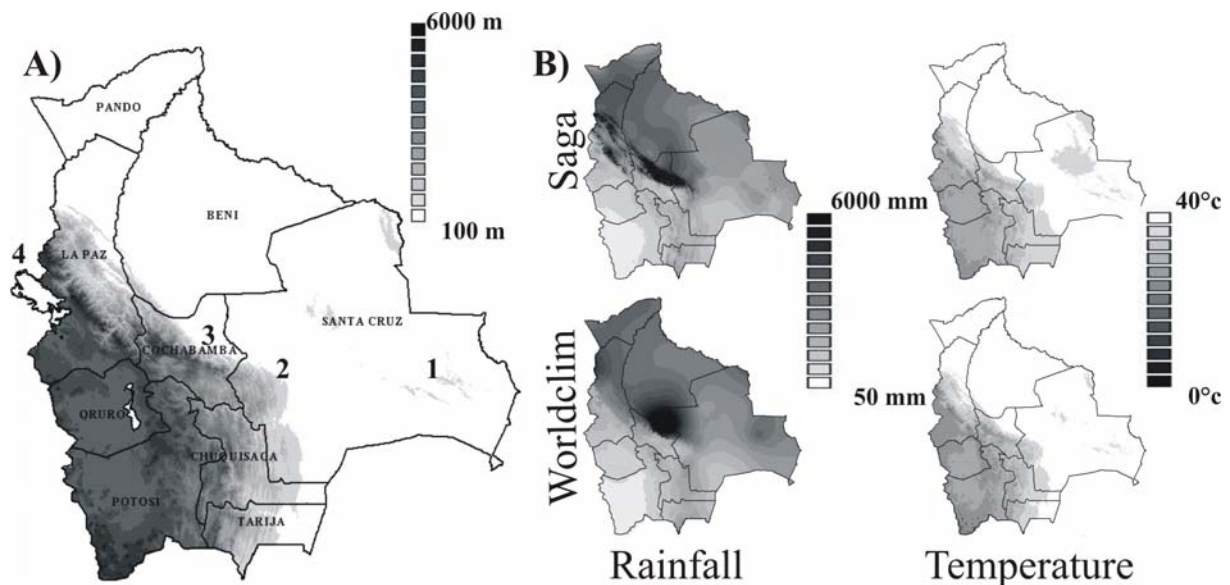


Figure 3.1. A) The study area detailing the administrative division of Bolivia and the digital elevational model of Bolivia. Numbers represent localities mentioned in the text: 1) Serranía de Santiago, 2) Andean Elbow, 3) the Chapare region, 4) Lake Titicaca. B) Climatic layers of mean annual precipitation (left) and temperature (right) predicted by the SAGA (top) and Worldclim (bottom) models.

bamba department, exceeding 6000 mm of annual rainfall. Humid montane forests are considered one of the most diverse ecoregions in Bolivia with high levels of endemism (Ibisch *et al.*, 2003), including birds (Herzog *et al.*, 2005) and ferns (Soria-Auza & Kessler, 2007, 2008). South of the Andean elbow, humid montane forests have a more patchy distribution, forming habitat islands in a matrix of seasonally dry forest. The north-westernmost distribution of seasonally dry forests reaches the central Andean region of La Paz department. At this latitude seasonally dry forests are fragmented and surrounded by either other high Andean vegetation types (puna grasslands) or humid montane forests (Herzog & Kessler, 2002, 2006; Ibisch & Mérida, 2003; Wood, 2006; Linares-Palomino & Kessler, 2009). Seasonally dry forests are the dominant vegetation in the subtropical lowlands of southern Bolivia, where several types of dry vegetations are commonly recognized (Chaco, Cerrado & Chiquitano dry forests) (Herzog & Kessler, 2002; Ibisch & Mérida, 2003). Tropical rain forests, on the other hand, occur in northern Bolivia and extend

along the eastern base of the Andes south to about 18°, forming a thin band limited to the east by the seasonally flooded grasslands of Beni (in central Bolivia).

For species distributional data, we used the database of Bolivian pteridophytes compiled by M. Kessler and A. R. Smith (www.fernsofbolivia.uni-goettingen.de), and the distributional database of birds of Bolivia of Asociación Armonia – BirdLife International. For the present study, 23 bird and 22 fern species were selected according to two criteria: (1) species characteristic of either humid montane forests north of the Andean elbow or seasonally dry forests, (2) species with at least 15 geographically independent records, and a relative good level of knowledge of their distribution. In total, we had 1840 locality records for all species combined, with an average of 38.3 ± 16.7 records per species. The number of records per species varied from 15 (*Myiopsitta monachus*) to 81 (*Polioptila dumicola*).

The subset of fern species characteristic of humid montane forests included six species of the genus *Cyathea* (tree ferns) that are tightly associated with humid montane forests. Although *Cyathea* species are not categorized as threatened, they are the only group of ferns experiencing direct human impact on their populations as their “trunks” are harvested to make flower pots. Of the 14 bird species characteristic of this habitat one is endemic to Bolivia (*Grallaria erythrotis*).

The subset of species characteristic of the seasonally dry forests was comprised of 15 and 12 species of ferns and birds, respectively. From this group of species, the Bolivian endemic *Cranioleuca henricae* is listed as endangered under IUCN Red List criteria. *Tarphonomus harterti* also is endemic to the country. The complete list of species is detailed in Table 3.2.

3.2.2 Selection of environmental variables and climate models

We used precipitation and temperature variables that describe the general pattern and annual variability of the climate estimated by both climate models at a resolution of 30 arc s. Variables included (1) annual precipitation, (2) mean precipitation during the three driest months, (3) mean precipitation during the three wettest months, (4) annual precipitation range (precipitation of the wettest month minus precipitation of the driest month), (5) mean annual temperature, (6) mean temperature during the three hottest months, and (7) mean temperature during the three coldest months. Because some of these environmental variables may be collinear, we checked for collinearity following the approach described by Blanchet

et al. (2009). We entered the variables one by one into a matrix and then computed at each step the determinant of its correlation matrix. Variables are completely collinear when the determinant's value equals zero. After this process we eliminated annual precipitation range and mean precipitation during the wettest month.

Worldclim (Hijmans *et al.*, 2005) is a comprehensive climate data set that covers most of the Earth's surface at a resolution of 30 arc s. Worldclim was compiled from available meteorological station networks. The authors used the thin-plate splines smoothing procedure available in ANUSPLIN 4.3, as described by Hutchinson (1995). A second-order spline was fitted using latitude, longitude and elevation as independent variables because this produced the lowest overall error (see Hijmans *et al.*, 2005 for more details). This technique has been used in several global studies, and performed relatively well in comparative tests of multiple interpolation techniques (New *et al.*, 1999, 2002).

Whereas the Worldclim approach is an interpolation technique rather than a modelling approach, the estimation of climate variables via SAGA uses an empirical modelling scheme. SAGA integrates statistical downscaling and terrain parameterization methods to enable the physically consistent estimation of climate layers. The statistical downscaling consists of linking data collected from meteorological stations to large-scale circulation patterns. Since spatio-temporal climate variations in mountainous environments also are significantly controlled by regional to local scale topography and other processes, digital elevation model (DEM) derived terrain parameters are integrated in order to increase the predictive power and the empirical congruence of the spatial transfer functions. The required data for this modelling process consist of circulation variables either derived from general circulation models (GCM) or from retroactively modelled atmospheric fields, a high resolution digital elevation model (DEM) and available time series data from meteorological station networks. A more comprehensive description of this modelling approach and its limitations are given in Böhner (2005).

3.2.3 Comparison of climate models

We randomly plotted 1000 points over the surface of Bolivia. In order to prevent pseudo-replication (more than a point from a single grid), points were at least 1 km apart from each other (the resolution of the climatic layers from SAGA and Worldclim). Then we imported this georeferenced file into DIVA GIS 5.4. The corresponding environmental variables of

each point were extracted from both climate models. We used SAM 3.0 to correlate the correspondent environmental variables from both climate models (e.g. mean annual temperature from Worldclim vs. that from SAGA). We used the adjusted p values following Dutilleul's (1993) correction to account for the effect of spatial autocorrelation (lack of spatial independence between some points).

3.2.4 Modelling species distribution

We used Maxent (Maximum Entropy) to model species distributions (Phillips *et al.*, 2006; Phillips & Dudík, 2008). This method has been reported to outperform other presence-only methods (Elith *et al.*, 2006), even with limited amounts of occurrence data (Pearson *et al.*, 2007). Auto features were maintained to find out the best relationship between species occurrence data and environmental variables, and settings were set to remove duplicate presence records at the resolution of the environmental layers.

Prior to modelling, we randomly partitioned the occurrence data of each species into two subsets. Seventy five percent of the records were used to model species distributions (training data), and 25% to evaluate the model (testing data). We repeated this procedure 20 times per species. The partition was performed randomly each time following a bootstrapping procedure. We therefore modelled 20 versions of each species' distribution (hereafter termed versions). In order to compare the modelled species distributions, and consequently, the estimated pattern of species richness by both climate models, we converted the probability values given by Maxent into presence-absence values using the maximisation of sensitivity and specificity values as threshold (Canran *et al.*, 2005). The final ranges of each species included only the grid cells predicted to potentially contain the species in all 20 versions. We used the area under the curve (AUC) to evaluate the general accuracy of every version modelled. This measure has been recommended for evaluating predicted species distributions because it avoids the supposed subjectivity of threshold-selection when continuous probability derived scores are converted into binary presence-absence (Fielding & Bell, 1997).

Wilcoxon tests were used to test for differences between AUC values produced by the modelled estimations from SAGA and Worldclim at the species level and between species. At the species level, each AUC value of a modelled version was considered a repetition, so we had 20 repetitions. At the between-species approach the averaged values of

AUC per species were considered repetitions. Finally, we also compared the differences in the predicted patterns of species richness estimated by each climate model. We created a map of disagreement between both maps of species richness by performing a cell-to-cell subtraction of SAGA minus Worldclim species richness values.

3.3 Results

3.3.1 Comparison between both climate models

Table 3.1. Bivariate correlations between environmental layers from the SAGA and Worldclim climate models. Degrees of freedom were corrected according to Dittuleul's criterion.

Environmental variables	R	P	DF (Dittuleul's corrections)
Annual precipitation	0.57	0.022	6.64
Annual precipitation range	0.46	0.023	5.95
Mean precipitation of the three driest months	0.69	0.021	8.85
Mean precipitation of the three wettest months	0.50	0.027	11.77
Mean annual temperature	0.99	< 0.001	4.36
Mean temperature of the three hottest months	0.99	< 0.001	4.57
Mean temperature of the three coldest months	0.98	< 0.001	4.20

Spatial correlations between corresponding environmental variables from both climate models yielded extremely high correlation values for temperature variables. The highest correlation values corresponded to the mean temperature during the three hottest months ($r = 0.99$, $p < 0.001$), the lowest to the mean temperature during the three coldest months ($r = 0.98$, $p < 0.001$). Precipitation variables returned lower but also significant correlations (range 0.46-0.69, Table 3.1, Fig. 3.2). A direct comparison of annual precipitation patterns between both climate models showed that Worldclim provides lower precipitation values than SAGA on the humid eastern slopes of the northern Bolivian Andes and in the adjacent lowlands. Worldclim, however, predicts higher rainfall for most of the southern lowlands and Andes, except for extreme south-western Bolivia (Fig. 3.2a). Although mean annual temperatures from both climate models also reported some spatial differences, these differences were not larger than 4°C (Fig. 3.2b).

3.3.2 Modelling species distributions

Average AUC values obtained for the final distribution maps of bird and fern species were notoriously high using both SAGA and Worldclim (> 0.84), although values based on SAGA were slightly higher (0.94 ± 0.03) than those using Worldclim (0.90 ± 0.03) (Table 3.2). This difference in favour of SAGA was homogeneous for species that are characteristic of humid

Table 3.2. Comparison between versions (intraspecific comparisons) and final maps constructed with Maxent using SAGA and Worldclim data layers. Each row shows the average and standard deviation of AUC values based on 20 Maxent runs, followed by z value (of the Wilcoxon test) and the corresponding p values. Bold values indicate significant differences, highlighting the higher values.

Species	Taxa	SAGA		Worldclim		Wilcoxon test	
		AUC	\pm SD	AUC	\pm SD	Z	p value
Humid montane forests							
<i>Andigena cucullata</i>	Bird	0.98	0.001	0.94	0.002	4.78	0.00
<i>Atlapetes rufinucha</i>	Bird	0.95	0.001	0.88	0.001	4.70	0.00
<i>Conirostrum ferrugineiventre</i>	Bird	0.96	0.001	0.88	0.001	4.40	0.00
<i>Cranioleuca albiceps</i>	Bird	0.95	0.001	0.89	0.001	4.70	0.00
<i>Cyanolyca viridicyanus</i>	Bird	0.93	0.001	0.89	0.001	4.57	0.00
<i>Cyathea austropallescens</i>	Fern	0.97	0.001	0.91	0.001	2.88	0.00
<i>Cyathea delgadii</i>	Fern	0.98	0.015	0.92	0.003	4.17	0.00
<i>Cyathea multiflora</i>	Fern	0.98	0.003	0.91	0.003	3.34	0.00
<i>Cyathea pungens</i>	Fern	0.96	0.004	0.86	0.005	3.61	0.00
<i>Cyathea squamipes</i>	Fern	0.92	0.002	0.94	0.002	3.74	0.00
<i>Cyathea subincisa</i>	Fern	0.94	0.001	0.86	0.001	4.34	0.00
<i>Delothraupis castaneiventris</i>	Bird	0.95	0.001	0.88	0.001	4.62	0.00
<i>Entomodestes leucotis</i>	Bird	0.95	0.001	0.88	0.003	4.78	0.00
<i>Eubucco versicolor</i>	Bird	0.99	0.002	0.89	0.002	4.72	0.00
<i>Grallaria erythrotis</i>	Bird	0.96	0.001	0.89	0.001	4.78	0.00
<i>Metallura aeneocauda</i>	Bird	0.96	0.001	0.86	0.001	4.70	0.00
<i>Myiornis albiventris</i>	Bird	0.95	0.002	0.86	0.001	3.70	0.00
<i>Psarocolius atrovirens</i>	Bird	0.96	0.001	0.90	0.002	4.78	0.00
<i>Scytalopus parvirostris</i>	Bird	0.98	0.002	0.90	0.001	4.30	0.00
<i>Zimmerius bolivianus</i>	Bird	0.96	0.002	0.87	0.002	3.87	0.00
subset of species		0.96	0.018	0.89	0.024	3.27	0.00
Seasonally dry forests							
<i>Adiantum rufopunctatum</i>	Fern	0.89	0.003	0.89	0.001	1.89	0.06
<i>Adiantopsis chlorophylla</i>	Fern	0.93	0.025	0.92	0.026	1.38	0.17
<i>Anemia australis</i>	Fern	0.87	0.006	0.86	0.006	0.05	0.96
<i>Anemia herzogii</i>	Fern	0.87	0.014	0.88	0.013	0.25	0.80
<i>Anemia ferruginea</i>	Fern	0.93	0.014	0.92	0.013	2.19	0.08
<i>Anemia myriophylla</i>	Fern	0.91	0.006	0.91	0.010	0.76	0.44
<i>Anemia tomentosa</i>	Fern	0.88	0.007	0.88	0.005	0.05	0.96
<i>Argyroschisma flava</i>	Fern	0.88	0.010	0.88	0.009	1.17	0.24
<i>Arremon flavirostris</i>	Bird	0.93	0.002	0.89	0.003	4.63	0.00

<i>Asplenium inaequilaterale</i>	Fern	0.87	0.059	0.87	0.058	2.09	0.04
<i>Asplenium lorentzii</i>	Fern	0.91	0.002	0.91	0.004	1.48	0.14
<i>Astrolepis sinuata</i>	Fern	0.93	0.052	0.92	0.007	0.87	0.39
<i>Cranioleuca henricae</i>	Bird	0.98	0.021	0.98	0.021	0.87	0.39
<i>Doryopteris lorentzii</i>	Fern	0.94	0.025	0.93	0.010	0.15	0.88
<i>Doryopteris raddiana</i>	Fern	0.94	0.017	0.94	0.015	1.07	0.28
<i>Formicivora melanogaster</i>	Bird	0.93	0.006	0.95	0.005	4.17	0.00
<i>Myiopsitta monachus</i>	Bird	0.97	0.003	0.97	0.002	1.66	0.10
<i>Nystalus maculatus</i>	Bird	0.96	0.003	0.96	0.004	1.50	0.13
<i>Pecluma filicula</i>	Fern	0.90	0.003	0.90	0.004	0.20	0.84
<i>Polioptila dumicola</i>	Bird	0.95	0.006	0.94	0.006	1.22	0.22
<i>Poospiza boliviana</i>	Bird	0.92	0.002	0.92	0.001	1.25	0.21
<i>Selaginella sellowii</i>	Fern	0.90	0.005	0.90	0.005	1.78	0.07
<i>Serpophaga munda</i>	Bird	0.89	0.004	0.92	0.002	4.17	0.00
<i>Stigmatura budytoides</i>	Bird	0.94	0.002	0.96	0.002	3.96	0.00
<i>Suiriri suiriri</i>	Bird	0.97	0.005	0.90	0.009	3.11	0.00
<i>Synallaxis scutata</i>	Bird	0.90	0.002	0.90	0.004	2.58	0.01
<i>Tarphononmus harterti</i>	Bird	0.88	0.012	0.90	0.033	4.78	0.00
subset of species		0.92	0.033	0.92	0.031	2.02	0.18
<i>All species</i>		0.94	0.034	0.90	0.030	2.02	0.04

montane forests, except for the fern *Cyathea squamipes*, which was the only species that showed significantly lower AUC values for SAGA than for Worldclim (Table 3.2). Differences between the models were not as strong for the set of species characteristic of seasonal dry forests. Twenty species did not show significant differences in AUC values (Table 3.2, $p > 0.05$), for two bird species (*Arremon flavirostris*, *Suiriri suiriri*) SAGA values were higher, whereas for four bird species Worldclim values were higher (*Formicivora melanogaster*, *Serpophaga munda*, *Stigmatura budytoides*, *Tarphononmus harterti*) (Table 3.2). When comparing the whole subset of species characteristics of this habitat, we did not find significant differences (Table 3.2).

Variability of AUC values between versions for species characteristic of humid montane forest were quite low, irrespective of which climate model was used (SAGA: standard deviation varied from ± 0.0001 for *Grallaria erythrotis* to ± 0.015 for *Cyathea delgadii*; Worldclim: from ± 0.001 for *Delothraupis castaneiventris* to ± 0.005 for *Cyathea pungens*). The variability for the subset of species characteristic of dry forests was somewhat higher but also did not differ between different climate data sets (SAGA: from ± 0.002 for *Asplenium lorentzii* to ± 0.059 for *Asplenium inaequilaterale*; Worldclim: from ± 0.001 for *Adiantum rufopunctatum* to ± 0.058 for *Asplenium inaequilaterale*; Table 3.2).

Diversity maps of bird and fern species characteristic of humid montane forests generated by both climate models predicted the species-richest cells on the humid east Andean slopes (Fig. 3.3a-b and 3.3d-e). Worldclim estimations, however, predicted the

occurrence of two bird species-rich centres south of the Andean elbow (up to 11 species) in (1) central Chiquisaca department and (2) at the border between northern Chuquisaca and western Santa Cruz departments. Worldclim also predicted the occurrence of three species of tree-ferns (*C. pungens*, *C. multiflora* and *C. delgadii*) in Amazonian lowlands (Fig. 3.3b and 3.3e). Larger differences resulted when comparing both patterns of species richness on a cell-to-cell basis. SAGA predicted higher species richness on the humid east Andean slopes for both taxa than Worldclim, whereas the latter suggested a higher number of bird species to occur in the cool and dry surroundings of Lake Titicaca (7 species) and the fragmented Andean seasonal dry forest (up to 11 species). Importantly, especially for ferns, Worldclim estimated the lowland Chapare region to have higher species richness than SAGA (Fig. 3.3c and 3.3f).

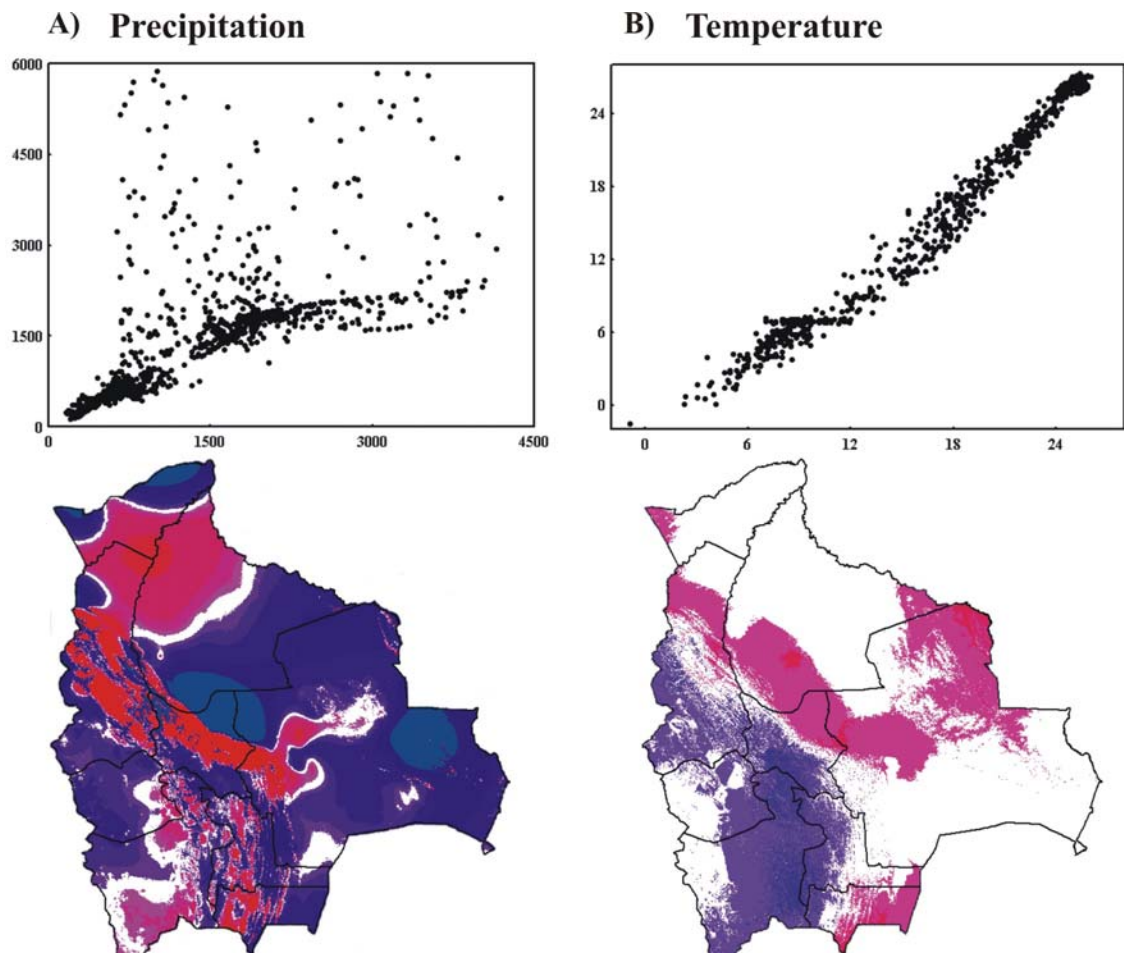


Figure 3.2. Graphic correlation between values of mean annual (A) precipitations and (B) temperatures. The Y axis represents data from the SAGA model, the X axis Worldclim values. The maps depict the geographical discordances between both climate models. Reddish tones indicate higher values of SAGA in relation to Worldclim, bluish tones the opposite.

Despite the lack of statistical differences in AUC values between climate models for species characteristic of seasonal dry forests, the overlapped maps of species richness showed clear differences, not just in the lowlands, but also in the Andes. Models based on SAGA calculated cells of higher numbers of co-occurring dry forest bird and fern species in sections of the northern Bolivian Andes (departments of La Paz and Cochabamba) where seasonal dry forests occur as isolated habitat fragments. Worldclim, on the other hand, produced a diffused pattern that was not able to contrast humid from dry habitats in this region of Bolivia (Fig. 3.3 g-h and 3.3j-k). In other words, models based on Worldclim tended to predict bird and fern species characteristic of dry habitats to occur on the wet Andean slopes north of the Andean elbow. Figures 3.3i and 3.3l show this tendency for both taxa in more detail. Here, the upper humid Andean slopes of the Chapare region were included within the ranges of bird and fern species from dry habitats by models based on Worldclim data. It is also apparent that Worldclim data resulted in predictions of higher diversity of birds and ferns at the upper end of dry Andean slopes south of the Andean elbow. In the dry lowlands, models based on SAGA data indicated higher species richness of birds in the central part of the Chiquitano dry forest and in the Cerrado in central Santa Cruz department when compared to models based on Worldclim data. Models using Worldclim data, on the other hand, predicted higher species richness at the northernmost extreme of the seasonal dry forests and in the Chaco region in southern Santa Cruz (Fig. 3.3i). Model predictions for ferns showed a more complicated spatial pattern in the lowlands. Whereas models based on Worldclim data predicted higher richness in central Santa Cruz, models using SAGA data identified the surroundings of the Serranía de Santiago and the Chiquitano dry forest around this area as having more species (Fig. 3.3l).

3.4 Discussion

3.4.1 Comparison between both climate models

It is not surprising that temperature layers from both climate models have good spatial concordance. Although slight local deflections due to vertical wind movements caused by difference in air-pressure in mountain areas may be expected, temperature is strongly negatively correlated with altitude, allowing little room for variation in regional-scale climate models (Killeen *et al.*, 2007). Rainfall patterns, on the other hand, are influenced by

a combination of other factors including wind currents, topography, and the diurnal cycle of solar radiation that changes air pressure, and therefore causes differential precipitations along altitudinal gradients (forcing factors in regional circulation models). Such complex interactions cause a more irregular spatial pattern of rainfall in mountain regions that is not directly correlated to either latitude or altitude. Instead, it is strongly influenced by factors shaping regional circulation patterns and the resulting windward/leeward differentiation. Figure 3.2 shows an interesting discordance between layers of annual rainfall as predicted by the two climate models. Whereas Worldclim estimates highest values of rainfall for the lowlands adjacent to the most humid area in Bolivia (Andean slopes of the Chapare regions), SAGA predicts maximum precipitation on the Andean slopes of the Chapare region. This pattern predicted by SAGA is supported by the effect of the South American low level jet that overpowers the South Atlantic convergence zone during the austral summer and transports humid winds from the Northern Andes to the foothills of the Chapare (Nieto-Ferreira, 2003; Vuille & Keimig, 2004; Killeen *et al.*, 2007). Outside the Chapare region, Worldclim predicts fairly uniform precipitation on the east Andean slope of the northern Bolivian Andes, failing to distinguish intersecting dry rain-shadow valleys in La Paz and Cochabamba departments.

The accuracy of Worldclim has been assessed in Europe, North America and several tropical regions, all of which have considerably higher densities of climatic field stations than most of the tropical regions in South America, Africa, and Asia (see Fig. 1a-c in Hijmans *et al.* 2005). Additionally, it is relatively common that field stations in tropical countries have not collected data continuously. This means that although it is possible to find areas with a relatively high density of field stations, not all of them contributed equally with data. Even more importantly especially in mountainous regions, climate stations tend to be located close to population centres which are typically found under climatic conditions most suitable to human habitation and agriculture and are rarely representative of the climatic conditions in the entire region. Consequently, estimating rainfall based only on data extracted from field stations may not result in accurate patterns for tropical areas with complex topography and limited numbers field stations.

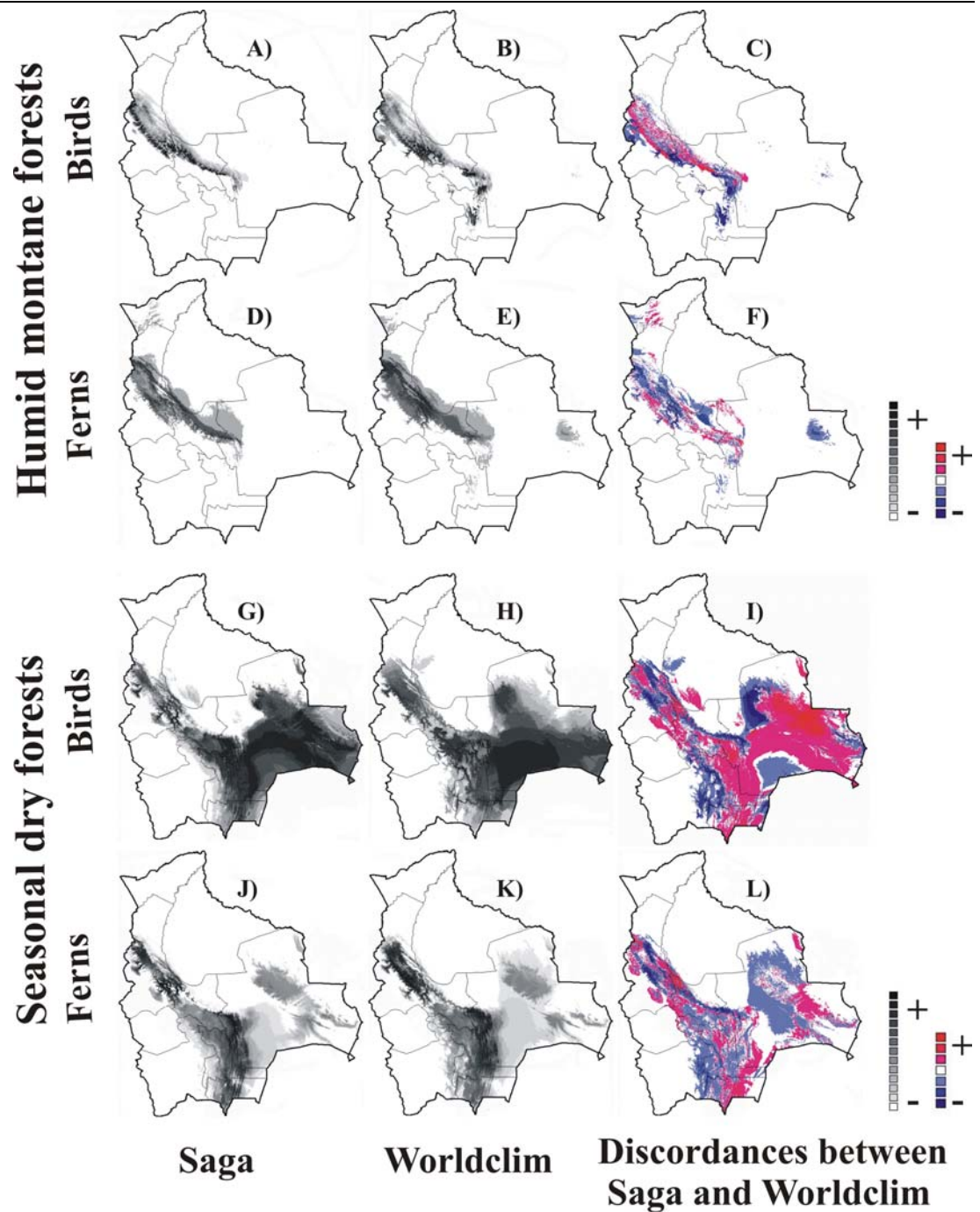


Figure 3.3. Patterns of species richness predicted by Maxent models based on climate data from SAGA (left) and Worldclim (centre) and tie geographical discordance between the two modelling approaches. Reddish tones indicate higher values based on SAGA data in relation to Worldclim data, bluish tones the opposite.

Unlike SAGA, Worldclim does not take into account the effect of topographically influenced regional circulation patterns in estimating the windward and leeward variations of rainfall patterns. We suggest that this methodological difference may be the source of the notable differences in predicted rainfall patterns between both climate models. Killeen *et al.* (2007) noted that centres of high rainfall predicted by Worldclim along the eastern Andes tend to have an artificial ovoid shape that extends into the more seasonal and drier lowlands.

SAGA does not depict this pattern. Instead, it mirrors the configuration of the eastern Andean cordillera, and resembles closely the cloud masks presented by Killeen *et al.* (2007: fig. 6 a-d). Although this may suggest that SAGA outperforms Worldclim in predicting rainfall patterns, it must be considered that the masks of cloudiness shown by Killeen *et al.* (2007) represent the mean pattern of cloudiness at four different times of the day from December to March. Although this period presumably covers most of the rainy season, this figure only offers a qualitative evaluation. A good alternative to evaluate rainfall layers from climate models may be the aggregation of clouds reaching temperatures lower than -65°C at the top. These clouds are closely related to centres of deep convective rain (Hastenrath, 1997; Killeen *et al.*, 2007). Therefore, a layer that summarizes the frequency of aggregation of clouds with such characteristic may be a reliable independent measure of rainfall. However, the contribution of other sources of precipitation (drizzle, horizontal precipitation, etc.) would still be underestimated.

3.4.2 Modelling species distributions and implications for conservation

Predicted ranges of species characteristic of humid montane forests had a higher model fit when modelled based on SAGA. Since the only difference in the modelling process was the use of different climatic models, we can attribute the higher fit of SAGA-based models to the climate data. In fact, the patterns of species richness produced by models based on SAGA are in closer correspondence to the survey-based knowledge of the distribution of humid montane forests in Bolivia (e.g. Navarro & Maldonado, 2002; Ibisch *et al.*, 2003). Models using Worldclim, on the other hand, predicted the occurrence of several bird and fern species in the surroundings of Lake Titicaca on the Bolivian altiplano, an area without forest cover where the actual climate is much dryer than in the montane humid forests and where none of these species are known to occur (e.g. Hennessey *et al.*, 2003). Importantly, models based on Worldclim also failed to predict the occurrence of some bird species in the humid montane forests of the Chapare region, whereas they wrongly predicted the presence of some humid montane forest species in the Chapare lowlands (ferns) and well south of the Andean elbow (birds). Field surveys suggest that the two centres of high bird species richness predicted by models based in Worldclim south of the Andean elbow are a modelling artefact and that the humid montane forest species modelled here do not occur in these areas (e.g. Hennessey *et al.* 2003; SKH unpubl.). The Andean elbow marks the

boundary between two distinct ecoregions of humid montane forest, the tropical Yungas of the northern Bolivian Andes and the more seasonal Bolivian-tucuman forests from the south, subtropical Boliviano-Tucuman forests of the southern Bolivian Andes (e.g. Navarro & Maldonado, 2002; Ibish *et al.*, 2003). Most humid montane forest species reach their southern range limit at the Andean elbow (e.g., Ridgely & Tudor, 1994; Fjeldså & Mayer, 1996; Hennessey *et al.*, 2003).

Despite the lack of statistical significance between the AUC values obtained by models based on Worldclim and SAGA for seasonal dry forest species ranges, crucial differences emerged between the maps of species richness based on the different climate models. For example, models using SAGA more clearly depicted the geographical configuration of the fragments of seasonal dry forests in the northern Bolivian Andes as also indicated by Herzog and Kessler (2002, 2006), Ibisch *et al.* (2003) and Wood (2006). These outcomes are remarkable since even the predicted ranges using Worldclim obtained values of AUC higher than the commonly indicated minimal acceptable threshold (0.75) (e.g. Fielding & Bell, 1997). If we look at the maps of discrepancies between the patterns of species richness (Fig. 3.3i and 3.3j) further critical differences are evident. This raises the question whether AUC is a suitable index by which to evaluate modelled ranges of species produced by presence-only methods. Although this question is beyond the scope of this study, it is evident that modelled ranges with high AUC values may still be unreliable (see also Lobo *et al.*, 2008; Peterson, 2008). Therefore, ground-truthing of predicted ranges should form an integral part of ecological niche modelling studies, especially if studies are aimed at determining priority areas for conservation action.

As subtle as the differences in species richness patterns between climate models may look, they may bear critical implications for conservation concern species. Current conservation policies commonly attempt to identify key areas so that efforts to conserve priority species can be maximised, while minimizing economic and social costs. Therefore, it is of vital importance to determine the most efficient way to identify centres that contain high densities of species of conservation concern such as range restricted species, habitat specialists, and threatened species. We found several areas where model predictions using the two climate data sets were not congruent. Although most species we modelled are of low conservation concern (We excluded threatened species because they have few records and are therefore difficult to model), they are geographically restricted to two biomes of high conservation priority (Ibisch *et al.*, 2003; Herzog *et al.*, 2005), which both harbour a significant number of species of conservation concern. Andean seasonal dry forest

fragments have high levels of endemism for several plant groups such as Cactaceae, Bromeliaceae (e.g. Bach *et al.*, 1999; Wood, 2006; Linares-Palomino & Kessler, 2009) and humid montane forests of the northern Bolivian Andes (Yungas) harbour by far the greatest number of bird species of conservation concern of all Bolivian ecoregions (Herzog *et al.*, 2005).

Previous studies on the reliability of species distribution models have focused on evaluating the disagreements of predictions produced by different species distribution models (e.g., Elith *et al.*, 2006; Peterson *et al.*, 2007) or assessed the effect of the spatial data structure (Loiselle *et al.*, 2007), but uncertainties introduced by climate layers have been largely overlooked so far. Our study shows that this uncertainty may have an important impact on the prediction of the distributions of tropical species, where species distribution modelling is increasingly being employed (Hernandez *et al.*, 2008; Hole *et al.*, 2009; Velazques *et al.* in prep.).

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3.5 References

- Araujo, M.B. & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677-1688.
- Araujo, M.B. & Rahbek, C. (2006) How does climate change affect biodiversity?. *Science*, 313, 1396-1397.
- Araujo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology and Evolution*, 22, 42-47.
- Araujo, M.B., Whittaker, R.J., Ladle, R.J. & Erhard, M. (2005) Reducing uncertainty in projections of extinction risk from climate change. *Global ecology and Biogeography*, 14, 529-538.
- Araujo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of biogeography*, 33, 1712-1728.
- Bach, K., M. Kessler & Gonzales, J., (1999) Caracterización preliminar de los bosques deciduos andinos de Bolivia en base a grupos indicadores botánicos. *Ecología en Bolivia*, 32: 7-22.
- Bahn, V. & McGill, B. (2007) Can niche-based distribution models outperform spatial interpolation?. *Global Ecology and Biogeography*, 16, 733-742.
- Bauermann, W., Saatchi, S., Smith, T.B., Zutta, B.R., Chaves, J.A., Milá, B. & Graham, C.H. (2008) Predicting species distributions across the Amazonian and Andean regions using remote sensing data. *Journal of Biogeography*, 35, 1160-1176.
- Blanchet, F. G., Legendre, P. & Borcard D. (2009) Forward selection of explanatory variables. *Ecology*, 89, 2623-2632.
- Böhner, J. (2005) Advancements and new approaches in climate spatial prediction and environmental modelling. *Arbeitsberichte des Geographischen Instituts der HU zu Berlin* 109, 49-90.
- Canran, L. P., Terence, M. B., Dawson, P. D. & Pearson, R. G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385-393.
- Carnaval, A.C. & Moritz, C. (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forests. *Journal of biogeography*, 35, 1187-1201.
- Cumming G.S. (2000) Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). *Journal of biogeography*, 27, 425-440.
- Dutilleul, P. (1993) Modifying the t test for assessing the correlation between two spatial processes. *Biometrics*, 49, 305-314.

- Elith, J., Grahm, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachertti-Pereira, R., Schap9hire, R.E. Soberon, J., Williams, S., Wisz, M.S., & Zimmermann N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Fielding, A.H. & J. F. Bell (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation*, 24 (1), 38-49.
- Fjeldså, J. & Mayer, S., (1996) Recent ornithological surveys in the Valles region, southern Bolivia - and the possible role of Valles for the evolution of the Andean avifauna. *DIVA Technical Report 1*. Rønde, Denmark.
- Graham, K.H., Moritz, C., Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforests fauna. *Proceedings of the National Academy of Sciences*, 103, 632-636.
- Hastenrath, S. (1997) Annual cycle of upper air circulation and convective activity over tropical Americas. *Journal of Geophysical Research*, 102, 4267-4274.
- Hennessey, A.B., Herzog, S.K. & Sagot, F. (2003) Lista anotada de las aves de Bolivia. 5th edición. *Asociación Armonía/BirdLife Internacional*, Santa Cruz de la Sierra, Bolivia, 238 pp.
- Hernandez, P.A., Franke, I., Herzog, S.K., Pacheco, V., Paniagua, L., Quinana, H.L. Soto, A., Swenson, J.J., Tovar, C., Valqui, T.H., Vargas, J. & Young, B.E. (2008) Predicting species distributions in poorly-studied landscapes. *Biodiversity Conservation*, 17, 1353-1366.
- Herzog, S.K. & Kessler, M. (2002) Biogeography and composition of dry forests bird communities in Bolivia. *Journal of Ornithology*, 143, 171-204.
- Herzog, S.K. & Kessler, M. (2006) Local *versus* regional control on species richness: a new approach to test for competitive exclusion at the community level. *Global Ecology and Biogeography*, 15, 163-172.
- Herzog, S.K., Soria-Auza, R. W. & Hennessey, A.B. (2005) Patrones ecorregionales de riqueza, endemismo y amenaza de la avifauna boliviana: prioridades para la planificación ecorregional. *Ecología en Bolivia*, 40(2), 27-40.

- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International journal of climatology*, 25, 1965-1978.
- Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, H.M., Collingham, Y.C., Rahbek, C. & Huntley, B. (2009) Projected impacts of climate change on continental-wide projected area network. *Ecological Letters*, 12, 420-431.
- Hutchinson M.F. (1995) Interpolating mean rainfall using thin plate smoothing splines. *International Journal of Geographical Information Systems*, 9, 385-403.
- Ibisch, P.L., Beck, S.G., Gerkmann, B. & Carretero, A. (2003) La diversidad Biologica-Ecoregiones y ecosistemas Pp. 47-53. In Ibisch P.L. & Merida G. (2003) Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación. *Editorial FAN*, Santa Cruz de la Sierra, Bolivia.
- Ibisch, P. L. & Mérida, G. (2003) Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación. Ministerio de desarrollo sostenible. *Editorial FAN*, Santa Cruz de la Sierra, Bolivia.
- Jiménez-Valverde, A. Lobo, J.M. & Hortal, J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and distributions*, 14, 885-890.
- Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen P. M. & Mejia, J. (2007) Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, 34, 1357-1373.
- Linares-Palomino, R & Kessler, M. (2009) The role of dispersal ability, climate and spatial separation in shaping biogeographic patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography*, 36, 280-290.
- Lobo, J. M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17, 145-151.
- Loiselle, B.A., Jørgensen, P.,M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G. & Montiel, O.M. (2007) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes?. *Journal of Biogeography*, 35, 105-116.
- Luoto, M., Virkkala, R. & Heikkinen, R. K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global ecology and biogeography*, 16, 34-42.

- Navarro, G. & Maldonado, M. (2002) Geografía ecológica de Bolivia: Vegetación y ambientes acuáticos. *Centro de ecología Simón I. Patiño*- Departamento de difusión. Cochabamba, Bolivia.
- New, M., Hulme, H. & Jones P. (1999) Representing twentieth-century space-time climate variability. Part I: Development of a 1961-90 mean monthly terrestrial climatology. *Journal of Climate*, 12, 829-856.
- New, M., Lister, D., Hulme, M. & Makin I. (2002). A high resolution data set of surface climate over global land areas. *Climate Research*, 21, 1-25.
- Nieto-Ferreira, R., Rickenbach, T.M., Herdies, D.L. & Carvalho, L.M.V. (2003) Variability of South American convective cloud systems and Tropospheric circulation during January-March 1998 and 1999. *American Meteorological Society*, 131, 961-973.
- Pearson, R. G., Raxworthy, C.J., Nakamura M. & Peterson A.T. (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography*, 34, 102-117.
- Peterson, A. T., Papes, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modelling. *Ecological Modelling*, 213, 63-72.
- Phillips, S. T., Anderson, R. P. & Schapire, R. E.(2006) Maximum entropy modelling for species geographic distributions. *Ecological Modelling*, 190, 231-259.
- Phillips, S. T & Dudík, M. (2008) Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161-175.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, 17, 403-414.
- Ridgely, R. S. & Tudor, G. (1994) The birds of South America, vol. 2. *Oxford University Press*, Oxford, UK.
- Soria-Auza, R.W. & Kessler, M. (2007) Estado del conocimiento y conservación de los helechos y plantas afines en Bolivia. *Ecología en Bolivia*, 42 (2), 136-147.
- Soria-Auza, R.W. & Kessler, M. (2008) The influence of sampling intensity on the perception of the spatial distribution of tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, 14, 123-130.
- Van Rensburg, B.J., Levin, N. & Kark, S. (2009) Spatial congruence between ecotones and range-restricted species: implications for conservation biogeography at the sub-continental scale. *Diversity and Distributions*, 15, 379-389.

- Vuille, M. & Keinig F. (2004) Interannual Variability of summertime convective cloudiness and precipitation in the central Andes derived from ISCCP-B3 data. *Journal of Climate*, 17, 3334-3348.
- Wood, J.R.I. (2006) Inter-Andean dry forests of Bolivia- Floristic affinities and patterns of endemism: Insights from Acanthaceae, Asclepiaceae and Labiateae. Pp. 235-256. In: Pennington R.T., Lewis, G.P. & Ratter, J.A. (2006) Neotropical Savannas and seasonally dry forests. *Press Boca Raton, FL*.

Chapter 4

Linking latitudinal and elevational patterns of bird species richness in the central Andes

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Abstract

We aimed to unravel the impact of climate, geometric constraints (latitudinal and elevational), and regional area in determining the patterns of bird species richness along latitudinal and elevational gradients in the central Andes. The study area covered from the extremely species rich humid Amazonian forests in the lowlands in southern Peru to the strongly seasonal, and less diverse lowland Chaco forest of south Bolivia, and the elevational gradients from the lowlands to the high Andes.

We mapped the bird species richness, topography and climate at a resolution of 15' x 15' (ca. 27 x 27 km) on the eastern Andean slopes from southern Peru to southern Bolivia. We performed spatial regression analysis of the species richness against the aforementioned variables. We additionally partitioned the study area into five regions and six elevational belts. The species richness was also partitioned into four quartiles, according to the species range-extension.

Species richness was higher at low to mid-elevations in the southern Peruvian Andes and decreased toward high elevations, and to the south. Dividing birds by range-size quartiles, the peak of species richness gradually shifted from high to low elevations as the range-size of the species increase. General species richness monotonically declined as elevation increase. But this pattern gradually changed toward a hump-shaped elevational pattern of species richness in a regional context southwards. Climate (precipitation) played the most important role in predicting the species richness. However, the other factors also played an important role that became evident when the study area was partitioned by regions and elevational belts. The effect of precipitation was more pronounced at lower elevations, as the strongest reductions of rainfall also occur there. Elevation (temperature) and habitat heterogeneity gained specially importance when we analyzed the data by regions. Narrow-ranged species on the other hand, showed different geographical patterns. The factors determining their distribution were also mainly precipitation followed by habitat heterogeneity. Our results suggest strong support in favour of the water-energy hypothesis as driver of species richness.

We show that diversity-parameter relationships recovered when the entire area is analyzed as a sole unit reflects the overwhelming dominance of the widespread species. Dissecting the study area into regions and elevational belts, and the species richness into quartiles let us to recover less frequent relationships that are valid for species of geographically restricted range. This also strongly suggest that continent-wide analyses of

diversity patterns run the risk of recovering patterns of the most common species (biomes), while neglecting the geographically restricted species (biomes) that are of priority for conservation.

Keywords: Altitude, Birds, Climate, Diversity gradients, Elevation, Mid-domain effect, Species richness

4.1 Introduction

Understanding the mechanisms determining global and regional gradients of species richness remains one of the major challenges of ecological and biogeographical research. Perhaps the best known richness pattern is that along the latitudinal gradient, with highest richness in the tropics for most taxa and decreasing richness toward higher latitudes (Rosenzweig, 1995; Gaston & Blackburn, 2000; Hillebrand, 2004), but patterns along elevational gradients are also increasingly being studied (e.g., Rahbek 1995, 2005, Lomolino 2001). Elevational gradients have the analytical advantage over the latitudinal gradient that they can be replicated at different sites across the globe and that they can each be studied within a given biogeographical and climatological region, thus excluding the potentially confounding effects of differences between regions (McCain, 2009). The elevational richness gradient was long believed to mirror the latitudinal gradient because both span a transition from warm to cold climatic conditions, and species richness was accordingly believed to decline monotonically from low to high elevations. It has now been shown that this perception was the result of an overemphasis on a few studies, and that about 50-75% of all elevational studies document hump-shaped richness patterns with maximum richness at some intermediate point of the gradient (Rahbek 1995, 2005; McCain, 2009). The remaining studies show either monotonic declines, constant richness to mid-elevations followed by declines, and (very rarely) increases or constant values. In contrast, latitudinal gradients typically show highest diversity at the equator.

Latitudinal and elevational richness patterns have been interpreted in the light of mainly four factor complexes, namely space involving regional area (e.g., Rosenzweig & Ziv, 1999) and geometric constraints (e.g., Colwell *et al.* 2004), current climate such as temperature and precipitation (e.g., Heaney, 2001; Kessler, 2001a; Bhattarai *et al.*, 2004; Kluge *et al.*, 2006) which in turn determine energy availability and ecosystem productivity (e.g., Hawkins *et al.*, 2003a; Currie *et al.*, 2004), biotic processes involving metapopulation interactions such as the Rapoport rescue hypothesis (e.g., Stevens, 1989) or source-sink effects (e.g., Kessler, 2000a; Grytnes, 2003), and historical and evolutionary processes (e.g., Hawkins *et al.*, 2003b, 2006; Ricklefs, 2004). Many of these aspects remain poorly explored, often due to the lack of suitable field or phylogenetic data (Kessler, 2009; McCain, 2009). Both along latitudinal and elevational gradients, all of the above-mentioned explanatory factors can lead to highest diversity at the equator or at mid-elevations, respectively, with the exception of area along elevation, since this generally declines

continuously with elevation (Körner & Paulsen, 2004). Thus, because many of the explanatory variables frequently covary along single gradients, discrimination between them is often impossible (e.g., Heaney, 2001; Bhattarai *et al.*, 2004; Kluge *et al.*, 2006).

Birds feature prominently in studies of regional and elevational species richness (e.g., Terborgh, 1977; Hawkins *et al.*, 2003a, 2003b; Evans & Gaston, 2005; McCain, 2009) because they are the taxonomically and biogeographically best known major group of organisms (e.g., Bibby *et al.*, 1992; Furness & Greenwood, 1993). Studies of latitudinal gradients of bird diversity have found little support for area (Hawkins & Porter, 2001) or the mid-domain effect (Hawkins *et al.*, 2005) as crucial factors, while current climate (e.g., Rahbek *et al.*, 2007) as well as historical and evolutionary factors including niche conservatism, the “time-for-speciation” hypothesis, and extinctions due to past climate change are supported (Hawkins *et al.*, 2006, 2007). Turning to mountains, in a recent meta analysis of 78 elevational bird gradient studies, McCain (2009) tested 18 predictions of theory diversity and obtained strong support for water-temperature limitations as crucial determinants, with weaker support for evolutionary niche conservatism; sampling effects, area, and the mid-domain effect were not supported. Both latitudinal and elevational studies thus appear to converge on a similar set of likely explanatory variables, although some differences are apparent.

This raises the question to which degree patterns of diversity along elevational and latitudinal gradients are determined by the same underlying mechanisms or whether different factors may apply. An important difference between them is their spatial extent, with latitudinal gradients extending over thousands of kilometres as opposed to usually tens of kilometres along elevational gradients. Thus population processes such as dispersal are more likely to influence elevational gradients over short time spans, while at evolutionary time scales, long-distance dispersal may be more important on a global scale (Kessler, 2009). A further problem in linking latitudinal and elevational gradients is that both types of gradients have so far mainly been studied independently of each other, and potential interactions between latitudinal and elevational diversity gradients remain unexplored. In particular, different factors may influence bird diversity in lowland versus montane regions, with topographic factors and small-scale ecological diversity probably being more important in mountains (Ruggiero & Hawkins, 2008). In addition, latitudinal and elevational studies typically differ in the number of spatial dimensions along which diversity is mapped: elevational studies typically use a one-dimensional approach of a single line along the gradient with single data points at each elevational step, whereas latitudinal studies mostly

use a two-dimensional approach, mapping diversity in numerous grid cells at each latitude. While it is well known that the scale and grain size at which diversity patterns are documented strongly impact our perception and interpretation of patterns (Rahbek, 2005), we are unaware of any study that has attempted to bridge this potential discrepancy between latitudinal and elevational studies.

In the central Andes, a number of field studies have documented bird species richness along extensive elevational gradients, uncovering different patterns along each gradient. From north to south, Terborgh (1977) found a hump-shaped pattern with a peak at about 1300 m in the Apurimac Valley of south-central Peru, Patterson *et al.* (1998) a roughly monotonical decrease with elevation in the Manu region, southern Peru, Kessler *et al.* (2001) a hump-shaped pattern with maximum richness at 2700 m in a dry valley system in northern Bolivia, and Herzog *et al.* (2005) a hump with maximum richness at ca. 1000 m in the very wet Chapare region of central Bolivia. These differences are partly due to the elevational extents of the studied transects, with those of Terborgh (1977) and Kessler *et al.* (2001a) being located in Andean valleys and those of Patterson *et al.* (1998) and Herzog *et al.* (2005) reaching to the lowlands, but striking differences remain even when only analogous transects are compared, with the more southern transects showing richness peaks at higher elevations than the more northern transects. The central Andes thus represent a region where different elevational bird richness patterns can be found along a latitudinal gradient.

In the present study, we set out to combine the analyses of latitudinal and elevational bird richness gradients in the central Andes. Our study region covers two strong bird richness gradients, namely the latitudinal gradient from the humid tropical Amazonian lowlands of southern Peru which harbour some of the world's richest avian communities (Terborgh *et al.*, 1990), to the relatively species poor seasonally dry, subtropical Chaco region of southern Bolivia (Stotz *et al.*, 1996), and the elevational gradient from the lowlands to the high Andes with peaks exceeding 6000 m in elevation. Our aim was to take advantage of this natural experiment of two superimposed diversity gradients to unravel the impacts of regional area, climate, and geometric constraints in determining bird richness patterns. We did not include primary productivity as a variable because suitable data are not available (McCain, 2009). Similarly, although evolutionary history is likely to play a role in determining bird diversity patterns (Hawkins *et al.*, 2006, 2007; McCain 2009), fully resolved and dated phylogenies, which are necessary to test the relevant hypotheses, are only available for a small subset of bird groups in the study region.

4.2. Methods

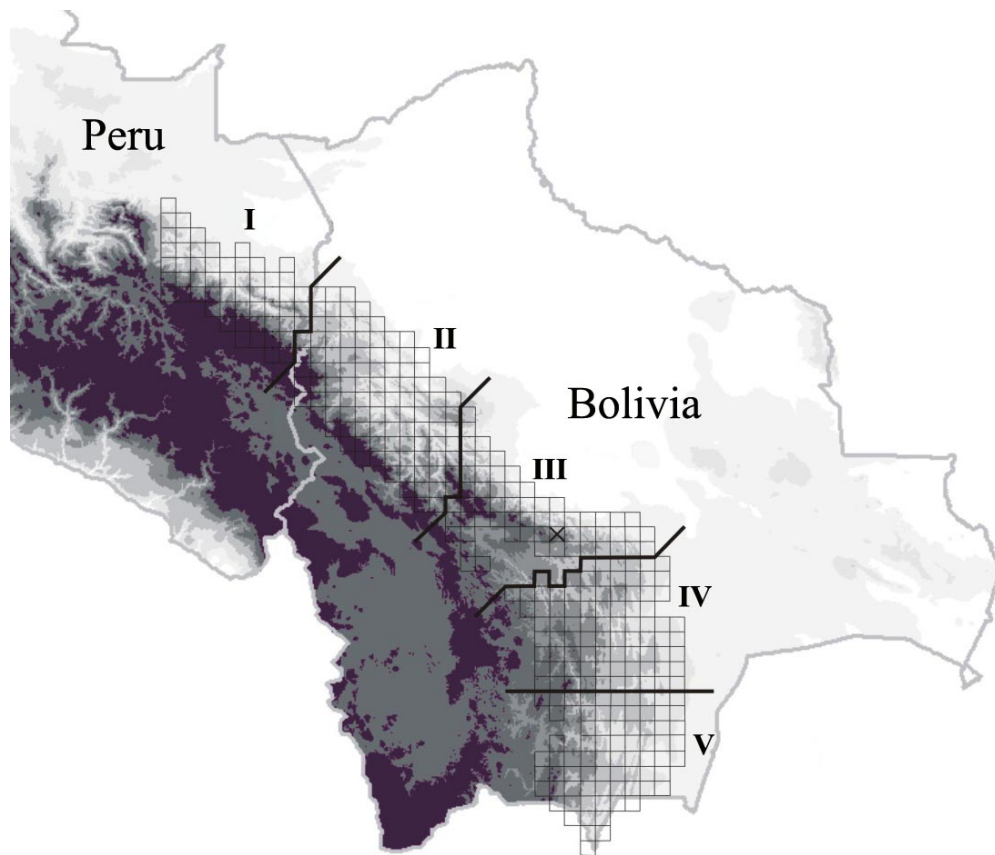


Figure 4.1. *Elevation model of the study area, showing the delimitation of the five study regions.*

We mapped bird species richness, topography and climate in a grid with a resolution of $15' \times 15'$ (ca. 27 km x 27 km) on the eastern Andean slope from the Manu region, southern Peru (12°S) to the southern Bolivian border with Argentina ($22^{\circ}30'\text{S}$) (Fig. 4.1). The lower elevational limit of the study region was defined as those cells including an elevation of at least 500 m, i.e., excluding cells situated exclusively in the lowlands. The upper limit was placed at those cells climatically directly influenced by the eastern trade winds, i.e., excluding rain-shadow inter-Andean valleys with strikingly different climatic and biogeographical conditions (Herzog & Kessler, 2002) as well as the Altiplano. For data analysis, the study region was divided into five topographically and climatically distinct latitudinal regions (I-V) and into six elevational zones (Fig. 4.1). Region I included the Peruvian part of the study region which has high precipitation levels and borders directly on the extensive Amazonian rainforest. Region II was the Yungas region of the northern

Bolivian Andes which is topographically more complex, has a more seasonal precipitation regime, and humid lowland forest restricted to a narrow band along the Andean foothills (with areas further east covered by seasonally flooded savannahs). Region III included the Chapare region of central Bolivia, a very wet region with extremely steep slopes, and lowland forests similarly restricted to the foothill zone. This region extends southeast to the “Andean elbow” at 18°S, which marks the transition from the humid tropical Andes to the seasonally dry subtropical Andes. Region IV covered the northern part of the subtropical Bolivian Andes south to 20°15’S, and region V the southern part (20°-22°30’S). Both of these regions included the western edge of the extensive arid Chaco lowlands. The six elevational zones were defined by the lowest elevation present in a given cell: to 500 m, 501-1000 m, 1001-1500 m, 1501-2000 m, 2001-2500 m, and > 2500 m.

All terrestrial breeding bird species were mapped individually based on the distributional database of Asociación Armonía – BirdLife International for Bolivia (ca. 60 000 records) and standard references (e.g., Fjeldså & Krabbe, 1990; Ridgely & Tudor, 1989, 1994; del Hoyo *et al.*, 1992-2007; Schulenberg *et al.*, 2007) for Peru. Ranges were interpolated between known records if suitable habitats were present. Because previous studies have shown that bird species of different range size show distinct biogeographic patterns (Jetz & Rahbek, 2002; Rabek *et al.*, 2007), we subdivided the birds into four range-size categories. For this, global range sizes were obtained from the unpublished geographical bird distributional database of the Zoological Museum of Copenhagen provided by J. Fjeldså (Rahbek & Graves, 2001) and the species then arranged by range size. They were then subdivided into quartiles, with the 1st quartile including the 25% most range-restricted species (endemics), and the 4th quartile the 25% most widespread species. Individual range maps were then overlaid to obtain the species richness for each cell, for all species combined and for each quartile separately.

We included seven predictor variables in the analysis: regional area, minimum elevation of each cell, variability of elevation (difference between highest at lowest elevation in a given cell), mean annual precipitation, variability of mean annual precipitation, richness predicted by an elevational MDE model, and richness predicted by a latitudinal MDE model (Fig. 4.2f-1).

Because the latitudinal extent of the study regions was roughly constant, regional area was expressed as the width of the elevational bands (Herzog *et al.*, 2005). The width of each elevational belt was determined for each study region as the mean distance in kilometres along five randomly placed transects set perpendicular to the main direction of

the Andean slope in each region (southwest to northeast in regions I-III, west to east in regions IV and V). The extent of the lowest belt was impossible to accurately define due to the huge size and ill-defined limits of the Amazon and Chaco forest regions. The width was therefore arbitrarily set at 500 km in the Amazon (region I) and Chaco (regions IV and V), and limited to the width of humid forest foothill belt in regions II and III.

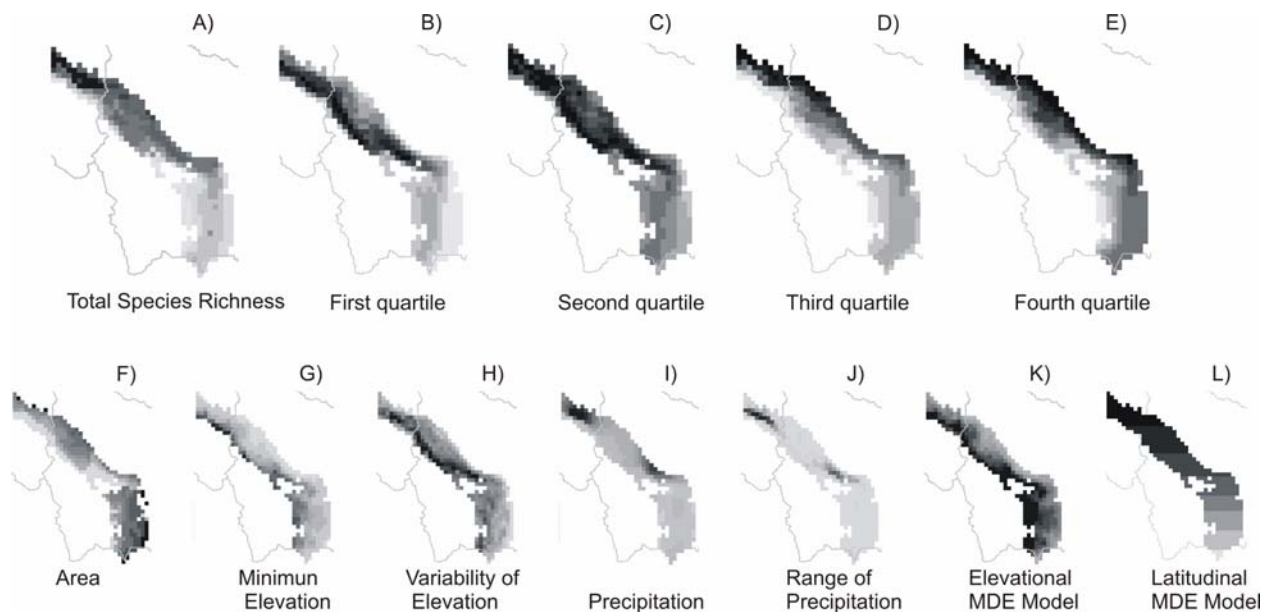


Figure 4.2. Number of total terrestrial breeding bird species per 15' x 15' cell (a), of bird species richness separated by range size quartile (b-e), and patterns of the seven explanatory variables (f-l). In all graphs, darker colours indicate higher numerical values.

Elevational data for each cell (lowest elevation, highest elevation, elevational midpoint, variability of elevation) were determined for each cell based on a digital elevation model of the study region with a resolution of 925 m x 925 m developed by J. Böhner (Dept. of Geography, Univ. Göttingen, Germany) was derived from SRTM-3 (Shuttle Topographic Radar Mission) public domain sources of the USGS (United States Geological Survey) by J. Böhner, Univ. Hamburg (Kessler *et al.*, 2007). Initial data exploration showed that minimum elevation of each cell was more closely correlated to bird species richness ($R = -0.57$, $P = 0.001$) than either maximum elevation ($R = -0.26$, $P = 0.001$) or elevational midpoint ($R = 0.39$, $P = 0.001$), and in an effort to reduce the number of collinear variables, the latter two factors were excluded.

Mean annual precipitation (maximum, minimum, mean of each cell) was extracted from the global climate data base Worldclim (Hijmans *et al.* 2005) that has a resolution of ca. 1 km x 1km. We initially computed the mean, minimum maximum and range of precipitation at a resolution of 15' x 15'. As for elevation, maximum precipitation per cell (hereafter named precipitation) ($R = 0.76$, $P = 0.001$) was selected as the most suitable precipitation parameter over mean precipitation ($R = 0.75$, $P = 0.001$) and minimum precipitation ($R = 0.70$, $P = 0.001$). Temperature was not included as an independent variable in the analysis because it was very closely correlated to elevation ($R = 0.98$, $P < 0.001$) and discrimination between both variables would have been impossible.

Richness as predicted by the MDE models was based on model 2 of Colwell & Hurtt (1994). For the elevational MDE model, we took sea level as lower elevational limit and 5000 m or, if lower (in regions IV and V), the maximum mountain height as upper limit. We did not use randomization of actual variability of elevations of the individual bird species to create MDE predictions as advocated by Colwell *et al.* (2004) because our raw data did not include precise elevational data for each species in each of the five study regions. For the latitudinal MDE model, we set the peak values at the equator and the lower limit at the southern tip of Tierra del Fuego.

Statistical analysis proceeded in three steps. First, we calculated correlations among all explanatory variables to explore interrelations between variables. Since all variables are spatially structured, we used Dutilleul's (1993)'s criterion to correct the correlations. Second, we conducted simple Spatial Autoregression Analyses (SAR) of bird species richness against each of the explanatory variables. Third, we used multiple Simultaneous Autoregressive Models (SAM) autoregressive models (Lichstein *et al.*, 2002) to search for multivariate models explaining as much as possible of the variance of bird species richness. We used Akaike's Information Criterion (AIC, Akaike 1977) to evaluate successive models in terms of their goodness-of-fit and number of parameters, spatial autocorrelation was controlled in the multi-model selection following the procedure proposed by Diniz-Filho *et al.* (2008)'s procedure. All analyses were first conducted for the entire study area and then separately for each of the five regions and six elevational belts.

Unlike Rahbek (2007) and Bachman *et al.* (2004) we did not first regress species richness against area, saving the residuals. This procedure reduces relative species richness at elevations with large surface area (especially the lowlands, but in our region also the high elevations), creating a more pronounced hump-shaped richness pattern. Rather, we preferred to include area as one of several potentially equally important predictor variables rather than

deciding *a priori* that area was the factor of major importance and only further analyzing the residuals once the effect of area had been accounted for. This approach would have eliminated the variance that may be explained by either area or some other factor under consideration, reducing the potential explanatory power of all other variables.

4.3 Results

In total, we mapped 1102 terrestrial bird species as breeding in the study region. Species richness per cell varied from a minimum of 89 on the edge of the high, arid Altiplano on the south-western border of the study area to a maximum of 652 at mid-elevations in the Manu region, right on the north-western limit of the study area (Fig. 4.2a). Generally speaking, richness was highest at low to mid-elevations in the tropical northern part of the study region, declining towards high elevations and to the south. Separating the birds by range-size quartiles showed that peaks of species richness gradually shifted from high (1st quartile: endemics) to low elevations (4th quartile: widespread species) (Fig. 4.2b-e).

Table 4.1. Pairwise correlation coefficients among the seven explanatory variables for the entire study area. * = $P < 0.05$, ** = $P < 0.01$ *** = $P < 0.001$.

	Area	MinElev	VarElev	Prec	RangePrec	LatMDE
MinElev	-0.24**	--				
VarElev	-0.21*	0.28**	--			
Prec	-0.07	-0.46**	0.18	--		
VarPrec	-0.06	0.16	0.62***	0.73***	--	
LatMDE	-0.21	0.00	0.24*	0.63*	0.38	--
ElevMDE	0.27*	0.82***	0.38***	-0.46**	0.06	0.18

Overall, there was a roughly monotonic decline of bird species richness with elevation (Fig. 4.3). However, when the study area was divided into five latitudinal regions, we found a shift from roughly monotonically declining species richness in regions I and II to increasingly hump-shaped patterns in regions III-V. Separating the species by range size quartiles revealed that the narrow-ranged species of the 1st and 2nd quartiles showed hump-shaped richness patterns in all regions, whereas the widespread species of the 3rd and 4th

quartiles mostly showed monotonic declines, except for species of the 3rd quartile in region V.

Overall, there was a roughly monotonic decline of species richness with increasing latitude (Fig. 4.4). However, when the study area was divided into six elevational belts, it became apparent that this decline was most pronounced at lower elevations. Around the Andean elbow at ca. 18°S most elevational belts showed an abrupt reduction of bird species richness. Separating the species by range size quartiles revealed that the narrow-ranged species of the 1st and 2nd quartiles had roughly similar latitudinal richness patterns at all elevations with abrupt declines at 18°S, whereas the widespread species of the 3rd and 4th quartiles showed monotonic declines below 1000 m, and roughly constant richness values above this elevation.

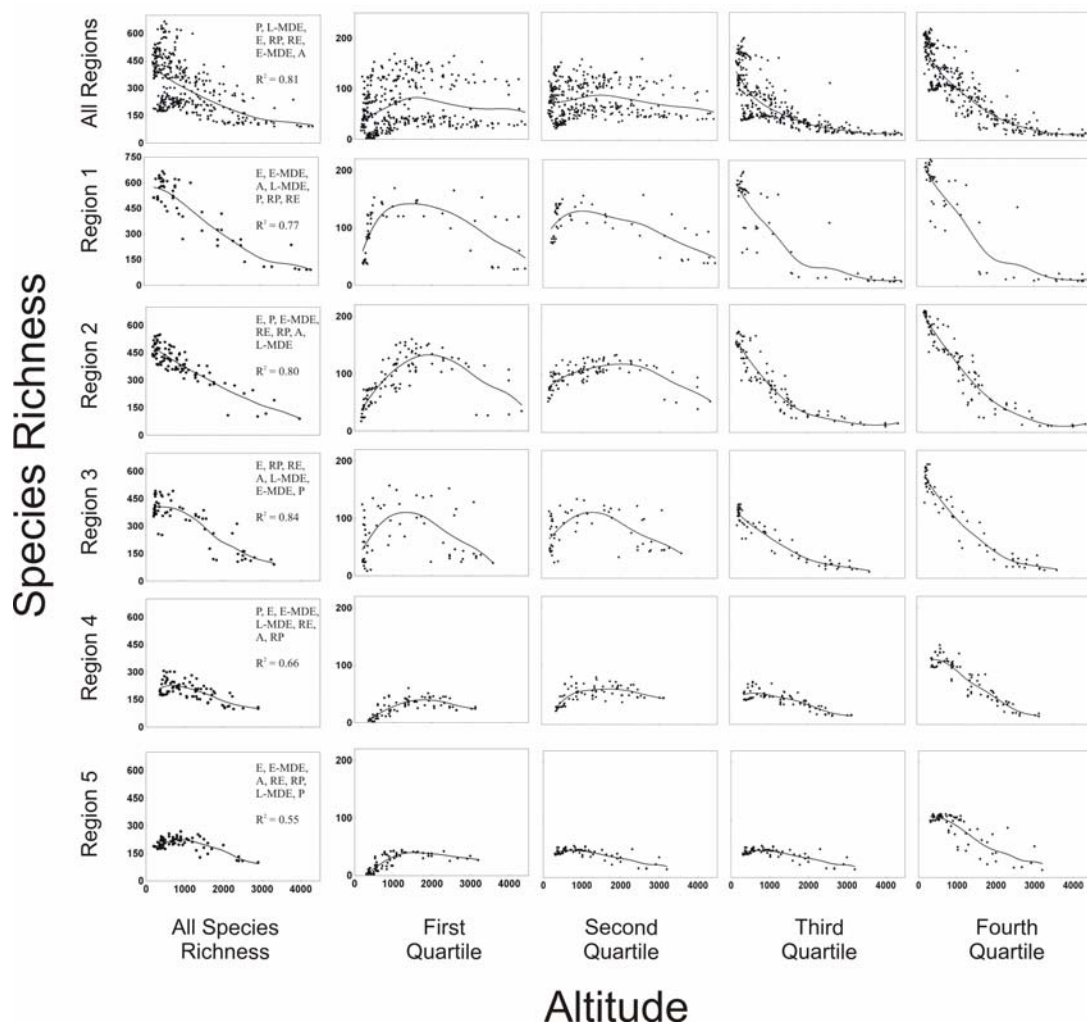


Figure 4.3. Elevational patterns of terrestrial breeding bird species richness per cell for the entire region and five latitudinally divided regions, for the entire avifauna and for the species separated into four range size quartiles. Trend lines were drawn by distance-weighted least squares smoothing with stiffness 0.16. Explanatory factors included in the MAM models (see appendix A2): A = area; E = elevation; E-MDE = Elevational MDE; L-MDE = latitudinal MDE; P = precipitation; RE = range precipitation.

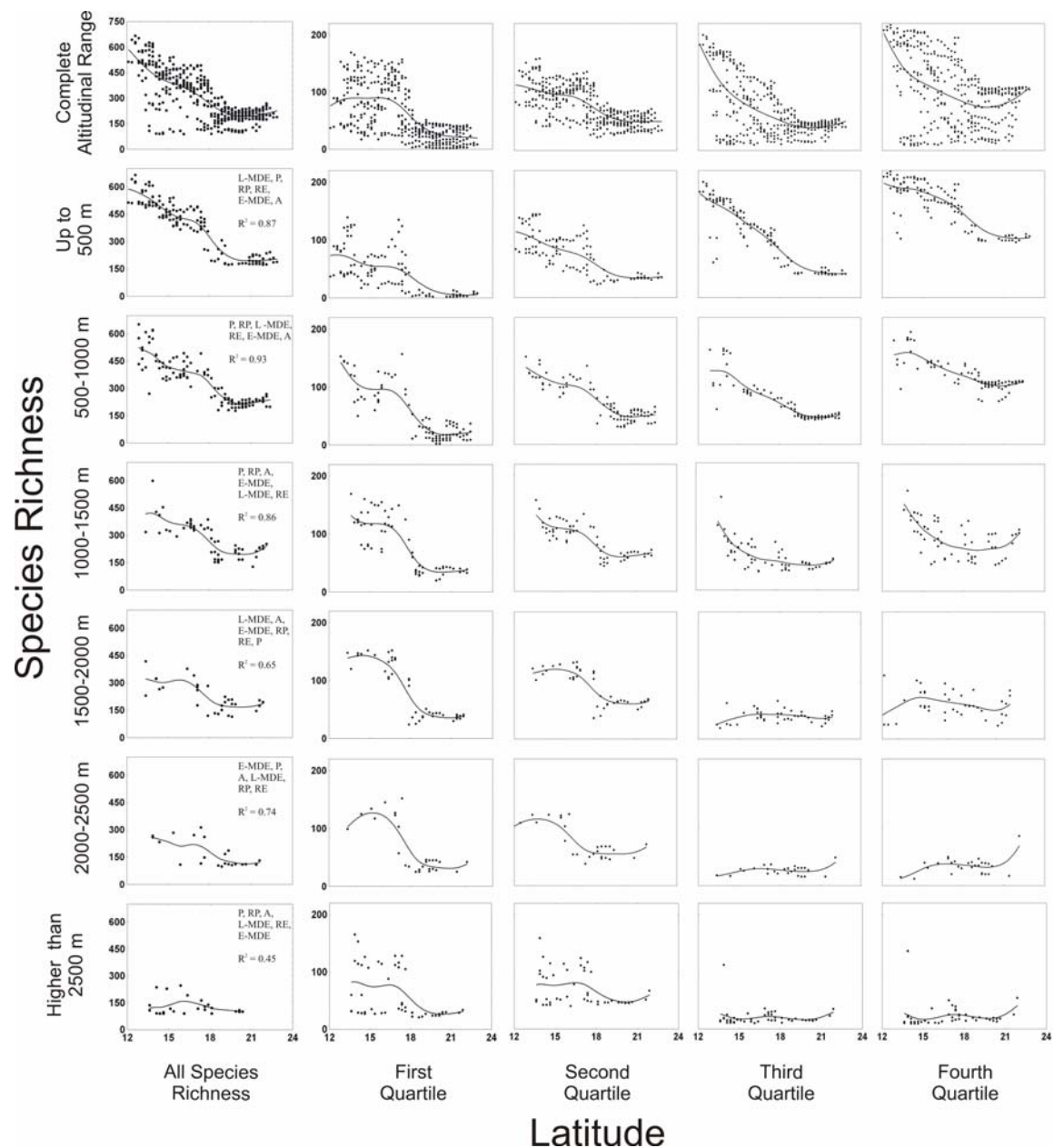


Figure 4.4. Latitudinal patterns of terrestrial breeding bird species richness per cell for the entire study region and five latitudinally divided regions, for the entire avifauna and for the species separated into four range size quartiles. Trend lines were drawn by distance-weighted least squares smoothing with stiffness 0.16. Explanatory factors included in the MAM models (see appendix A3): A = area; E = elevation; E-MDE = Elevational MDE; L-MDE = latitudinal MDE; P = precipitation; RE = range precipitation

Focussing on the explanatory variables, for the entire study area 12 of 21 pairwise combinations of variables showed significant correlations (Table 4.1). Broadly similar relationships were found for each of the five study regions (data not shown).

Simple autoregressive analyses for the entire study area revealed a strong relationship of bird species richness with precipitation ($R^2 = 0.63$), followed by latitudinal MDE model predictions ($R^2 = 0.47$), elevational MDE ($R^2 = 0.33$) and minimum elevation and ($R^2 = 0.29$) (Table 4.2). However these relationships differed between narrow-ranges species and widespread species (Appendix A1). The best multiple autoregressive model included all variables with the following order of importance: precipitation, latitudinal MDE, minimum elevation, variability of precipitation, elevational MDE, variability of elevation and area ($R^2 = 0.87$) (Fig. 4.3; see also Appendix A2).

Table 4.2 Determination coefficients (R^2 -values) of the relationship of bird species richness to seven explanatory variables. The highest value in each line is marked in bold and underlined, the second highest is in bold. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Species Richness	Area	MinElev	Range Elev	Prec	Range Prec	LatMDE	ElevMDE
Central Andes Regions	0.01	0.29***	0.01	<u>0.63</u> ***	0.19***	0.47 ***	0.33***
Region I	0.01	<u>0.76</u> ***	0.01	0.54 ***	0.08*	0.33***	0.48***
Region II	0.50***	<u>0.77</u> ***	0.09*	0.66 ***	0.00	0.24***	0.65***
Region III	0.06	<u>0.69</u> ***	0.00	0.61***	0.49***	0.27***	0.62 ***
Region IV	0.00	0.38 ***	0.00	<u>0.58</u> ***	0.11**	0.03	0.31***
Region V	0.04	0.22 **	0.01	<u>0.26</u> **	0.06*	0.07*	0.09*
Elevational belts							
< 500	0.12**	0.03	0.07*	0.43 **	0.07*	<u>0.77</u> **	0.01
500-1000	0.04	0.01	0.09*	0.42 **	0.03	<u>0.76</u> ***	0.02
1000-1500	0.44**	0.02	0.02	0.61 **	0.19*	<u>0.63</u> ***	0.16*
1500-2000	0.28*	0.15*	0.04*	0.34 **	0.18*	<u>0.51</u> **	0.13*
2000-2500	0.16	0.04	0.29**	<u>0.55</u> ***	0.47 ***	0.29**	0.46***
>2500	0.02	0.06	0.34***	0.49 ***	<u>0.51</u> ***	0.10*	0.02

Dividing the study area into the five latitudinal regions, minimum elevation of each cell was the best single explanatory variable in regions I-III and second-highest in regions IV and V, whereas precipitation had the highest values in regions IV and V, the second-highest in regions I and II, and the third-highest in region III (Table 4.2). Elevational MDE model predictions had the third highest values in all regions except in region III where it was second. Minimal adequate models (MAM) per regions were not confidently identified. The relative high degree of collinearity between the explanatory variables (Table 4.1) resulted in a high degree of uncertainty, with more than one competing MAMs (Appendix

A2). Multiple autoregressive analyses based on averaged models selected minimum elevation as the main predictor variable in all regions except region IV (second most important variable). Elevational MDE was the second most important variable twice (Regions I and V), and precipitation and range of precipitation once (Regions II and III respectively) (Appendix A2).

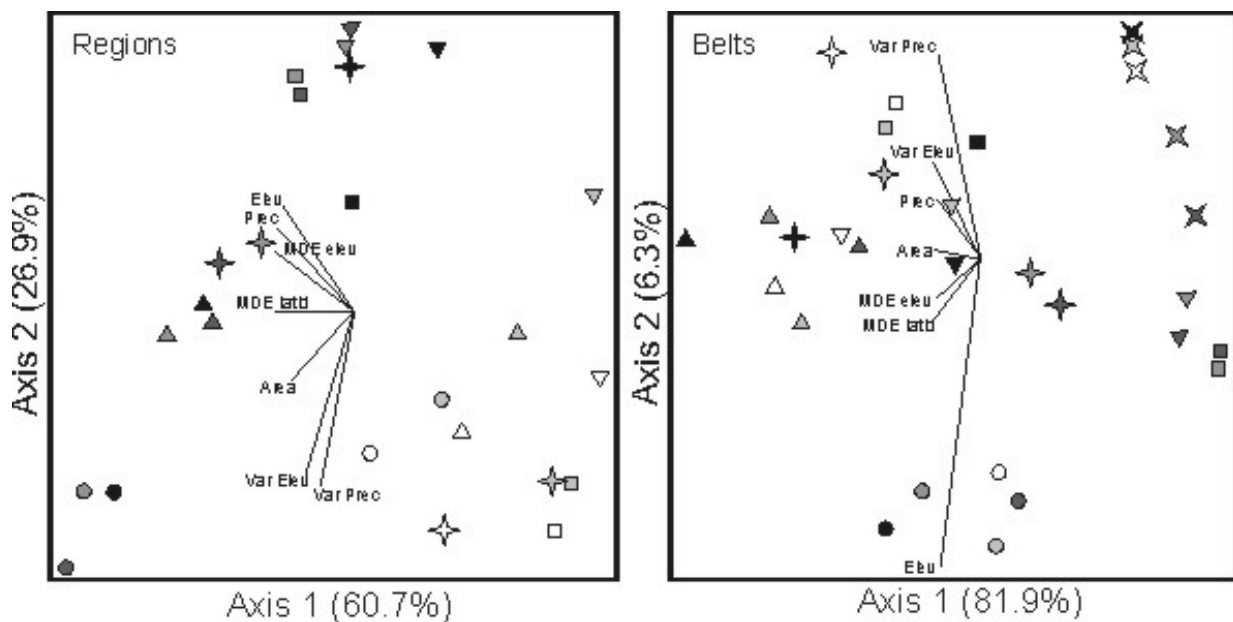


Figure 4.5. Visualization through Principal Component Analyses (PCAs) of the relative contribution of different explanatory variables in determining the species richness of birds in different regions and elevational belts (different symbols) on the eastern Andean slope of Peru and Bolivia, separated for the species of the four range size quartiles (different shadings) and all species combined (black symbols). Symbols: region 1 = inverted triangles, region 2 = crosses, region 3 = squares, region 4 = triangles, region 5 = circles; <500 m = circles, 500-1000 m = triangles, 1000-1500 m = upright crosses, 1500-2000 m = inverted triangles, 2000-2500 m = squares, >2500 m = diagonal crosses; endemics of quartile 1 = white symbols to widespread species of quartile 4 = dark gray symbols.

Regarding the six elevational belts, the single variables with the highest predictive power shifted from latitudinal MDE (first) and precipitation (second) in the lowermost four belts (< 500 to 2000 m.) to precipitation (first) and range of precipitation (second) for the belt 2000-2500 and vice versa for higher than 2500 m (Table 4.2). Visualization through principal component analyses (PCAs) of the relative contribution of the seven explanatory variables to bird species richness patterns showed that when the study area was divided into regions, the main distinction along PCA axis 1 is between the narrow-ranged species of the 1st and 2nd quartiles on the one hand (left) and the widespread species of the 3rd and 4th

quartiles on the other (right) (Fig. 4.5). This pattern was mainly correlated to minimum elevation, precipitation, and elevational and latitudinal MDE model predictions. Within this main separation, there was a secondary gradient along PCA axis 2 that spread out the data points by region from north (top of graph) to south (bottom). This axis was mainly correlated to variability of elevation and precipitation, and to area. Overall species richness closely tracked the pattern of the latter two quartiles.

The PCA analysis dividing the study area into six elevational belts showed a contrasting pattern (Fig. 4.5). Here, the main distinction was between the belts and only secondarily by quartiles. Axis 1 was mainly correlated to area and elevational as well as latitudinal MDE model predictions, whereas axis 2 was correlated to elevation, variability of both elevation and precipitation, and precipitation.

4.4 Discussion

4.4.1 General patterns

This is the first detailed analysis of superimposed latitudinal and elevational patterns of bird richness patterns, and further considering different range size categories. Our approach thus follows the suggestions of, e.g., Pimm & Brown (2004), Oomen & Shanker (2005), and Rahbek (2005) that progress in macroecology depends on the consideration of multiple mechanisms and scales. We found that analyses of different geographical subsets of the overall dataset revealed the differential impacts of various factors at different scales and in different regions. In a general sense, this is a rather trivial result (Rahbek, 2005), yet when applied in a systematic way, it can lead to important insights. For example, by restricting the area to comparatively narrow regions, factors that change latitudinally such as latitudinal MDE model predictions or precipitation became less important, allowing us to address the subset of variation of species richness and explanatory variables that one observes along elevational transects. At the other extreme, by subdividing the study area into elevational belts, factors changing primarily with elevation became irrelevant and latitudinal changes more prominent.

In our most general analysis, involving all species over the entire study region, which methodologically corresponds to commonly used macroecological analyses at continental to global scales (e.g., Jetz & Rahbek, 2002; Hawkins *et al.*, 2003b; Ruggiero &

Hawkins, 2008), the multivariate analysis included all seven explanatory variables. Although these were ranked according to their contribution to the model, the conclusion from such an analysis might simply have been that climate, in particular precipitation, is the most important factors but that everything else also plays a role to some degree. In contrast, three of four studies of bird diversity along elevational gradients in the same region have so far failed to mention precipitation as a determinant of bird diversity (Terborgh, 1977; Patterson *et al.*, 1998; Herzog *et al.*, 2005; but see Kessler *et al.* 2001). One might conclude that latitudinal and elevational patterns of bird diversity are determined by different factors. Indeed, when we divided our study region into latitudinal regions and elevational belts it became apparent that the effect of precipitation was primarily due to the latitudinal decline of precipitation at low elevations. Conversely, the importance of elevation and habitat heterogeneity were only evident once regions and elevational belts were analyzed independently. Let us now consider these aspects in detail.

4.4.2 Explanatory parameters

We found that in the central Andes, elevational patterns of bird species richness gradually change latitudinally, from essentially monotonically declining in the north to increasingly hump-shaped patterns as one goes southwards. This corresponds to differential declines of species richness at different elevations. In the lowlands at the base of the Andes, species richness declines by about 65% from the northern to the southern limit of our study region, whereas above 2500 m this decline is negligible (Fig 4.4). The decline was particularly pronounced around the elbow of the Andes at about 18°S, corresponding to the rather abrupt transition from the humid, tropical climate of the Peruvian and northern Bolivian Andes to the seasonally dry, subtropical climate of the southern Bolivian and northern Argentinean Andes. Such regional shifts of elevational richness patterns coincide with previous studies of plants in Norway (Grytnes, 2003), and of mammals (McCain, 2005; 2007), birds (McCain, 2009) and ferns (Kessler *et al.*, unpubl. data) on a global scale.

A similar result was obtained by McCain (2009) in her global analysis of bird elevational diversity, where hump-shaped patterns were predominantly found in arid mountains, whereas humid regions mostly had highest diversity at or close to the bottom of the transects. The reduced negative effect of aridity on bird diversity at higher elevations has two reasons. First, precipitation tends to increase with elevation in arid mountains as a result

of convective precipitation (e.g., Lauer, 1986). Second, as temperature declines with elevation, evapotranspiration also decreases, reducing the effect of limited precipitation. As a result, pockets of humid forest can be found in the southern Bolivian Andes at 1200-3000 m on exposed, east-facing mountain ranges capturing moisture brought in by the eastern trade winds, at latitudes where the lowlands only support thorn scrub (Kessler, 2000b; Krömer *et al.*, 2006; Fjeldså & Mayer, 1996). Although impoverished relative to humid montane forests further north, these montane bird communities are still comparatively richer than those inhabiting the adjacent but much drier Chaco lowlands, leading to the observed richness peak at mid-elevations.

In addition to precipitation levels, elevation as such also played a major role in the simple and multi autoregressive analyses when the data set was divided into five latitudinal regions (Appendix A1 & A2). This mainly reflects the roughly linear decline of bird species richness observed along the upper portions of all transects. Not surprisingly, the relationship of elevation to richness was relatively lower in southern Bolivia, where richness patterns were humped, as compared to roughly linear patterns in the north (Fig. 4.3).

Latitudinal MDE model predictions also played an important role when the study region was divided into elevational belts (except for the higher two elevational bands) (Table 4.2). In contrast, elevational MDE played a secondary role, even in southern Bolivia where richness patterns were hump-shaped (Table 4.2; Fig. 4.2 and 4.3). Regional area was irrelevant overall, but played an important role in some elevational belts and latitudinal regions, mainly for species with restricted geographical ranges.

Our analysis also included two measures of environmental heterogeneity, namely variability of precipitation and of elevation in each cell. Overall, these two factors were of subordinate importance in explaining bird species richness, although they became prominent at higher elevations when the study region was divided into elevational belts. This pattern can be readily interpreted: cells with a higher number of habitats (elevational zones and/or humidity classes) can harbour a higher number of bird species.

An exact quantification of the contribution of the different explanatory factors to regional bird species richness patterns is impossible due to the rather high correlations between most explanatory variables. However, the consistently high explanatory power of precipitation and of elevation (i.e., temperature) strongly suggests that these are the main factors determining bird species richness in the study region. We are thus faced with a pattern of highest richness in warm and humid regions and lower richness in dry and cold habitats. The same pattern has previously been found for the latitudinal richness patterns

among a variety of plant and animal groups, where richness is usually limited by low temperatures at high latitudes and by water availability at low latitudes (Francis & Currie, 2003; Hawkins *et al.*, 2003a; McCain, 2007, 2009). Together, these studies thus all support the idea that the water-temperature balance crucially determines species richness of many taxa. Whether this is due to direct physiological limitations of the organisms, availability of food or other energetic resources, or historical or evolutionary trends, remains to be explored. The classical interpretation is that under extreme climatic conditions fewer species can exist, but the actual mechanisms limiting richness are unclear (Evans *et al.*, 2005; Mittelbach *et al.*, 2001). Hawkins *et al.* (2006) have shown that basal bird clades are overrepresented in the warm, wet tropics of the New World, whereas drier regions and higher latitudes are mainly inhabited by species from more recent, evolutionary derived clades. The analysis of Hawkins *et al.* (2006) did not specifically target the elevational gradient as such, but it is likely that the same pattern also applies here as is evident from their figures 2 and 3 (Hawkins *et al.*, 2006: 775, 776). A combination of macroecological approaches as the one taken here with more explicit phylogenetic analyses and with physiological studies of climatic tolerances of birds from different biomes may help to unravel the potentially crucial impact of evolutionary processes in determining regional richness patterns.

4.4.3 Range size

The above considerations apply to overall species richness and largely to the more widespread species of the 3rd and 4th quartiles whereas the range-restricted species of the 1st and 2nd quartile showed quite distinct patterns, as has previously been shown for, e.g., African birds (Jetz & Rahbek, 2002) and American palms (Kreft *et al.*, 2006). However, whereas previous studies often have found that the richness of endemic species is more difficult to explain than that of widespread species, in our study this was not the case. Endemic species typically are concentrated in localized habitats and mountainous regions (e.g. Rahbek *et al.*, 2007), as is also the case in our study, where endemics have highest richness at high elevations (Fig. 4.2b, c). Also, they show a drastic decline of species richness along the Andean elbow at about 18°S. This is related to a decline in precipitation, but a direct causal relationship is difficult to establish in this case, because this zone represents the boundary between two biogeographical zones, the humid tropical zone to the north and the seasonally dry subtropical zone to the south. Because the separation by range

size implies that species inhabiting geographically extensive biomes will not be included among the endemic species even if they are restricted to this biome, the decline of endemics at this boundary might reflect the spatial extends of the biogeographic areas, rather than any direct relationship between species richness and environmental parameters. Despite this caveat, our study shows that a separation by range size provides important additional information about the interaction of range size and potential explanatory factors of species richness.

4.5 Conclusions

Our study shows that the diversity-parameter relationships recovered when we analyzed the entire species set over the entire study region resulted in a very simplified pattern which unsurprisingly was dominated by the most frequent species (the widespread ones) and the most common environmental conditions (mainly the lowlands). It was only by separating the data set into range size classes, latitudinal zones, and elevational belts that less frequent relationships became evident. For range size, this effect has repeatedly been stressed (Jetz & Rahbek, 2002; Kreft *et al.*, 2006) and it is now well known that overall patterns of species richness are dominated by a relatively small proportion of widespread species, neglecting the idiosyncratic patterns of range-restricted taxa. Along a similar line of reasoning, continent-wide analyses of diversity patterns (e.g., Jetz & Rahbek, 2002; Ruggiero & Hawkins, 2008) run the risk of only recovering the patterns of the geographically dominant biome or biomes, while neglecting geographically restricted regions where different patterns and processes may be found. Here a meaningful subdivision of the data set may provide important additional insight.

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4.6 References

- Bachman, S., Baker, W.J., Brummitt, N., Dransfield, J. & Moat, J. (2004) Elevational gradients, area and tropical island diversity: an example from the palms of New Guinea. *Ecography*, 27, 299–310.
- Bhattarai, K.R., Vetaas, O.R. & Grytnes, J.A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31, 389–400.
- Bibby, C. J., Collar, N. J., Crosby, M. J., Heath, M. F., Imboden, C., Johnson, T. H., Long, A. J., Stattersfield, A. J. & Thierygood, S. J. (1992) *Putting biodiversity on the map: priority areas for global conservation*. ICBP, Cambridge, U.K.
- Colwell, R.K., & Hurtt, G.C. (1994) Nonbiological gradients in species richness and a spurious Rapoport effect. *American Naturalist*, 144, 570–595.
- Colwell, R.K., Rahbek, C., & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far?. *American Naturalist*, 163, E000–E023.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134.
- Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, 17, 479–488.
- Dutilleul, P. (1993) Modifying the t test for assessing the correlation between two spatial processes. *Biometrics*, 49, 305–314.
- Evans, K.L. & Gaston, K.J. (2005) People, energy and avian species richness. *Global Ecology and Biogeography*, 14, 187–196.
- Fjeldså, J. & Krabbe, N. (1990) *Birds of the high Andes*. Apollo Books, Svendborg.
- Fjeldså, J., & Mayer, S. (1996) *Recent ornithological surveys in the Valles region, southern Bolivia - and the possible role of Valles for the evolution of the Andean avifauna*. DIVA Technical Report 1. Rønde.
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness climate relationship for angiosperms. *American Naturalist*, 161, 523–536.
- Furness, R. W. & Greenwood, J. J. D. (eds.) (1993) *Birds as monitors of environmental change*. Chapman & Hall, London.

- Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and process in Macroecology*. Blackwell Science. Cambridge, UK.
- Grytnes, J.A. (2003) Species richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography*, 26, 291-300.
- Hawkins, B.A. & Porter, E.E. (2001) Area and the latitudinal diversity gradient for terrestrial birds. *Ecology letters*, 4, 595-601.
- Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003a) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, 84, 1608-1623.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guègan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003b) Energy, water & broad-scale geographic patterns of species richness. *Ecology*, 84, 3105–3117.
- Hawkins, B.A., Diniz-Filho, J.A.F. & Weis, A.E. (2005) The mid-domain effect and diversity gradients: is there anything to learn? *American Naturalist*, 166, E140–E143.
- Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. & Soeller, S.A. (2006) Post-Eocene climate, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography*, 33, 770-780.
- Hawkins, B.A., Diniz-Filho, J.A.F., Laramillo, C.A. & Soeller, S.A. (2007) Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist*, 170, s16-s27.
- Heaney, L.R. (2001) Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography*, 10, 15–39.
- Herzog, S.K., & Kessler, M. (2002) Biogeography and composition of dry forest bird communities in Bolivia. *Journal für Ornithologie*, 143, 171-204.
- Herzog, S.K., Kessler, M. & Bach, K. (2005) The elevational gradient in Andean bird species richness at the local scale: a foothill peak and a high-elevation plateau. *Ecography*, 28, 209–222.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of climatology*, 25, 1965-1978.

- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American naturalist*, 163, 192-211.
- del Hoyo, J., Elliott, A. & Sargatal, J. (1992-2002) *Handbook of the Birds of the World*, vol. 1-7. Lynx Edicions, Barcelona.
- del Hoyo, J., Elliott, A. & Christie, D.A. (2003-2005) *Handbook of the Birds of the World*, vol. 8-10. Lynx Edicions, Barcelona.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, 297, 1548-1551.
- Kessler, M. (2000a). Upslope-directed mass effect in palms along an Andean elevational gradient: a cause for high diversity at mid-elevations?. *Biotropica*, 32, 756-759.
- Kessler, M. (2000b) Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. *Plant Ecology*, 149, 181-193.
- Kessler, M. (2001a) Patterns of diversity and range size of selected plant groups along an elevational transect in the Bolivian Andes. *Biodiversity and Conservation*, 10, 1897-1920.
- Kessler, M. (2001b) Pteridophyte species richness in Andean forests in Bolivia. *Biodiversity and Conservation*, 10, 1473-1495.
- Kessler, M. (2009) The impact of population processes on patterns of species richness: Lessons from elevational gradients. *Basic and applied Ecology*, 10, 295-299.
- Kessler, M., Herzog, S.K., Fjeldså, J. & Bach, K. (2001a) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity, and land use in the Bolivian Andes. *Diversity and Distributions*, 7, 61-77.
- Kessler, M., Böhner, J. & Kluge, J. (2007) Modelling tree height to assess climatic conditions at tree lines in the Bolivian Andes. *Ecological Modelling*, 207, 223-233.
- Kluge, J., Kessler, M. & Dunn, R.R. (2006) What drives elevational patterns of diversity? A test of geometric constraints, climate, and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, 15, 358-371.
- Körner, C., & Paulsen, J. (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31, 713-723.
- Kreft, H., Sommer, J.H. & Barthlott, W. (2006) The significance of geographic range size for spatial diversity patterns in Neotropical palms. *Ecography*, 29, 21-30.

- Krömer, T., Kessler, M. & Herzog, S.K. (2006) Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. *Biotropica*, 38, 183-195.
- Lauer, W. (1986) Klimatische Grundzüge der Höhenstufung tropischer Gebirge. *Tagungsber Wiss. Abh 40 Dt Geographentag Innsbruck*, 1975, 76-90.
- Lichstein, J.W., Simons, T.R., Shriver, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autorregressive models in Ecology. *Ecological Monographs*, 72, 445-463.
- Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3-13.
- McCain, C.M. (2005) Elevational gradients in diversity of small mammals. *Ecology*, 86, 366-372.
- McCain, C.M. (2007) Area and mammalian elevational diversity. *Ecology*, 88, 76-86.
- McCain, C.M. (2009) Global Analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346-360.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dobson, S.I., Gough, L. (2001) What is the observed relationship between species richness and productivity?. *Ecology*, 82, 2381-2396.
- Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W., & Pacheco, V. (1998) Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, 25, 593-607.
- Oomen, M.A. & Shanker, K. (2005) Elevational species richness patterns emerge from multiple local mechanism in Himalayan woody plants. *Ecology*, 86, 3039-3047.
- Pimm, S.L., & Brown, J.H. (2004) Domains of diversity. *Science*, 304, 831-833.
- Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, 18, 200-205.
- Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224-239.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences*, 98, 4534-4539.
- Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society, Series B*, 274, 165-174.
- Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7, 1-15.

- Ridgely, R.S., & Tudor, G. (1989) *The Birds of South America, vol. 1*. Oxford University Press, Oxford.
- Ridgely, R.S., & Tudor, G. (1994) *The Birds of South America, vol. 2*. Oxford University Press, Oxford.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L., & Ziv, Y. (1999) The echo pattern of species diversity: pattern and process. *Ecography*, 22, 614-628.
- Rugiero, A. & Hawkins, B.A. (2008) Why do mountains support so many species of birds?. *Ecography*, 31, 306-315.
- Stevens, G.C. (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, 133, 240-256.
- Schulenberg, T.S., Stotz, D.F., Lane, D.F., O'Neill, J.P. & Parker, T.A. (2007) *Birds of Peru*. Princeton University Press. Princeton, USA.
- Stotz, D.F., Fitzpatrick, J.W., Parker, T.A., III & Moskowitz, D.K. (1996) *Neotropical Birds: ecology and conservation*. University of Chicago Press, Chicago.
- Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58:1007-1019.
- Terborgh, J., S.K. Robinson, T.A. Parker III, C.A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian bird community. *Ecological Monographs* 60:213-238.

Chapter 5

Modelled Quaternary dispersal and vicariance of habitat-endemic fern and bird species in Seasonally Dry Tropical Forests of the Bolivian Andes

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Abstract

Aim: To model the probable Quaternary geographical connections of inter-Andean dry forests, a currently geographically fragmented type of seasonally dry tropical forest (SDTF), and to model patterns of colonization of these fragments by a set of bird and fern species endemic to SDTFs in the Bolivian Andes.

Location: Bolivia

Methods: We mapped the distribution of the SDTFs under the present climatic conditions (warm-wet) using the climate model SAGA. Then we modified SAGA following estimations of the most contrasting Quaternary climates (cold-wet, cold-dry and warm-dry), and modelled the past distribution of the SDTFs under each climate scenario. Distributions of 27 bird and fern species were modelled with MAXENT for each climate scenario.

Results: The fragments of inter-Andean SDTFs were modelled to be connected to SDTFs in the central Bolivian lowlands during cold-dry and warm-dry conditions. The latter offered favourable conditions to colonize the Andean SDTFs from the southern lowlands, but the central Andes represented a barrier that limited dispersal north-westwards. Wet climates were associated with the most restricted distribution of SDTFs. Species inhabiting Andean SDTF fragments were modelled to have had connections via lowlands, highlands, or both. Cold-dry climates presented the favourable conditions for connections via the lowlands while connections via the highlands occurred during warm periods. Species that today have a higher mid elevational range are those that were able to colonize the fragments through the central Andes, whereas species with lower elevational range colonized the fragments via the lowlands.

Main conclusions: The fragments of inter-Andean dry forests are remnants of the more extensively distributed SDTFs that occupied the central Bolivian lowlands and Andean valleys during the Quaternary dry climates. Wet climates restricted the SDTFs to the drier lowlands of southern Bolivia, isolating them from fragments in the Andes. The modelled distributions of the species suggest that vicariance, rather than long-distance dispersal, may have played an important role in determining the current species distributions across the SDTFs in the Bolivian Andes.

Keywords: Birds, Bolivia, Climate model, Dispersal, Ferns, Long-distance dispersal, MAXENT, Pleistocene, Seasonally dry tropical forests, Species distributions, Vicariance.

5.1 Introduction

The impacts induced by past climate fluctuations on the global distribution of diversity have been widely discussed (e.g. Peterson *et al.*, 2004; Wiens & Donoghue, 2004). In the South American Andes, the elevational tree-line was lower than today in the northern and central Andes during the last glacial period (Mourguiart & Lebru, 2003; Hooghiemstra & Van der Hammen, 2004; Niemann & Behling, 2008). Likewise, the late Pleistocene was also a period with significantly different distributions of the biomes in the lowlands, with the evergreen Amazonian forest contracted to its minimum extension, more septentrional distribution of the Seasonally Dry Tropical Forests (SDTFs), and a grassland-dominated landscape in the southern part of the current SDTFs' distribution (Mayle 2004; Mayle *et al.*, 2004).

The history of the SDTFs since the Last Glacial Maximum (LGM) is noteworthy in this regard. Based on the fragmented current distribution of this biome and the scattered presence of some biome-endemic taxa in some of these fragments, Prado & Gibbs (1993) and Pennington *et al.* (2000) suggested that the present distribution of the SDTFs in South America has resulted from a climatically-driven process of fragmentation of the 'pleistocenic dry forest' (i.e., vicariance). This 'pleistocenic dry forest' together with savanna-like vegetations (e.g. Behling & Hooghiemstra 2001) are assumed to have been more extensively distributed on the continent, while the Amazon forest was restricted and fragmented (i.e., the Amazonian pleistocenic refugia hypothesis; Haffer, 1969). However, later evidence suggests that vicariance may have not been the causal process of the current fragmented distribution of the SDTFs (Pennington, 2004). Modelling studies indicate that the present distribution of species associated to SDTFs may have resulted from long-distance dispersal processes since the LGM (e.g. Mayle, 2004; Mayle & Beerling, 2004; Mayle *et al.*, 2004). The lack of evidence for allopatric speciation expected from vicariance during the Pleistocene and the post-Pleistocene appearance of *Anadenanthera colubrina*, a key species used for the formation of the dry forest refugia hypothesis (Prado & Gibbs, 1993; Pennington *et al.*, 2000), supports this alternative long-distance dispersal hypothesis.

In Bolivia, the fragmented configuration of the inter-Andean dry forests, a type of STDFs in the Andes, is particularly interesting (Fig. 5.1a). Biogeographic studies indicate that the vegetation of the Bolivian inter-Andean dry forests is related to dry vegetation formations from central-southern South America (López, 2003). However, other studies demonstrated a strong differential influence of other neighbouring vegetation types upon the

community composition of the inter-Andean dry forests. The southern Andean dry forests, for example, have important Chaco components, whereas the northern fragments, which are surrounded by humid montane forests, appear to have more important lowland components and some species in common with the Cerrado and Chiquitano dry forest (Fig. 5.1a) (Bach *et al.*, 1999; Kessler & Helme, 1999). Similarly, Herzog and Kessler (2002) also reported isolated populations of several bird species that are typical of the Cerrado, Chiquitania and Chaco vegetation types (e.g., *Formicivora melanogaster*, *Synallaxis scutata*) in some of the SDTF fragments (Figs. 5.1c-h). Recently, Linares-Palomino and Kessler (2009) proposed that the inter-Andean dry forests can be divided into two groups, a northern and a southern one, based on the community composition of several plant families of poor dispersal ability (Acanthaceae, Bromeliaceae and Cactaceae) (Fig. 5.1a). This suggests that vicariance, rather than dispersal, may have determined these distributions. However, it is unclear where and when past connections between currently fragmented SDTF areas may have occurred. Such connections may theoretically have taken place either through the lowlands, with lowland forests reaching the Andean base and Andean forests extending downwards, or across Andean passes if Andean SDTFs reached higher elevations than at present.

In this context, we set out to reconstruct the potential past distribution of the SDTFs in Bolivia, including a set of species endemic to this biome, under contrasting Quaternary climatic scenarios. We aimed to assess if the fragments of inter-Andean dry forests may be remnants of a larger SDTF that was once distributed throughout the lowlands of central Bolivia during the dry climate of the Quaternary. On the individual species level, lowland connections may be expected to have occurred during the cold climates, whereas connections through the Andes would be expected to have happened during the warm and dry climates. To test these predictions, we modelled the distributions of a set of fern and bird species that are endemic to the SDTFs. Birds and ferns are phylogenetically distant groups with good dispersal ability which allows them to track climatically-driven habitat modifications (Herzog & Kessler, 2002; Linares-Palomino & Kessler, 2009).

The four climate scenarios we used are cold-wet, cold-dry, warm-dry and warm-wet. These scenarios roughly correspond to conditions during the LGM (25 to 17 kyr BP), the Younger Dryas (YD; 12.5 to 11 .5 kyr BP), the early Holocene (9 to 6 kyr BP) and the late Holocene (LH; present). Quaternary climatic reconstructions for the Neotropic are in some cases contrasting (e.g. Maslin & Burns, 2000; Baker *et al.*, 2001). Therefore, these climatic scenarios should be seen as conservative estimations of the most contrasting climates that

repeatedly occurred across the entire Quaternary (Sigman & Boyle, 2000), instead of directly relating them to specific periods.

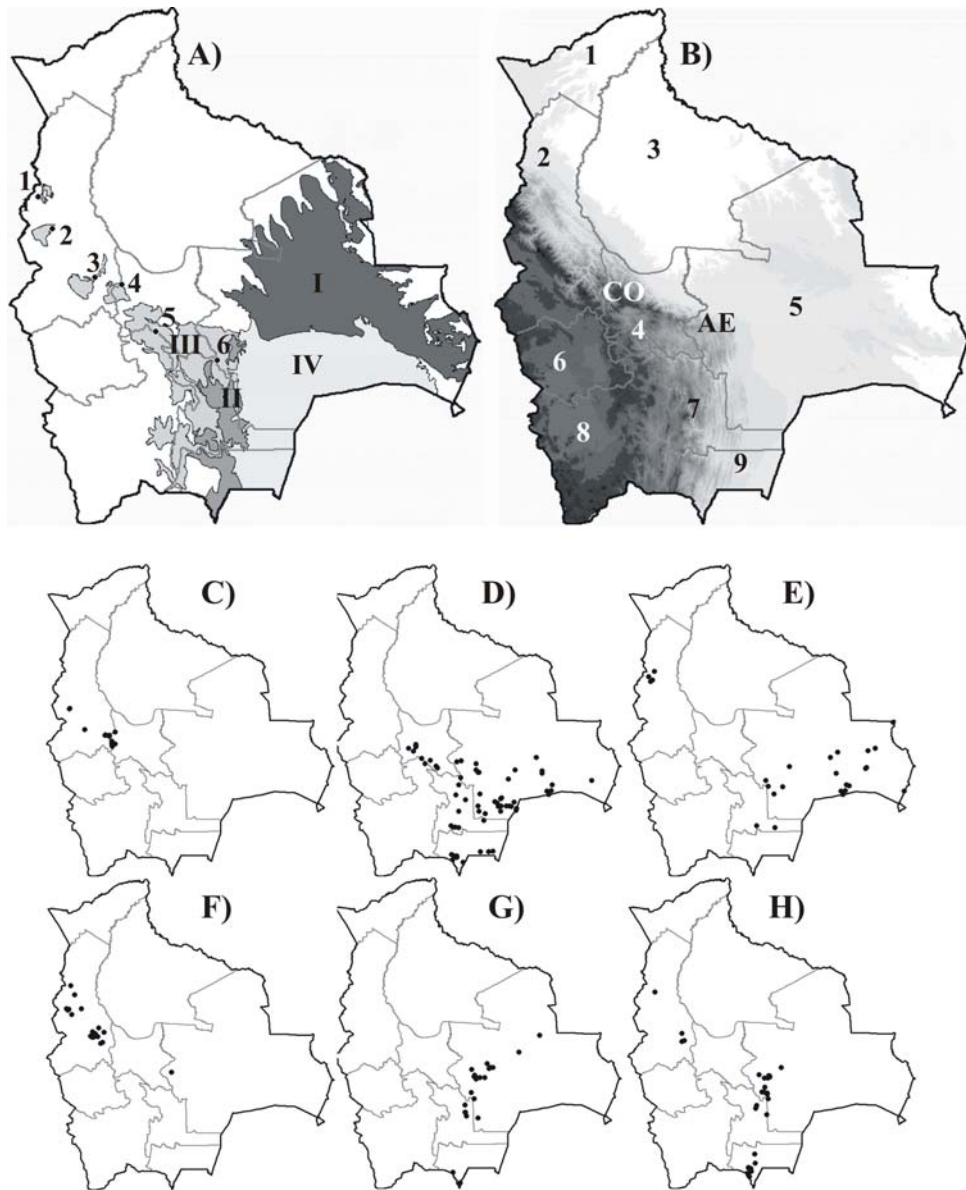


Figure 5.1. A) Map of seasonally dry vegetation types in Bolivia (after Olson et al., 2001). (I) The Chiquitano dry forest, (II) the Southern Andean Yungas, (III) the Bolivian montane dry forest and (IV) the dry Chaco. The numbers point to some important sites of SDFs: 1. Río Tuichi, 2. Camata and Consata, 3. Chamaca, Mecapaca, and Miguillas, 4. Cotacajes and Inquisivi, 5) Río Caine, 6) Río Grande. B) Digital elevational model of Bolivia. Numbers represent the departments of Bolivia, 1. Pando, 2. La Paz, 3. Beni, 4. Cochabamba, 5. Santa Cruz, 6. Oruro, 7. Chuquisaca, 8. Potosí, 9. Tarija, CO = Cordillera of Cochabamba and AE = Andean elbow. C) to H) Geo-referenced Bolivian records of species endemic to SDFs: *Cranioeluca henricae* (bird), *C. pyrrhophia* (bird), *Formicivora melanogaster* (bird), *Adiantum rufopunctatum* (fern), *Anemia herzogii* (fern) and *Pecluma filicula* (fern).

5.2 Methods

5.2.1 Current distribution of the SDTFs in Bolivia

SDTFs grow in climatically seasonal areas where rainfall is less than 1600 mm per year and with six months of dryness (less than 100 mm per month) (Gentry, 1995; Grahan & Dilcher, 1995). SDTFs cover most of the subtropical lowlands of Bolivia, with their northernmost extension at approximately 18°S near the Andean elbow (Fig. 5.1b) and approximately 15°S further east in the lowlands. Their distribution in the Andes is restricted to areas of low precipitation and is strongly associated with the catchment areas of important rivers that drain into the lowlands (Wood, 2006; Linares-Palomino & Kessler, 2009). SDTF habitats are diverse in Bolivia and are differentiated into several types such as Chaco (low thorn forest of the SE lowlands), Chiquitano dry forests (taller forests of the central lowlands), and inter-Andean dry forests (Ibisch *et al.*, 2003: Fig. 3.1; Pennington, 2004; Wood, 2006). SDTFs are of lower stature, have lower basal area than evergreen rain forests (Murphy & Lugo, 1986), have lower net primary productivity due to the restricted growth season (Pennington, 2004), and thorny species are a significant component of the plant communities. In our study, we included the Cerrado-Chiquitano and Cerrado-Chaqueño that are structurally a mosaic of savanna and Chiquitano or Chaco vegetations respectively (vegetation units recognized by Ibisch *et al.*, 2003), and occur under similar climatic, but different edaphic, conditions.

5.2.2 Species distributions

For the analyses of individual species, we selected 27 species that are (1) endemic to the seasonally dry tropical forests, (2) that have a fairly well established taxonomy, thereby guaranteeing that species records are reliable, and (3) that have a relatively large number of confidently georeferenced records. Species data for ferns were extracted from the database of Bolivian pteridophytes compiled by M. Kessler and A.R. Smith (www.fernsofbolivia.uni-goettingen.de), and for birds from the distributional database of Asociación Armonía – BirdLife International. We selected 13 bird species (*Arremon flavirostris*, *Cranioleuca henricae*, *Cranioleuca phyrrophia*, *Formicivora melanogaster*, *Myiopsitta luchi*, *Myiopsitta monachus*, *Nystalus maculatus*, *Polioptila dumicola*, *Poospiza boliviana*,

Serpophaga munda, *Stigmatura budytoides*, *Suiriri suiriri* and *Synallaxis scutata*) and 14 fern species (*Adiantopsis chlorophylla*, *Adiantum rufopunctatum*, *Anemia australis*, *A. ferruginea*, *A. herzogii*, *A. myriophylla*, *A. tomentosa*, *Asplenium inaequilaterale*, *A. lorentzii*, *Astrolepis sinuata*, *Doryopteris lorentzii*, *D. raddiana*, *Pecluma filicula* and *Selaginella sellowii*). After intensively filtering the data (described in Soria-Auza & Kessler, 2008), the 27 species retained a total of 1361 georeferenced records. *Synallaxis scutata* had the highest number of records (146), whereas *C. henricae* had the lowest (17). Eighteen of the 27 species had more than 30 records and the average number of records per species was 48 ± 32 .

5.2.3 Modelling the distribution of SDTFs

We first mapped the current distribution of SDTFs in Bolivia based on the literature (Ibisch *et al.*, 2003; Pennington, 2004; Wood 2006; Linares-Palomino & Kessler, 2009). We then overlaid raster layers of annual precipitation and mean annual temperature at a resolution of 30 arc s. (ca. 1 km) on the distribution map of SDTFs to quantify the climatic limits of the forests. Climate data was obtained from the climate model SAGA (Böhner *et al.*, 2005; Kessler *et al.*, 2007). Unlike Worldclim, SAGA does not show the artificial ovoid-shaped centres of humidity geographically displaced to the lowlands adjacent to the Andes (Killeen *et al.*, 2007) that are associated with a lower predictive power when estimating species ranges (R. Soria-Auza *et al.*, unpubl. data). Initially, we assumed SDTFs to be present when values of both climatic variables met the ranks indicated by other authors for these habitats (see above). However, in this process we found that distributions of SDTFs are overpredicted using the climatic data available. Therefore, we settled on the following climatic parameters to define the envelopes for SDTFs in Bolivia: in lowlands (<1000 m) mean annual temperatures were set at 22-25°C and mean annual precipitation at 300-1.300 mm (precipitations levels below 800 mm corresponded to Chaco thorn forests and those >800 mm to the Chiquitano forests and the Cerrado). In the Andes (>1000 m), temperature ranges were lower (12-22°C), whereas precipitation limits remained the same as in the lowlands. Our delimitation of SDTFs thus embraced the whole range of such habitats in Bolivia (including most of the mosaic of Cerrado-Chiquitano and Cerrado-Chaco vegetation types). We must point out that we delimited the potential distribution of the habitat free of

the anthropogenic impacts that have severely reduced the current distribution of SDTFs in the Bolivian Andes (Wood, 2006).

To estimate the past distribution of SDTFs in Bolivia, we modified the environmental layers following estimations of past climates by focussing on the situations that most strongly deviate from present conditions. Present day climate in Bolivia can be characterized as warm and wet (Graf 1992; Mayle *et al.*, 2000; Mourguiart & Lebru, 2003), and we modelled conditions for cold-wet, cold-dry and warm-dry conditions. These scenaria roughly correspond to conditions during the LGM, Younger Dryas and early Holocene (Maslin & Burns, 2000; Thompson *et al.*, 2000; Baker *et al.*, 2001; Mourguiart & Ledru, 2003), respectively. However, these climatic scenarios occurred repeatedly along the Quaternary (Sigman & Boyle, 2000), and therefore they should not be associated specifically to any specific period of the Quaternary. We modified the present day conditions by reducing precipitation and temperature levels based on indications from pollen studies (Mourguiart & Ledru, 2003), sedimentology (Baker *et al.*, 2001), ice-core isotopes (Thompson *et al.*, 2000), and glacial and snow lines (Clapperton *et al.*, 1997; Klein *et al.*, 1999). Independent reconstruction of palaeoclimatic scenarios was not possible due to the lack of detailed palaeocirculation models. Temperature for cold periods was set at 6°C lower than present, which is in accordance with the majority of palaeoclimatic studies focussing on the northern and central Andes (e.g., Graf, 1992; Clapperton *et al.*, 1997; Klein *et al.*, 1999; Mourguiart & Ledru, 2003), although reductions by as much as ca. 8°C (Thompson *et al.*, 2000) or even ca. 12°C (Hooghiemstra & Ran, 1994) have also been proposed. Precipitation reduction was more difficult to quantify because palaeoecological studies commonly discern between periods of elevated or reduced humidity but do not provide absolute measures of precipitation change since, unlike temperature data, there are no directly quantifiable indicators. We therefore set dry periods at 70% of the current precipitation levels, roughly corresponding to the shifts between vegetation types documented for the Holocene in eastern Bolivia (Mayle *et al.*, 2000) and southeast Brazil (Behling, 1995; Behling & Lichte, 1997), and to the rainfall scenario presented by Graf (1992: 126). Our scenaria should be considered to be conservative as it is likely that even more extreme climatic conditions occurred during the Pleistocene in the central Andes.

5.2.4 Modelling of species distributions

We used Maxent 3.2.19 (Phillips *et al.*, 2006; Phillips & Dudik, 2008) to model species distributions. This technique outperforms other standard presence-only methods (Elith *et al.*, 2006). Maxent looks for the most probable distribution based on the theory of maximum entropy. Detailed information on the mathematical fundamentals is provided by Phillips *et al.* (2006) and Phillips & Dudik (2008). We removed duplicated presence records closer than 1 km that corresponds to the pixel resolution of the environmental raster layers, and the logistic output format was chosen to depict the raster maps for the species due to its intuitive interpretation (Phillips & Dudik, 2008).

Mean annual temperature and annual precipitation (simple climatic model) are the two climatic variables we used to model the species distributions for the present and past climate scenarios. Although more climatic variables of ecological significance (e.g. variables that give information about seasonality) should yield better fitted maps, we decided to limit our analysis to these two variables as information from past climates only provide estimations of these two climatic variables. Moreover, we also modelled the species ranges using a total of 8 climatic variables (complex climatic model; see supplementary material) that included information about the seasonality of precipitation and temperature, as well as the annual range of both variables to control for the quality of the ranges modelled with the simple climatic model for the present climate (warm-wet). We used the maximum training sensitivity plus specificity threshold (Canran *et al.*, 2005) for delimiting the ranges constructed with the simple climatic model.

To model the distributions of species for the past scenarios, we used the modified layers of temperature and precipitation to project the distributions into the other climatic scenarios (see Maxent for more detailed information). In addition, the same thresholds were applied to the ranges estimated for these other periods. To evaluate the modelled species ranges, we randomly partitioned the occurrence data into two subsets; 75 % of the records were used to build range estimation, and the remaining 25 % to evaluate them. The index we used to evaluate the estimated ranges was the AUC as it is threshold independent (Fielding & Bell, 1997; Phillips *et al.*, 2006).

5.3 Results

5.3.1 Distribution of SDTFs in the present warm-wet climate

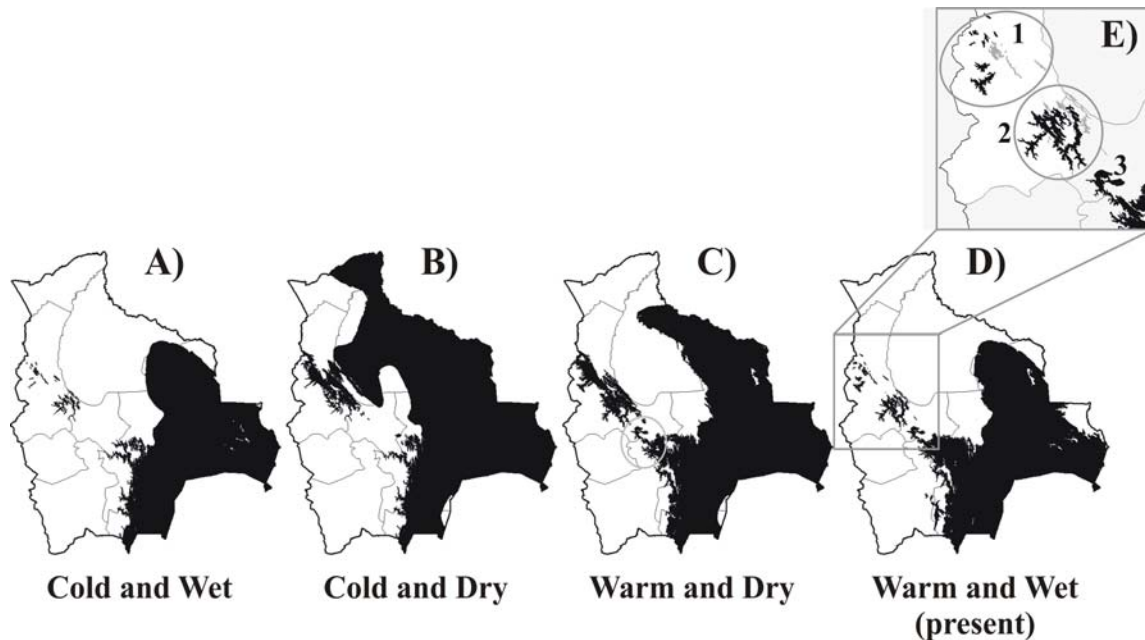


Figure 5.2. Modelled climatically determined distribution of SDTFs in Bolivia under each of four contrasting climatic scenarios (A-D) defined for the Pleistocene. Map E shows the fragments of inter-Andean dry forests of the north-western Bolivian Andes in detail. (1) Group Camata, Consata and Río Tuichi fragments, (2) group Chamaca, Cotacajes, Inquisivi, Mecapaca and Miguillas fragments, and (3) shows the valley of Cochabamba

The estimated map of the SDTFs during the current period of warm-wet climate accurately reproduced all the known Inter-Andean dry forests. The isolated inter-Andean dry forests in La Paz and Cochabamba may more or less be combined into two groups (Fig. 5.2d). Firstly, the northernmost fragments placed in the rain-shadow valleys that are surrounded by the humid montane forests, and are altitudinally limited by other high Andean vegetation. This group is composed of the Camata, Consata, Río Tuichi and other surrounding smaller fragments. Secondly, the other group of fragments clumped in the rain-shadow valleys of the humid eastern cordillera are composed by the Chamaca, Cotacajes, Inquisivi, Mecapaca and Miguillas valleys (Fig. 5.2e). The southern inter-Andean dry forests that are an extension of the SDTFs from the lowlands were placed south of the Andean elbow. The north-westernmost extension of this dry Andean formation is the valley of Cochabamba and is connected to the larger dry Andean forests via the Río Caine basin (Fig. 5.2d-e). SDTFs

in the lowlands extend to most of the departments of Santa Cruz, Chuquisaca, and Tarija. The northernmost extension of the SDTFs in the lowlands includes the south-eastern part of the department of Beni (see Fig. 5.1b for descriptions of the regions and important geographic characteristics; see Fig. 5.2d for the estimated distribution of the SDTFs).

Table 5.1. Current elevational distribution of the species that were modelled as establishing contacts to the forest fragments in the northern Bolivian Andes, and periods in which the contacts took place. B = birds, F = ferns.

Species	Taxon	Min elev	Max elev	Median elev	Mean elev	Range	Period of contact
Species that established connections through the lowlands							
<i>Adiantum rufopunctatum</i>	F	574	3154	1599	1597	2580	cold-dry
<i>Anemia herzogii</i>	F	339	1995	894	877	1656	cold-dry
<i>Arremon flavirostris</i>	B	83	2673	930	1007	2590	cold-dry
<i>Asplenium inaequilaterale</i>	F	958	3276	1546	1669	2318	cold-dry
<i>Doryopteris lorentzii</i>	F	798	2364	1460	1522	1566	cold
<i>Doryopteris raddiana</i>	F	113	1691	888	844	1578	cold-dry
<i>Formicivora melanogaster</i>	B	84	1778	321	570	1694	dry
<i>Nystalus maculatus</i>	B	82	2658	356	554	2576	warm-dry
<i>Pecluma filicula</i>	F	428	2270	1340	1387	1842	cold-dry
<i>Polioptila dumicola</i>	B	82	2939	335	523	2857	warm-dry
<i>Synallaxis scutata</i>	B	84	1971	783	796.62	1887	warm
Mean		330	2434	950	1031	2104	
Species that established connections through the highlands							
<i>Anemia myriophylla</i>	F	113	3403	2177	2149	3290	warm
<i>Asplenium lorentzii</i>	F	1504	3842	2421	2512	2338	warm-wet
<i>Astrolepis sinuata</i>	F	888	3708	2087	2075	2820	warm
<i>Cranioleuca henricae</i>	B	1583	3180	2581	2494	1597	cold
<i>Cranioleuca pyrrhophia</i>	B	129	3693	918	1265	3564	all
<i>Myiopsitta luchsii</i>	B	1364	2939	2645	2520	1575	dry
<i>Poospiza boliviana</i>	B	1261	3911	2634	2657	2650	warm
<i>Serpophaga munda</i>	B	82	3546	836	1064	3464	all
<i>Stigmara budytoides</i>	B	206	2940	529	1122	2734	all
Mean		792	3462	1870	1984	2670	
Species that did not establish connections							
<i>Myiopsitta monachus</i>	B	80	785	303	285	705	-

5.3.2 Distribution of the SDTF during the past climatic scenarios of the Quaternary

Dry climates of the Quaternary were associated with larger extensions of the SDTFs than today (Fig. 5.2b-c). The cold-dry climate was the period in which the SDTFs showed their maximal extension in the lowlands. During this period, the inter-Andean dry forests in the north-west Andes of Bolivia (in La Paz and Cochabamba) were modelled as directly connected to the SDTFs (department of Beni) (Fig. 2b). The central Andean region of Bolivia (e.g., valley of Cochabamba and Río Caine) were modelled as not having favourable climatic condition to maintain SDTFs. Moreover, the upper altitudinal limit of the SDTFs along the southern Andean range (south of the Andean elbow) was significantly lower than today. The warm-dry climate, on the other hand, was predicted to offer the conditions needed by the SDTFs in order to colonize the Andes while simultaneously they experienced significant reductions in the lowlands (although they still remained larger than today) (Fig. 5.2c). The valleys of Cochabamba and Río Caine were modelled as being colonized by SDTFs under these conditions, so that the configuration of the SDTFs in the Andes approximately resembled their current distribution, except for the larger extension of the fragments in the north-west Bolivian Andes (Fig. 5.2c). The most reduced extension of the SDTFs was modelled for the cold-wet climate. Under these conditions, the fragments of SDTFs in the north-west Bolivian Andes were even smaller than today and the upper altitudinal limit south of the Andean elbow were at the lowest level. The extension of the SDTFs in the lowlands, on the other hand, was similar to the present modelled distribution of this biome (Fig. 5.2a).

5.3.3 Patterns of colonization of the Andean fragments of SDTFs

Species distributions estimated with the simple climatic model (mean temperature and annual precipitation) produced similar values of AUC to the modelled ranges constructed with the complex climatic model (see supplementary material). The average difference of AUC values between the ranges constructed with the complex and simple climatic model was of 0.02 and ranged from -0.006 (*Anemia tomentosa*, *Doryopteris raddiana* and *Selaginella sellowii*) to 0.103 (*Formicivora melanoleuca*). Although these numerical differences are small, the resultant ranges generated with the simple climatic model tended to predict more spatially restrictive ranges, especially in the lowlands (Appendix A4 & A5).

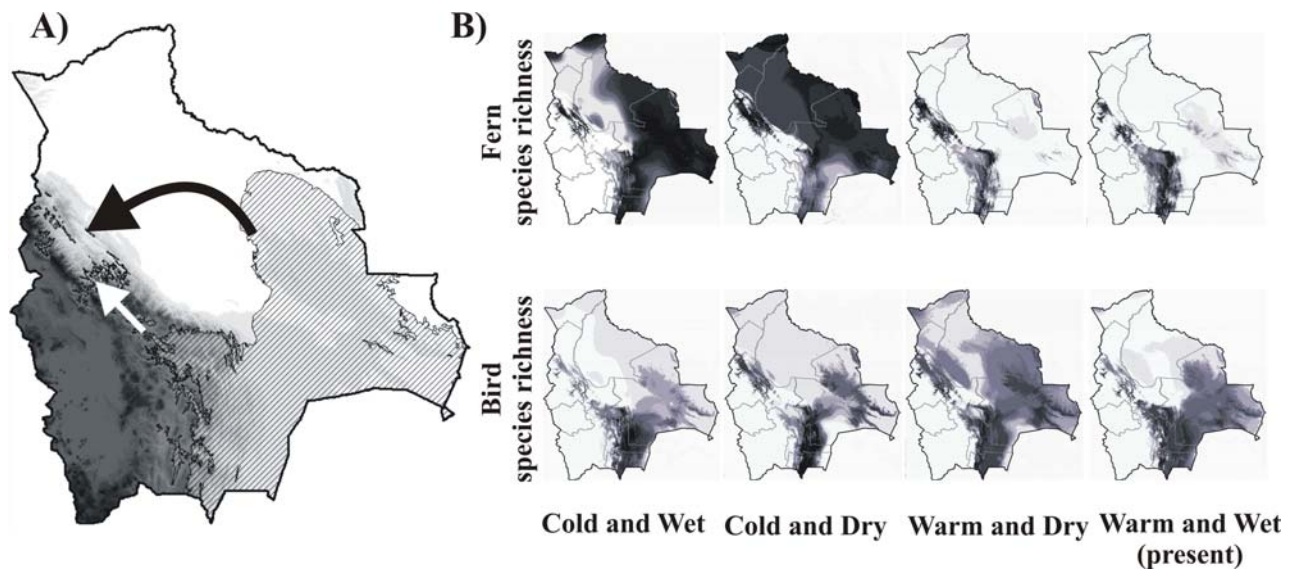


Figure 5.3. A) Present-day distribution of the SDFs in Bolivia with arrows indicating the two potential routes of colonization of inter-Andean SDFs of the northwestern Bolivian Andes. B) Cumulative species richness of 27 modelled birds and fern species under each of the contrasting climates of the Pleistocene (individual species ranges in appendix 1.5).

Two routes of connections between species' populations inhabiting the northern fragments of dry forests in the Andes and the rest of the SDFs were established: (1) connections through the SDFs that were widely spread over the central Bolivian lowlands during dry periods (see above), and (2) connections through the high central Andes (Cordillera of Cochabamba) during cold periods (Fig. 5.3a). An extensive area of suitable habitat for eleven species (five bird and six fern species, see Table 5.1) was modelled as being present across the central lowlands of Bolivia that reached the north Andean fragments of dry forests. Two species of birds (*Arremon flavirostris* and *Formicivora melanogaster*) and six species of ferns (see Table 5.1) from this group reached their maximum level of connectivity during dry climates (especially cold-dry climates), while four species reached their highest extension during warm-dry climates (Table 5.1). Two of these species do not have current populations in the fragments of inter-Andean dry forests (*Polioptila dumicola* and *Anemia herzogii*).

Table 5.2. Current elevational distribution of the species that were modelled as establishing contacts to the forest fragments in the northern Bolivian Andes both through the low- and highlands, and periods in which the contacts took place. B = birds, F = ferns.

Species	Taxa	Min elev	Max elev	Median elev	Mean elev	Range	Periods of contact through the lowlands	Periods of contact through the Andes
Species that established connections through both the lowlands and the Andes								
<i>Adiantopsis chlophylla</i>	F	113	2969	1111	1097	2856	Cold-dry	warm-wet
<i>Anemia australis</i>	F	267	3370	1869	1818	3103	Cold-dry	warm-wet
<i>Anemia ferruginea</i>	F	113	2155	1066	1034	2042	Cold-dry	warm-wet
<i>Anemia tomentosa</i>	F	143	3102	1072	1270	2959	Cold-dry	warm
<i>Selaginella sellowii</i>	F	258	4064	1589	1529	3806	Cold-dry	warm
<i>Suiriri suiriri</i>	B	84	2985	440	803	2901	warm-dry	warm-dry
Mean		163	3108	1191	1258	2945		

Nine species showed range expansions across the high central Andes and, therefore, were able to maintain populations on both sides of the central Cordillera of Cochabamba (Table 5.1). The expansion of suitable habitat for these species across the central Andes was established during the warm periods (Fig. 5.3b), except for *Serpophaga munda* which was modelled as maintaining populations on both sides of the central Andes across the four climatic scenarios and *C. henricae* which had larger ranges during the cold periods (see appendix A5). Although *Myiopsitta luchsii* and *Stigmatura budytoides* do not maintain current populations in the isolated fragments of dry forests northwest of the cordillera of Cochabamba, some tracts of potentially suitable habitat exist in several of the fragments of dry forests (see appendix A5).

A third group of species comprised by six species (1 bird and 5 fern species) established range expansions through the central Andes and the central lowlands of Bolivia. Connections throughout the lowlands were established during the cold-dry period, whereas warm periods fostered range expansions throughout the Andes, especially warm-wet climates (Table 5.2). *Suiriri suiriri* was the exception since the maximal range extension of this species was modelled for the warm periods.

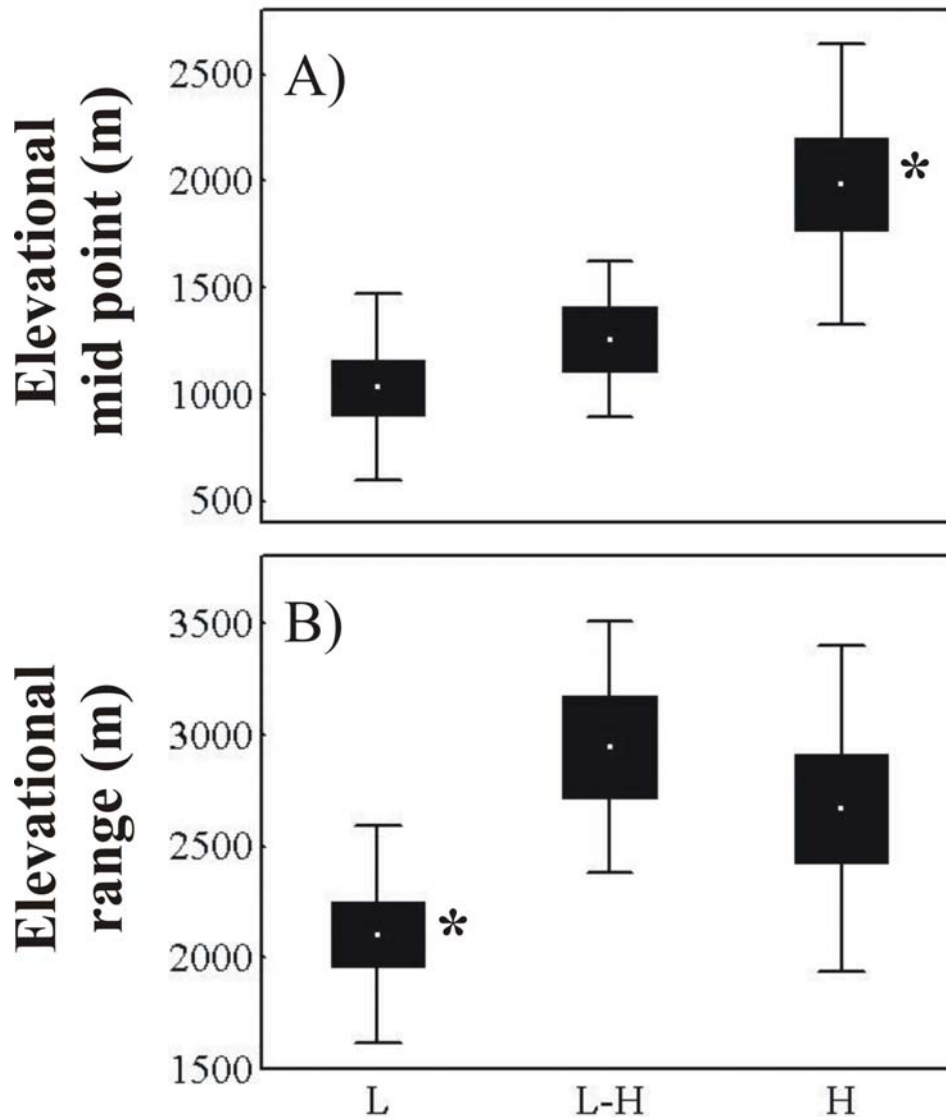


Figure 5.4. Comparison of elevational mid points (A) and elevational ranges (B) of species that were modelled to have colonized the north-west fragments of inter-Andean dry forests through the lowlands (L), the central Andes (H) or both (L-H). Asterisks indicate the groups that are statistically different from the remainder (Kruskal-Wallis, $p < 0.05$).

The current elevational mean point of the species elevational range was higher for species that established connections between the inter-Andean dry forests through the central Andes (Kruskal-Wallis; $H = 9.52$; $P < 0.01$; Fig. 5.4a). Conversely, the elevational ranges were lower for species that were modelled to have reached the Andean fragments through the central lowlands of Bolivia (Kruskal-Wallis; $H = 7.91$; $P < 0.05$; Fig. 5.4b).

5.4 Discussion

5.4.1 The distribution of the SDTFs throughout the Quaternary to the present

The climatically-determined map of the SDTFs for the present climate (warm-wet) coincided with the distribution of (1) the Chaco (low thorn forest of the SE lowlands), (2) the Chiquitano dry forests (low thorn forests on the south-eastern lower Andean slopes) and (3) the complex mosaic of Cerrado-Chiquitano dry forests and Cerrado-Chaco (see Ibisch *et al.*, 2003: Fig. 3.1). All these vegetation types are strongly seasonal and are structurally more similar to each other than to wetter vegetations such as the Amazonian rainforests, the seasonally flooded savannas of Moxos in central Bolivia, or the Pantanal in east Bolivia (Ibisch *et al.*, 2003) (see Fig. 5.1a). However, the northernmost extreme of our map in the lowlands (east Bolivia) also included the southernmost portion of the rainforest located in the northern extreme of the department of Santa Cruz and southern Beni. This area is covered by a type of transitional rainforest between the Chiquitano dry forests from central Santa Cruz and the Amazonian rainforests of northern Bolivia. Although this area is slightly wetter than the southern lowlands (south-north gradient of precipitation from 200 mm to 1200 mm), it is difficult to climatically discriminate this transitional rainforest from the Chiquitano dry forests without problems in delimiting the remainder of SDTFs.

If we compare our maps of the cold periods with Mayle's (2004) and Mayle & Beerling's (2004) estimations of a progressive southward advance of the rainforests since the LGM, then our map of the SDTFs for the cold-wet climate seems to be a subestimate (Fig. 5.2a). According to Mayle's (2004) estimations, the SDTFs covered most of the Bolivian lowlands during the LGM, which would roughly correspond with our cold-wet scenario. A determinant factor for the results of Mayle (2004) and Mayle & Beerling (2004) is the incorporation of CO₂ atmospheric levels (Colinveaux *et al.*, 2001; Cowling *et al.*, 2001; Siegenthaler *et al.*, 2005) in modelling the distribution of the biomes, which was not included in our analysis.

If we order the four mapped distributions of the SDTFs chronologically for the past 20.000 years, then, except for the distribution of the SDTFs during the cold-wet climate, our estimated SDTFs' distributions correspond to previous findings of a progressive southwards advance of the Amazonian rainforests at the expense of SDTFs and savannas (Mayle, 2004; Mayle & Beerling, 2004; Burbridge *et al.*, 2004). This supports the idea of a connection between the fragments of inter-Andean dry forests of north-western Bolivia to SDTFs from

the lowlands. The lower tree line mentioned by Moughiart & Lebru (2003) is, on the other hand, consistent with the lower upper altitudinal limit of SDTFs for this period. Other authors also found indications of the presence of Andean species (e.g. *Podocarpus* and *Alnus*) in the lowlands during the cold periods of the Pleistocene (Behling, 2001; Colinveaux *et al.*, 2001) and also interpreted this as a signal of a lower tree line due to the lower temperatures during this period. The persistence of fragments of SDTFs in the north-west Andean slopes of Bolivia suggests that these areas might correspond to ecoclimatically fairly stable areas associated with high levels of endemism in the high Andes (Fjelds  *et al.*, 1999). Our models suggest that these areas were stable enough to have maintained dry vegetation types, and hence also high levels of diversity characteristic of SDTFs in the north-west Bolivian Andes throughout the Quaternary (Fig. 5.3b).

The north-western expansion of Cerrado-like vegetations would explain the presence of Cerrado components (e.g., *Hemipogon sprucei*; Wood, 2006: Fig. 10.4) that still persist in the Tuichi fragment of Andean dry forests (Fig. 5.1a) and additionally, the isolated Cerrado-like vegetation in the lowlands of the department of La Paz, named by Ibisch *et al.* (2003) as Cerrado Pace o (Ibisch *et al.*, 2003: Fig. 3.1). This expansion would also explain the isolated populations of *F. melanogaster* and *S. scutata* that do not inhabit elevations above 1800 m in the Andes (Herzog & Kessler, 2002; Hennessey *et al.*, 2003).

5.4.2 The distributions of species during the Quaternary

Our discussion is, so far, limited to the last cycle of climate variation of the Pleistocene (e.g. Mayle, 2004; 2006; Mayle & Beerling, 2004; Pennington *et al.*, 2000; 2004). The entire Quaternary (Pleistocene and Holocene) covers a time span of approximately 1.8 million years, until present times. Consequently, drastic changes have taken place several times as at least four glacial and interglacial periods have been reported in the last 450.000 years (Sigman & Boyle, 2000) that coincide with fluctuations of atmospheric levels of CO₂ (Barnola *et al.*, 1987; Petit, 1999) and the Milankovich cycles (Hays *et al.*, 1976; Berger *et al.*, 1984; Paillard, 1998).

Although the climatically-determined vegetation maps suggest that the fragments of Andean SDTFs were connected to the once widely distributed SDTFs of the central Bolivian lowlands, some species presumably reached these fragments through the central Bolivian Andes. Cold climatic conditions (especially cold-dry) were modelled to offer conditions to support species expansions through the lowlands, while warm climates

allowed some species to disperse across the central Andes of Bolivia (Cordillera of Cochabamba; Table 5.1; Fig. 5.3b; see also appendix 5.1 for maps of individual species). At present, the central Andes of Bolivia represent a massive barrier of inhospitable environments for species inhabiting the SDTFs in southern Bolivia. Only species that today are well adapted to Andean environments were modelled to have the capacity to cross the central Andes (*Asplenium lorentzii*, *Cranioleuca henricae* and *Poospiza boliviana*) (Table 5.1; Fig.5.4).

Especially interesting are the predicted distributions of both species of *Cranioleuca* (*C. henricae* and *C. pyrrhophia*). According to the work of García-Moreno *et al.* (1999), the radiation of this group has taken place within the last million years, which places this genus within the genera of birds with a Pleistocenic origin (Klicka & Zink, 1997). García-Moreno *et al.* (1999) suggested that the cyclic climatic variations led to population isolation, and subsequent speciation, at some point within the Pleistocene. Although the modelled ranges for these two species have poor resolution (in comparison with the ranges estimated with the complex climatic model), especially for *C. henricae*, it is probable that during cold periods of the Pleistocene, these two species were geographical vicariants of the same group that started to differ from each other as consequence of population isolation driven by climate change. Furthermore, *C. pyrrhophia* is today comprised of two phylogenetic distinct subgroups, one inhabiting the Andes and the other distributed in the lowlands (García-Moreno *et al.*, 2000). Our modelled distributions also support this separation.

5.5 Conclusions

In conclusion, we found evidence supporting the hypothesis that the cyclic climatic conditions of the Quaternary resulted in repeated connections and disjunctions of Andean SDTFs from those in the central Bolivian lowlands. Individual analyses at species level showed that species adapted to cold climates were able to cross the central Andes and reach these fragments during warm periods. Species adapted to warm-dry environments, on the other hand, reached the north-west Andean fragments of dry forests via lowlands of central Bolivia. This suggests that the fragmented distribution of species specialized to SDTFs may be largely determined by vicariance, rather than by long-distance dispersal. Although this statement may apparently contrast the findings of other authors (i.e. long-distance dispersal of the SDTFs southwards; Mayle, 2004; Mayle & Beerling, 2004), we think both results are complementary. Previous studies have been performed at larger spatial scales and lower

resolutions, covering the whole continental area (e.g. 2.8° of latitudinal x 2.8° of longitudinal resolution; Mayle, 2000; Mayle & Beerling, 2004). Consequently, we do not deny the possibility of long-distance dispersal between SDTFs at the continental scale, but in addition suggest that vicariance may have played an important role in the Bolivian Andes.

Acknowledgments

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5.6 References

- Bach, K., M. Kessler & J. Gonzales (1999) Caracterización preliminar de los bosques deciduos andinos de Bolivia en base a grupos indicadores botánicos. *Ecología en Bolivia* 32: 7-22.
- Baker, P.A., Seltzer, G.O., Fritz, S.C., Dumbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D. & Broda, J.P. (2001) The history of tropical South American climate for the past 25,000 yr from the sedimentary record of lake Titicaca (Bolivia/Peru). *Science* 291, 640-643.
- Barnola, J.M., Raynaud, D., Korotkevich, Y.S. & Lorius, C. (1987) Vostok ice core provide 160,000-year record of atmospheric CO₂. *Nature*, 329, 408-414.
- Behling, H. (1995) A high resolution Holocene pollen record from Lago do Pires, SE Brazil: vegetation, climate and fire history. *Journal of Paleolimnology*, 14, 253-268.
- Behling, H. (2001) Late Quaternary environmental changes in the Lagoa da Curuça region (eastern Amazonia, Brazil) and evidence of Podocarpus in the Amazon lowland. *Vegetation History and Archaeobotany*, 10, 175-183.
- Behling, H. & Hooghiemstra, H. (2001) Neotropical savanna environments in space and time: Late quaternary interhemispheric comparisons. *Interhemispheric Climate linkages* (ed. by V. Markgraf), pp. 307-323. Academic Press, San Diego, California
- Behling, H. & Lichte M. (1997) Evidence of dry and cold climatic conditions at glacial times in tropical southeastern Brazil. *Quaternary research*, 48, 348-358.
- Berger, A., Imbrie, J., Hays, J., Kukla, G. & Saltzman, B. (1984). *Milankovich and climate-Understanding the responses to astronomical forcing*. Reidel, Dordrecht.
- Burbridge, R., Mayle, F.E., Killeen, T.J. (2004) Fifty-thousand-year vegetation and climate history of Noel Kempff Mercado National park, Bolivian Amazon. *Quaternary Research*, 61, 215-230.
- Canran, L., Berry, P. Dawson, T.P. & Pearson, R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385-393.
- Clapperton, C.M., Clayton, J.D., Benn, D.I., Marden, C.J. & Argollo, J. (1997) Late Quaternary glacial advances and paleolake highstands in Bolivian Altiplano. *Quaternary International*, 38/39, 49-59.
- Cowling, S.A., Maslin, M.A. & Sykes, M.T. (2001) Palaeovegetation simulations of lowland amazonia and implications for Neotropical allopatry and speciation. *Quaternary Research*, 55, 140-149.

- Elith, J., Grahman, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachertti-Pereira, R., Schap9hire, R.E. Soberon, J., Williams, S., Wisz, M.S., & Zimmermann N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24, 38-49.
- Garcia-Moreno, J., Arctander, P. & Fjeldså, J. (1999) A case of Rapid Diversification in the Neotropics: Phylogenetic relationships among Cranioleuca Spinetails (Aves: Furnariidae). *Molecular Phylogenetics and Evolution*, 12, 273-281.
- Fjeldså, J., Lambin, E. & Mertens, B. (1999) Correlation between endemism and local ecoclimática stability documented by comparing Andean bird distributions and remotely sensed land surface data. *Ecography*, 22, 63-78.
- Gentry, A.H. (1995) Diversity and floristic composition of Neotropical dry forests. *Seasonally dry tropical forests* (ed. by S.H. Bullock, H.A. Mooney & E. Medina), pp. 146-194. Cambridge University press.
- Graf, K. (1992) Pollediagramme aus den Anden. Eine Synthese zu Klimageschichte und Vegetationsentwicklung seit der letzten Eiszeit. *Physische Geographie* (Georg. Inst. Univ. Zürich), 34: 1-138.
- Graham A. & Dilcher, D. (1995) The Cenozoic record of tropical dry forests in northern Latin America and southern United States. *Seasonally dry tropical forests* (ed. by S.H. Bullock, H.A. Mooney and E. Medina), pp. 124-145. Cambridge University press.
- Ibisch, P.L., Beck, S.G., Gerkmann, B. & Carretero, A. (2003) La diversidad Biológica-Ecoregiones y ecosistemas. Biodiversidad: la riqueza de Bolivia. Estado de conocimiento y conservación (ed by P.L. Ibisch and G. Merida), pp. 47-53. FAN, Santa Cruz de la Sierra, Bolivia
- Haffer, J. (1969) Speciation in Amazonian forest birds. *Science*, 165, 131-137.
- Hays, J.D., Imbrie, J. & Shackleton, N.J. (1976) Variations in the Earth's orbit: Pacemakers of the ice Ages. *Science*, 194, 1121-1132.
- Hennessey, A.B., Herzog, S.K. & Sagot, F. (2003) *Lista anotada de las aves de Bolivia*. 5th edn. Asociación Armnía/BirdLife Internacional, Santa Cruz de la Sierra, Bolivia.

- Herzog, S.K. and Kessler, M. (2002) Biogeography and composition of dry forest bird communities in Bolivia. *Journal of Ornithology*, 143, 171-204.
- Hooghiemstra, H. & Ran, E.T.H.(1994) Late Pliocene-Pleistocene high resolution pollen sequence of Colombia: an overview of climatic change. *Quaternary International*, 21, 63-80.
- Hooghiemstra, H. & Van der Hammen, T. (2004) Quaternary Ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philosophical Transactions of the Royal Society of London. Series B*, 359, 173-181.
- Kessler, M. & Helme, N. (1999) Floristic diversity and phytogeography of the central Tuichi Valley, an isolated dry forest locality in the Bolivian Andes. *Candollea*, 54, 341-366.
- Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen P. M. & Mejia, J. (2007) Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, 34, 1357-1373.
- Klein, A.G., Seltzer, O.G. & Isacks, B.L. (1999) Modern and last local glacial maximum snowlines in the central Andes of Peru, Bolivia and northern Chile. *Quaternary Sciences Reviews*, 18, 63-84.
- Klicka, J. & Zink, R.M. (1997) The importance of recent ice ages in speciation: A failed paradigm. *Science*, 277, 1666-1669.
- Linares-Palomino, R. & Kessler, M. (2009) The role of dispersal ability, climate and spatial separation in shaping biogeographical patterns of phylogenetically distant plant groups in seasonally dry Andean forests of Bolivia. *Journal of Biogeography*, 280-290.
- López, R.P. (2003) Phytogeographical relationships of the Andean dry valleys of Bolivia. *Journal of Biogeography*, 30, 1659-1668.
- Maslin, M.A. & Burns (2000) Reconstruction of the Amazon basin effective moisture availability over the past 14,000 years. *Science*, 290, 2285-2287.
- Mayle, F.E. (2004) Assessment of the neotropical regugia hypothesis in the light of palaeoecological data and vegetation model simulations. *Journal of Quaternary Sciences*, 19, 713-720.
- Mayle, F.E. (2006) The late Quaternary biogeographical history of South American Seasonally dry tropical forests: insights from tropical forests: Insights from paleoecological data. *Neotropical Savannas and seasonally dry forests. Plant diversity, biogeography and conservation* (ed. by T. Pennington, G.P. Lewis and J.A. Ratter), pp. 395-416. Taylor and Francis group. United States of America.

- Mayle, F.E. And Beerling, D.J. (2004) Late quaternary changes in amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography, palaeoclimatology, Palaeoecology*, 214, 11-25.
- Mayle, F.E., Burbridge, R. & Killeen, T.J. (2000) Millennial-scale Dynamics of Southern Amazonian rain forests. *Sciences*, 290, 2291-2294.
- Mayle, F.E., Beerling, D.J., Gosling, W.D. & Bush, M.B. (2004) Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society of London, Series B*, 359, 499-514.
- Mourguiart, P. & Ledru, M.P. (2003) Last glacial maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia). *Geology*, 31, (3), 195-198.
- Murphy, P. & Lugo, A.E. (1986) Ecology of tropical dry forests. *Annual Review of Ecology and Systematics*, 17, 67-88.
- Niemann, H. & Behling H. (2008) Late quaternary vegetation, climate and fire dynamics inferred from the El Tiro record in the southeastern Ecuadorian Andes. *Journal of Quaternary Science*, 23, 203-212.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, D.N., Powel, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allmutt, T.F., Ricketts, T.H., Kura, Y., Lamereoux, J.F., Wettengel, W.W., Hedao, P. & Kassen, K.R. (2001) Terrestrial ecoregions of the world: a new map of the life on Earth. *Biosciences* 51, 933-938.
- Paillard, D (1998) The timing of Pleistocene glaciations from a simple multiple-state climate model. *Nature*, 391, 378-381.
- Pennington, R.T., Prado, D.E. & Pendry, C.A. (2000) Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography*, 27, 261-273.
- Pennington, R.T., Lavin, M., Prado, D.E., Pendry, C.A., Pell, S.K. & Butterworth, C.A. (2004) Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society of London, Series B*, 359, 515-537.
- Peterson, A.T., Martínez-Meyer, E. & Gonzáles-Salazar, C. (2004) Reconstructing the pleistocene geography of *Aphelocoma* jays (Corvidae). *Diversity and Distributions*, 10, 237-246.
- Petit, J.R. Jozuel, J., Raynaud, D., Barkov, N.I., Barnola, J.M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmonte, M., Kotlyakov, V.M., Legrand,

- M., Lipenkov, V.Y., Lorius, C., Pépin, L., Ritz, C., Saltzman, E. & Stievenard, M. (1999) Climate and Atmospheric history of the past 42,000 years from the Vostok ice core, Antarctica. *Nature*, 399, 429-436.
- Phillips, S. T & Dudík, M. (2008) Modeling of species distributions with maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161-175.
- Phillips, S. T., Anderson, R. P. & Schapire, R. E. (2006) Maximum entropy modelling for species geographic distributions. *Ecological Modelling*, 190, 231-259.
- Prado, D.E. & Gibbs, P.E. (1993) Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden*, 80, 902-927.
- Siegenthaler, U., Stocker, T.F., Monnin, E., Lüthi, D., Schwander, J., Stauffer, B., Rynaud, D., Barnola, J.M., Fischer, H., Masson-Delmotte, V. & Jouzel, J. (2005). Stable Carbon Cycle-climate Relationship during the Late Pleistocene. *Science*, 310, 1313-1317.
- Sigman, D.M. & Boyle, E.A. (2000) Glacial/interglacial variations in atmospheric carbon dioxide. *Nature*, 407, 859-869.
- Soria-Auza, R.W. & Kessler, M. (2008) The influence of sampling intensity on the perception of the spatial distribution of the tropical diversity and endemism: a case study of ferns from Bolivia. *Diversity and Distributions*, 14, 123-130.
- Thompson, L.G., Mosley-Thompson, E. & Henderson, K.A. (2000) Ice-core paleoclimates in tropical South America since the Late Glacial Maximum. *Journal of Quaternary Science*, 15, 377-394.
- Wiens, J. J. & Donoghue, M.J. (2004) Historical Biogeography, ecology and species richness. *Trends in ecology and evolution*, 19, 639-644.
- Wood, J.R.I. (2006) Inter-Andean dry forests of Bolivia- Floristic affinities and patterns of endemism: Insights from Acanthaceae, Asclepiaceae and Labiateae. *Neotropical Savannas and seasonally dry forests* (ed. by T. Pennington, G.P. Lewis and J.A. Ratter), pp. 235-256. Taylor and Francis group. United States of America.

Chapter 6

General Conclusions

6.1 A Summary of the major Findings

6.1.1 *The Geographic Bias of the sampling intensity and biodiversity patterns*

In spite of the fragmentary and geographically biased field data, the general patterns of species richness of pteridophytes in Bolivia were already confidently well estimated since early nineties. The humid montane forests are by far, the most diverse region, while the lowlands, as well as other high Andean dry areas are poor in species richness. The patterns of species richness were positively correlated with sampling intensity across time, as several studies also found (e.g., Freitag, *et al.*, 1998; Reddy & Dávalos, 2003). However, the relative higher difference between the estimated and recorded species richness in the heavily studied cells than in the poorly studied cells, indicate that most of these species-rich cells are expected to harbour even more species than the poorly studied cells. In any case, this expectancy will not modify drastically the already drawn pattern of species richness.

Local surveys also indicate high levels of fern diversity at mid elevations in the northern humid montane forests that gradually decline southwards (Kessler, 2000, 2001; Kessler *et al.*, 2001a, b). Although these studies are not statistically comparable, they also indicate a strong dependency of fern diversity upon humidity that is in accordance with other studies (e.g., Bhattarai *et al.*, 2004; Karst & Lechowicz, 2005; Bickford & Laffan, 2006; Kluge *et al.*, 2006). Bolivian lowlands, except for the north Bolivian rainforests (rainforests are more humid, but still seasonal), are also seasonal. Therefore, ferns inhabiting these areas are expected to experience a high water stress during the dry season. Since pteridophytes are strongly associated to humidity, seasonality may be a limiting factor for most fern species in the lowlands.

Endemism on the other hand, was not as strongly correlated with sampling intensity as species richness was. Again, the humid montane forests hold most of the endemic fern species, but their distributions within this area were much more irregular. Endemism is known to be less predictable than species richness in other taxa (Jetz *et al.*, 2004; Kreft *et al.*, 2006). This may reflect the presumably effect of historical factors that determine the evolution and distribution of species with restricted ranges.

Summarising, although the absolute values of species richness can not be estimated from incomplete data, it is possible to draw reliable general patterns of species richness. This is not the case for endemism.

6.1.2 *The impact of the quality of climate models and their impacts on niche modelling*

Since niche modelling use environmental variables to predict species ranges, Climate models (or data sets) may be considered as the hearth of these methods. The explosion of niche modelling techniques and their discordant results have lead scientist to explore the different sources of potential errors. Discrepancies between methods have been thoroughly studied (Elith *et al.*, 2006; Tsoar *et al.*, 2007), also the effect of the amount of available records (Araujo & Guisan, 2006) as well as the geographical disposition of records (Loiselle *et al.*, 2007) have been studied. The dispersal characteristics and the geographical extent of the species under study have also been investigated (Pöyry *et al.*, 2008). The amount of environmental variables used also has been identified as a source of discrepancies (Luoto *et al.*, 2007). However, the spatial pattern of the environmental variables used to extrapolate the species ranges have been neglected so far.

In the Chapter 3 we showed that the discrepancies between the spatial patterns estimated by different climate models are also an important source of error. The patterns of temperature between SAGA and Worldclim resulted to be quite similar. Rainfall patterns, on the other hand, resulted significantly different. These discrepancies are attributed to the procedure used to extrapolate these patterns. SAGA incorporate the effect of topography and regional circulation models in predicting the patterns of rainfall, while Worldclim does not. This result supports the previous observations of Killeen *et al.* (2007), who suggested that rain patterns of Worldclim do not reflect the real patterns of rainfall that are heavily influenced by the regional wind currents and topography.

The resultant predicted species ranges estimated using SAGA and Worldclim also were different. The species richness patterns predicted for species characteristic of the humid montane forests were outstandingly discrepant. This region was precisely pointed by Killeen *et al.* (2007) out as the area were Worldclim reproduces an ‘artificial ovoid-shaped’ centre of heavy precipitation. Although discrepancies between the species richness patterns for species characteristic of the seasonally dry forests estimated by SAGA and Worldclim were not significantly different. Detailed analysis revealed that Worldclim is not able to accurately discriminate the fragments of seasonally dry forests in the north Bolivian Andes, and over predict the occurrence of species in the high Andes. Although the species we used in this study are of secondary conservation priority. We expect that these discrepancies may be larger if the most important areas for conservation-priority species are to be identified using niche modelling.

6.1.3 *The latitudinal and elevational gradients of bird species richness in the Central Andes*

By combining the elevational and latitudinal gradients of species richness across the central Andes, we found that species richness decrease from the mid-lowland humid forest of south Peru to the dry highlands of south Bolivia. This general pattern resulted from differential changes of species richness at different elevations from the northern to the southern extremes of the study area. The northernmost regions, for example, exhibited a monotonic elevational decrease of species richness that gradually turned into a hump-shaped curve in the southernmost extreme of the study area. Similarly, the overall latitudinal gradient of species richness consisted of a decrease of species richness from north to south. This decrease was very pronounced for the lower elevational belts (up to 1500 m) and almost imperceptible for the upper altitudinal belts.

We found that the described pattern is largely determined by climatic factors (precipitation). The other variables, however, also play a role to some degree. The regional and elevational division of the study area revealed that the primary effect of precipitation over the species richness was due to the latitudinal decline of precipitation at lower elevations. On the other hand, elevation (temperature) and habitat heterogeneity gained importance when regions and elevations were analyzed independently. The abrupt reduction of species richness at low elevations around the Andean elbow, also coincide with the rather abrupt transition from the humid tropical montane forests of Peru and the northern Bolivian Andes to the seasonally dry and subtropical climate of southern Bolivia and northern Argentina. Such regional shifts have been also reported by other authors for mammals (e.g., McCain, 2005, 2007), birds (McCain, 2009) and ferns (Kessler et al., unpubl. data) on global scales. Hump-shaped curves have been reported to be typical for arid mountains (McCain, 2009), where mid elevations are relatively more humid than at lower elevations (Lauer, 1986). The partial collinearity between the explanatory variables makes difficult the evaluation of each variable's impact alone. However, the consistently high explanatory power of precipitation and temperature (elevation) strongly suggest that these two factors determine bird species richness in the region. Such pattern in which water availability is the limiting factor at low latitudes, while temperature plays this role at high latitudes has been reported for several groups of plants and animal groups (Francis & Currie, 2003; Hawkins *et al.*, 2003; McCain, 2007, 2009). However, the mechanisms behind this pattern remain to be studied.

We also found that the neotropical range-restricted bird species showed distinct patterns. Endemic species responded strongly to precipitation and habitat heterogeneity. They are known to be concentrated in localized habitats and mountain regions (e.g., Rahbek *et al.*, 2007). The same abrupt decline of the range-restricted species richness around the Andean elbow (18°S) was also reported for endemic species, which of course, was also related to the reduction of precipitation. However, because this area is also the transition area between the tropical humid montane forests and the subtropical and seasonally dry montane forests, this may also reflect the extension of this biomes rather than the association between endemic bird species and precipitation.

The overall diversity-parameter relationship of bird species richness is overwhelmingly dominated by the widespread species, and the most common environmental conditions. Dissecting the study area into regions, elevational belts, and also the species richness into quartiles let us recover less frequent relationships. This shows that continent-wide analyses of diversity patterns run the risk, if not analyzed separately, of neglecting geographically restricted species and biomes that are by nature of priority for conservation.

6.1.4 Historical distributions of the seasonally dry tropical forest in the Bolivian Andes

The seasonally dry tropical forests (SDTFs) that today are dispersed in the rain-shadow valleys of the north Bolivian Andes are vestiges of the more extensively distributed pleistocenic seasonally dry forest that covered most of the Bolivian lowlands, including important sectors of the Andes during the dry periods of the quaternary. Although this was already well established (e.g., Mayle, 2004; Mayle & Beerling, 2004), the geographical pattern of colonization of the rain-shadow valleys of the northern Bolivian Andes remained a point of discussion that we tackled by using a modelling approach.

We found that the SDTFs colonized the northern Bolivian Andes through the central Bolivian lowlands during the dry periods of the quaternary. Neither the cold-dry nor the warm-dry climates offered the suitable conditions for these seasonal vegetation to colonize the nowadays fragments by crossing the central Bolivian Andes, that surpass the 4500 m of elevation. Cold periods especially limited the elevational upper limit of the SDTFs in the Andes, while wet periods restricted their extension mainly in the lowlands. These patterns of distribution are in accordance with previous estimated past distributions of the SDTFs in the continent (Moughiart & Lebru, 2003; Mayle, 2004; Mayler & Beerling, 2004). However,

the scale and resolution at which we performed our study, let us to conclude that the nowadays fragments of SDTFs in the north Bolivian Andes resulted from a process of vicariance of the SDTFs that were distributed in the central lowlands of Bolivia. These findings do not contradict the already established process of long-distance dispersal of the SDTFs at a continental scale (e.g. Mayle, 2004; Mayle & Beerling, 2004). The significantly lower resolution of the previous studies prevented the authors to be conclusive for the central Andean region.

The modelled distributions of the set of species endemic to the SDTFs showed several patterns of colonization of the fragments that today are dispersed in the northern Bolivian Andes. Cold climates (especially cold-dry) offered the conditions to support species expansions through the central Bolivian lowlands, while warm climates favoured some species to disperse across the central Andes. This differential capacity to disperse through the Andes was obviously related to the biogeographical affinity of the species. Species of Andean affinity (i.e., species whose elevational upper limit is higher) were able to cross the central Andes during the warm periods (when the upper limit of the SDTFs reached the maximum elevational upper limit), while species mainly distributed across the lowland SDTFs were not able to cross the Andes. This Also explains the higher proportion of species of Andean biogeographic affinity at higher altitudes found by Wood (2006), and the proportionally higher percentage of species of Cerrado affinity in the northernmost fragment of SDTFs (e.g. Bach *et al.*, 1996; Kessler & Helme, 1999; Herzog & Kessler, 2002; Wood, 2006) that has a lower elevational range than the others (Herzog & Kessler, 2002).

6.2 Implications and limitations of these research

As we showed in the chapter two, data availability is the most limiting factor for macroecological and biogeographical research in the tropics. Although it was possible to draw the general pattern of fern species richness by analyzing the temporal development of sampling intensity, the resultant pattern was largely fragmented. But more importantly, the geographical pattern of endemism remained obscure.

Therefore, Methods that offer the possibility to fill these gaps of information are required in order to achieve further advances in Biogeography. Niche modelling has been recurrently pointed as the group of methods oriented to tackle the data deficiency. However, niche modelling also experience several sources of potential errors and uncertainties. In the

introductory part of the chapter three we detailed the several sources of potential bias when modelling species ranges. After controlling for the possible effects of these sources of biases, we found that (1) Worldclim present geographically biased patterns of precipitation in relation to Saga and the independent estimations of rainfall showed in Killen *et al.* (2007), (2) when species ranges of a set of species were estimated using Worldclim and Saga, ranges estimated with Worldclim excluded areas where species are known to inhabit and included other where species definitively do not inhabit. Although the biased pattern of rainfall of Worldclim was already superficially observed by Killen *et al.* (2007), most of the modelling studies after this publication still used Worldclim to model species ranges, and to estimate the impact of climate change over species distributions.

However, niche modelling techniques tend to produce low quality ranges when few records from the species are available. Consequently, manual extrapolations of the ranges, as we did in chapter four with birds, offer a reasonable solution at significantly lower resolutions. We were able to disentangle in detail the diversity-parameter relationships at different scales and for the different components of the bird community (range-restricted and widespread species). The overall relationships and consequently the overall patterns of diversity were overwhelmingly determined by the widespread species. Range-restricted species presented other diversity patterns that are shadowed in general regional and continental analyses. Additionally, since manual extrapolation requires a profound knowledge of species and habitat distributions. It is probable that extrapolating maps for rare or range-restricted species may be challenging.

Finally, we showed that when data is available, niche modelling is a powerful tool to disentangle the historical biogeographic distribution of the seasonally dry tropical forests. Although the seasonally dry tropical forests were modelled to be more extensively distributed in the Bolivian lowlands, colonizing the nowadays Andean fragments of dry forests through the lowlands, individual species were able to colonize this fragments through the highlands by crossing the Central Andes. This may explain the complicate affinity of the fragments of Andean dry forests (the seasonally dry tropical forests in the Andes) that share affinities with several other vegetations of the Andes and the lowlands. Therefore, in order to establish The patterns of colonization of these fragments by species characteristic of the SDTFs in detail, it would be necessary to model a larger set of species from different taxonomic groups and differential dispersal capacities. Finally, in this modelling study we assumed that climate changes homogeneously across the study area. If climate varied differentially across the study area, this may imply that the historical process

we found may be biased. Although it is probable that climate changes were not totally homogeneous, these local differences were due to a temporal displacement of the changes. The information from past climates still fragmentary and more research is needed in this area to increase the resolution of historical biogeographic studies.

6.3 References

- Araujo, M.B. & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, 33, 1677-1688.
- Bach, K., M. Kessler & J. Gonzales (1999) Caracterización preliminar de los bosques deciduos andinos de Bolivia en base a grupos indicadores botánicos. *Ecología en Bolivia* 32: 7-22.
- Bhattarai, K.R., Vetaas, O. R. & Grytnes, J. A. (2004) Fern species richness along a central Himalayan elevational gradient, Nepal. *Journal of Biogeography*, 31, 389-400.
- Bickford, S. A & Laffan, S. W. (2006) Multi-extent analysis of the relationship between pteridophyte species richness and climate. *Global Ecology and Biogeography*, 15, 588-601.
- Elith, J., Grahani, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachertti-Pereira, R., Schapshire, R.E. Soberón, J., Williams, S., Wisz, M.S., & Zimmermann N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Francis, A.P. & Currie, D.J. (2003) A globally consistent richness climate relationship for angiosperms. *American Naturalist*, 161, 523-536.
- Freitag, S., Hobson, C., Biggs, H. C. & Van Jaarsveld, A. S. (1998) Testing for potential survey bias: the effect of roads urban areas and nature reserves on Southern African mammal data set. *Animal Conservation*, 1, 119-127.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, 297, 1548-1551.
- Jetz, W., Rahbek, C. & Colwell, R.K. (2004) The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters*, 7, 1180-1191.
- Hawkins, B.A., Porter, E.E. & Diniz-Filho, J.A.F. (2003) Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, 84, 1608-1623.
- Karst, J., Gilbert, B. & Lechowicz, M. J. (2005) Fern community assembly: the role of chance and the environment at local and intermediate scales. *Ecology*, 86, 2473-2486.
- Herzog, S.K. and Kessler, M. (2002) Biogeography and composition of dry forest bird communities in Bolivia. *Journal of Ornithology*, 143, 171-204.

- Kessler, M. (2000) Elevational gradients in species richness and endemism of selected plant groups in central Bolivian Andes. *Plant ecology*, 149, 181-193.
- Kessler M. (2001) Pteridophyte species richness in Andean forest in Bolivia. *Biodiversity and Conservation*, 10, 1473-1495.
- Kessler, M. & Helme, N. (1999) Floristic diversity and phytogeography of the central Tuichi Valley, an isolated dry forest locality in the Bolivian Andes. *Candollea*, 54, 341-366.
- Kessler M., Parris, B.S. & Kessler, E. (2001a) A comparison of the tropical montane Pteridophyte floras of mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. *Journal of Biogeography*, 28, 611-622.
- Kessler, M. Herzog, S. K., Fjeldså, J. & Bach, K. (2001b) Species richness and endemism of plant and bird communities along two gradients of elevation, humidity and land use in the Bolivian Andes. *Diversity and distributions*, 7, 61-77.
- Killeen, T.J., Douglas, M., Consiglio, T., Jørgensen P. M. & Mejia, J. (2007) Dry spots and wet spots in the Andean hotspot. *Journal of Biogeography*, 34, 1357-1373.
- Kluge, J. & Kessler, M. (2006) Fern endemism and its correlates: contribution from an elevational transect in Costa Rica. *Diversity and Distributions*, 12, 535-545.
- Kreft, H., Sommer J. H. & Barthlott, W. (2006) The significance of geographic range for spatial diversity patterns in Neotropical palms. *Ecography*, 29, 21-30.
- Lauer, W. (1986) Klimatische Grundzüge der Höhenstufung tropischer Gebirge. *Tagungsber Wiss. Abh 40 Dt Geographentag Innsbruck*, 1975, 76-90.
- Loiselle, B.A., Jørgensen, P.,M., Consiglio, T., Jiménez, I., Blake, J.G., Lohmann, L.G. & Montiel, O.M. (2007) Predicting species distributions from herbarium collections: does climate bias in collection sampling influence model outcomes?. *Journal of Biogeography*, 35, 105-116.
- Luoto, M., Virkkala, R. & Heikkinen, R. K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global ecology and biogeography*, 16, 34-42.
- Mayle, F.E. (2004) Assessment of the neotropical regugia hypothesis in the light of palaeoecological data and vegetation model simulations. *Journal of Quaternary Sciences*, 19, 713-720.
- Mayle, F.E. And Beerling, D.J. (2004) Late quaternary changes in amazonian ecosystems and their implications for global carbon cycling. *Palaeogeography, palaeoclimatology, Palaeoecology*, 214, 11-25.

- McCain, C.M. (2005) Elevational gradients in diversity of small mammals. *Ecology*, 86, 366–372.
- McCain, C.M. (2007) Area and mammalian elevational diversity. *Ecology*, 88, 76-86.
- McCain, C.M. (2009) Global Analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18, 346-360.
- Mourguiart, P. & Ledru, M.P. (2003) Last glacial maximum in an Andean cloud forest environment (Eastern Cordillera, Bolivia). *Geology*, 31, (3), 195-198.
- Pöyry, J., Luoto, M., Heikkinen, R.K., Saarinen, K. (2008) Species traits are associated with the quality of bioclimatic models. *Global Ecology and Biogeography*, 17, 403-414.
- Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L.V.B. & Graves, G.R. (2007) Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society, Series B*, 274, 165-174.
- Reddy, S. & Dávalos, L. M. (2003) Geographical sampling bias and its implications for conservation priorities in Africa. *Journal of Biogeography*, 30, 1719-1727.
- Tsoar, A., Allouche, O., Steinitz, O., Rotem, D., Kadmon, R. (2007) A comparative evaluation of presence only methods for modelling species distribution. *Diversity and Distributions*, 14, 397-405.
- Wood, J.R.I. (2006) Inter-Andean dry forests of Bolivia- Floristic affinities and patterns of endemism: Insights from Acanthaceae, Asclepiaceae and Labiateae. *Neotropical Savannas and seasonally dry forests* (ed. by T. Pennington, G.P. Lewis and J.A. Ratter), pp. 235-256. Taylor and Francis group. United States of America.

Appendices

A1. Appendix A1 to Chapter 4

Coefficients of determination (R^2 -values) of the relationship of bird species richness to seven explanatory variables. The spatial autoregressive analyses (SAR) were initially performed for the entire study region, then by regions (I to V) and by elevational belts. We also calculated the R^2 values for each quartile. The 1st quartile represent the geographically most restricted species, 4th the most widespread species. The highest value in each line is marked in bold and underlined, the second highest is in bold. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

	Area	MinElev	Range Elev	MaxPrec	Range Prec	LatMDE	ElevMDE
Entire study area							
All species	0.01	0.29***	0.01	<u>0.63</u> ***	0.19***	0.47 ***	0.33***
1st quartile	0.07***	0.06*	<u>0.43</u> ***	0.19***	0.30***	0.36 ***	0.02*
2nd quartile	0.08***	0.00	0.27***	0.33 ***	0.27***	<u>0.43</u> ***	0.00
3rd quartile	0.00	0.44***	0.04***	0.52 ***	0.04**	0.23**	<u>0.53</u> ***
4th quartile	0.01	0.70***	0.11***	0.38 ***	0.03	0.12	<u>0.75</u> ***
Regions							
Region I							
All species	0.01	<u>0.76</u> ***	0.01	0.54 ***	0.08*	0.33***	0.48***
1st quartile	0.01*	0.02*	<u>0.29</u> ***	0.07	0.28 ***	0.02	0.08**
2nd quartile	0.04	<u>0.31</u> ***	0.04	0.30 ***	0.14**	0.05	0.05
3rd quartile	0.07	<u>0.77</u> ***	0.11*	0.42***	0.00	0.43***	0.73 ***
4th quartile	0.07	<u>0.79</u> ***	0.08**	0.50***	0.02	0.45***	0.73 ***
Region II							
All species	0.50***	<u>0.77</u> ***	0.09*	0.66 ***	0.00	0.24***	0.65***
1st quartile	0.52 ***	0.11*	<u>0.57</u> ***	0.07*	0.51***	0.20***	0.33***
2nd quartile	0.23***	0.00	<u>0.43</u> ***	0.00	0.42 ***	0.08**	0.11*
3rd quartile	<u>0.85</u> ***	0.71***	0.38***	0.60***	0.17	0.42***	0.82 ***
4th quartile	0.87 ***	0.80***	0.41***	0.62***	0.16**	0.33***	<u>0.89</u> ***
Region III							
All species	0.06	<u>0.69</u> ***	0.00	0.61***	0.49***	0.27***	0.62 ***
1st quartile	0.25***	0.00	0.47 ***	0.06	<u>0.49</u> ***	0.03	0.01
2nd quartile	0.23***	0.01	0.36 ***	0.08*	<u>0.47</u> ***	0.03	0.00
3rd quartile	0.35*	<u>0.88</u> ***	0.125*	0.59***	0.09*	0.27*	0.82 ***
4th quartile	0.46***	<u>0.89</u> ***	0.193*	0.49***	0.05	0.19*	0.83 ***
Region IV							
All species	0.00	0.38 ***	0.00	<u>0.58</u> ***	0.11**	0.03	0.31***
1st quartile	0.12*	0.32	<u>0.45</u> ***	0.00	0.05	0.01	0.40 *
2nd quartile	0.14*	0.11*	<u>0.34</u> *	0.07*	0.04	0.00	0.16
3rd quartile	0.03	<u>0.64</u> ***	0.02	0.57***	0.10*	0.06*	0.60 ***
4th quartile	0.06*	<u>0.85</u> ***	0.14	0.46***	0.02	0.00	0.81 ***

Appendices

Region V							
All species	0.04	0.22**	0.01	0.26**	0.06*	0.07*	0.09*
1st quartile	0.31**	0.34**	0.44**	0.07*	0.05	0.00	0.49***
2nd quartile	0.32**	0.23**	0.43**	0.04	0.08	0.00	0.38**
3rd quartile	0.00	0.52**	0.12*	0.37**	0.02	0.07*	0.35**
4th quartile	0.07*	0.71***	0.36**	0.44**	0.00	0.08*	0.62***
Elevational belts							
< 500							
All species	0.12**	0.03	0.07*	0.43**	0.07*	0.77**	0.01
1st quartile	0.16**	0.00	0.37**	0.56***	0.43**	0.36**	0.08*
2nd quartile	0.15**	0.00	0.20**	0.51**	0.20**	0.50**	0.03
3rd quartile	0.05*	0.17**	0.00	0.18**	0.00	0.78***	0.08*
4th quartile	0.79**	0.31**	0.00	0.14**	0.00	0.68**	0.16**
500 - 1000							
All species	0.04	0.01	0.09*	0.42**	0.03	0.76***	0.02
1st quartile	0.05*	0.03	0.37**	0.68**	<u>0.35**</u>	0.64***	0.00
2nd quartile	0.05*	0.04	0.27*	0.57**	0.18**	0.69***	0.00
3rd quartile	0.02	0.00	0.00	0.21**	0.00	0.71***	0.12**
4th quartile	0.01	0.02	0.00	0.13**	0.00	0.59**	0.22**
1000-1500							
All species	0.44**	0.02	0.02	0.61**	0.19*	0.63***	0.16*
1st quartile	0.74***	0.01	0.33**	0.45**	0.27*	0.59**	0.00
2nd quartile	0.70**	0.00	0.23**	0.59**	0.32**	0.57**	0.03
3rd quartile	0.09*	0.07	0.03	0.41**	0.05	0.34*	0.18**
4th quartile	0.00	0.13	0.12*	0.24**	0.01	0.19*	0.26**
1500 - 2000							
All species	0.28*	0.15*	0.04*	0.34**	0.18*	0.51**	0.13*
1st quartile	0.45**	0.00	0.34**	0.50**	0.41**	0.67**	0.00
2nd quartile	0.48*	0.04	0.31**	0.43**	0.34**	0.55**	0.00
3rd quartile	0.03	0.17*	0.27**	0.02	0.09*	0.00	0.12*
4th quartile	0.01	0.20**	0.20*	0.01	0.07	0.00	0.21*
2000 - 2500							
All species	0.16	0.04	0.29**	0.55***	0.47***	0.29**	0.46***
1st quartile	0.23*	0.01	0.35**	0.70***	0.63***	0.50***	0.33***
2nd quartile	0.24**	0.02	0.37**	0.67***	0.56***	0.39**	0.37***
3rd quartile	0.01	0.08	0.00	0.01	0.00	0.02	0.35***
4th quartile	0.03	0.08	0.01	0.02	0.02	0.07	0.24**
> 2500							
All species	0.02	0.06	0.34***	0.49***	0.51***	0.10*	0.02
1st quartile	0.02	0.00	0.30***	0.47***	0.39***	0.21**	0.00
2nd quartile	0.02	0.04	0.36***	0.47***	0.46***	0.12	0.00
3rd quartile	0.00	0.15	0.19**	0.30**	0.42***	0.00	0.05
4th quartile	0.00	0.18	0.14**	0.18**	0.32***	0.00	0.03

A2. Appendix A2 to Chapter 4

Autoregressive averaged and minimum adequate models (MAM) that better explain the patterns of bird species richness in the eastern slopes of the central Andes, from southern Peru to southern Bolivia.

Models were calculated first for the entire study area and then for each of the five regions.

Variables are arranged according to the value of their standardized coefficient. The standardized coefficient indicates the relative importance of each variable in the models (averaged or the minimum adequate). The most important factor are placed on the top, while the least important is placed at the bottom.

R^2 and the Akaike information criterion (AIC) of the models are showed at the bottom of the models.

Below the minimum adequate models (MAM) are displayed the correspondent R^2 and AIC values. Additional to these values we also show the Moran's I of autocorrelation that exist if non autoregressive models are performed, the level of uncertainty that the MAM is actually the best model (expressed in percentage), and the number of alternative competing models.

REGIONS												
AVERAGED MODELS	All	Coef	Region 1	Coef	Region 2	Coef	Region 3	Coef	Region 4	Coef	Region 5	Coef
	MaxPrec	0.40	MinElev	-0.81	MinElev	-0.51	MinElev	-0.61	MaxPrec	0.61	MinElev	-1.08
	LatMDE	0.39	ElevMDE	-0.17	MaxPrec	0.32	VarPrec	0.53	MinElev	-0.54	ElevMDE	0.69
	MinElev	-0.23	Area	-0.11	ElevMDE	-0.16	VarElev	-0.35	ElevMDE	0.38	Area	-0.43
	VarPrec	-0.20	LatMDE	-0.08	VarElev	0.13	Area	-0.24	LatMDE	0.13	VarElev	-0.31
	VarElev	0.16	MaxPrec	-0.06	VarPrec	-0.12	LatMDE	0.23	VarElev	0.11	VarPrec	0.28
	ElevMDE	-0.15	VarPrec	-0.05	Area	-0.06	ElevMDE	0.13	Area	-0.11	LatMDE	-0.26
	Area	-0.05	VarElev	-0.03	LatMDE	0.06	MaxPrec	-0.08	VarPrec	-0.10	MaxPrec	-0.15
R ²		0.81		0.77		0.80		0.84		0.66		0.55
AIC		4172.598		689.589		1079.575		687.236		785.857		694.934
Minimal Adequate Model (MAM)												
	All	Coef	Region 1	Coef	Region 2	Coef	Region 3	Coef	Region 4	Coef	Region 5	Coef
	MaxPrec	0.40	ElevMDE	0.58	MinElev	-0.57	MinElev	-0.58	MinElev	-0.66	MinElev	-1.13
	LatMDE	0.39	Area	0.10	MaxPrec	0.29	VarPrec	0.52	MaxPrec	0.63	ElevMDE	0.81
	MinElev	-0.23	MinElev	0.01			VarElev	-0.34	ElevMDE	0.44	Area	-0.41
	VarPrec	-0.20				Area	-0.25	LatMDE	0.10	VarElev	VarElev	-0.33
	ElevMDE	-0.15				LatMDE	0.22			VarPrec	LatMDE	0.28
	VarElev	0.15										-0.22
	Area	0.05										
R ²		0.87		0.83		0.84		0.88		0.70		0.57
AIC		4041.151		665.999		1049.756		666.419		770.449		691.001
Moran's I		0.59		0.52		0.39		0.29		0.51		0.55
Certidumbre %		91		14		10		55		9		24
N° competing Models		1		3		6		1		12		3

A3. Appendix A3 to Chapter 4

Autoregressive averaged and minimum adequate models (MAM) that better explain the patterns of bird species richness in the eastern slopes of the central Andes by elevational belts, from southern Peru to southern Bolivia.

Models were calculated for each of the six elevational belts detailed in the methodology section of chapter four.

Variables are arranged according to the value of their standardized coefficient. The standardized coefficient indicates the relative importance of each variable in the models (averaged or the minimum adequate). The most important factor is placed on the top, while the least important at the bottom.

R^2 and the Akaike information criterion (AIC) of the models are showed at the bottom of the models.

Below the minimum adequate models (MAM) are displayed the correspondent R^2 and AIC values. Additional to these values we also show the Moran's I of autocorrelation that exist if non autoregressive models are performed, the level of uncertainty that the MAM is actually the best model (expressed in percentage), and the number of alternative competing models.

Elevational Belts												
AVERAGED MODELS	< 500		500-1000		1000-1500		1500-2000		2000-2500		>2500	
	All	Coef	All	Coef	All	Coef	All	Coef	All	Coef	All	Coef
LatMDE	LatMDE	0.59	MaxPrec	0.89	MaxPrec	0.79	LatMDE	0.49	ElevMDE	0.42	MaxPrec	0.22
MaxPrec	MaxPrec	0.50	VarPrec	-0.68	VarPrec	-0.44	Area	-0.38	MaxPrec	0.30	VarPrec	0.16
VarPrec	VarPrec	-0.47	LatMDE	0.35	Area	-0.30	ElevMDE	-0.24	Area	-0.28	Area	-0.16
VarElev	VarElev	0.38	Elev int	0.34	ElevMDE	-0.17	VarPrec	-0.19	LatMDE	0.25	LatMDE	0.13
ElevMDE	ElevMDE	-0.06	ElevMDE	-0.08	LatMDE	0.15	VarElev	-0.06	VarPrec	0.08	VarElev	0.09
Area	Area	-0.01	Area	0.00	Elev int	0.06	MaxPrec	0.00	VarElev	0.03	ElevMDE	-0.01
R ²		0.87		0.93		0.86		0.65		0.74		0.45
AIC		1202.035		861.305		620.326		480.507		309.916		576.617
Minimal Adequate Model (MAM)												
	< 500	Coef	All	Coef	All	Coef	All	Coef	All	Coef	All	Coef
LatMDE	LatMDE	0.59	MaxPrec	0.89	MaxPrec	0.74	LatMDE	0.52	ElevMDE	-0.45	MaxPrec	0.26
MaxPrec	MaxPrec	0.50	VarPrec	-0.68	VarPrec	-0.39	Area	-0.38	Area	-0.30	Area	-0.17
VarPrec	VarPrec	-0.45	LatMDE	0.34	Area	-0.27	ElevMDE	-0.23	LatMDE	0.28		
VarElev	VarElev	0.37	Elev int	0.34	ElevMDE	-0.17	VarPrec	-0.15				
ElevMDE	ElevMDE	-0.06	ElevMDE	-0.084	LatMDE	0.142						
R ²		0.91		0.95		0.89		0.90		0.87		0.78
AIC		1153.22		828.49		603.69		426.08		283.62		520.91
Moran's I		0.56		0.38		0.54		0.44		0.20		0.82
Certidumbre %		46		74		39		31		29		9
N° competing Models		2		1		2		4		3		8

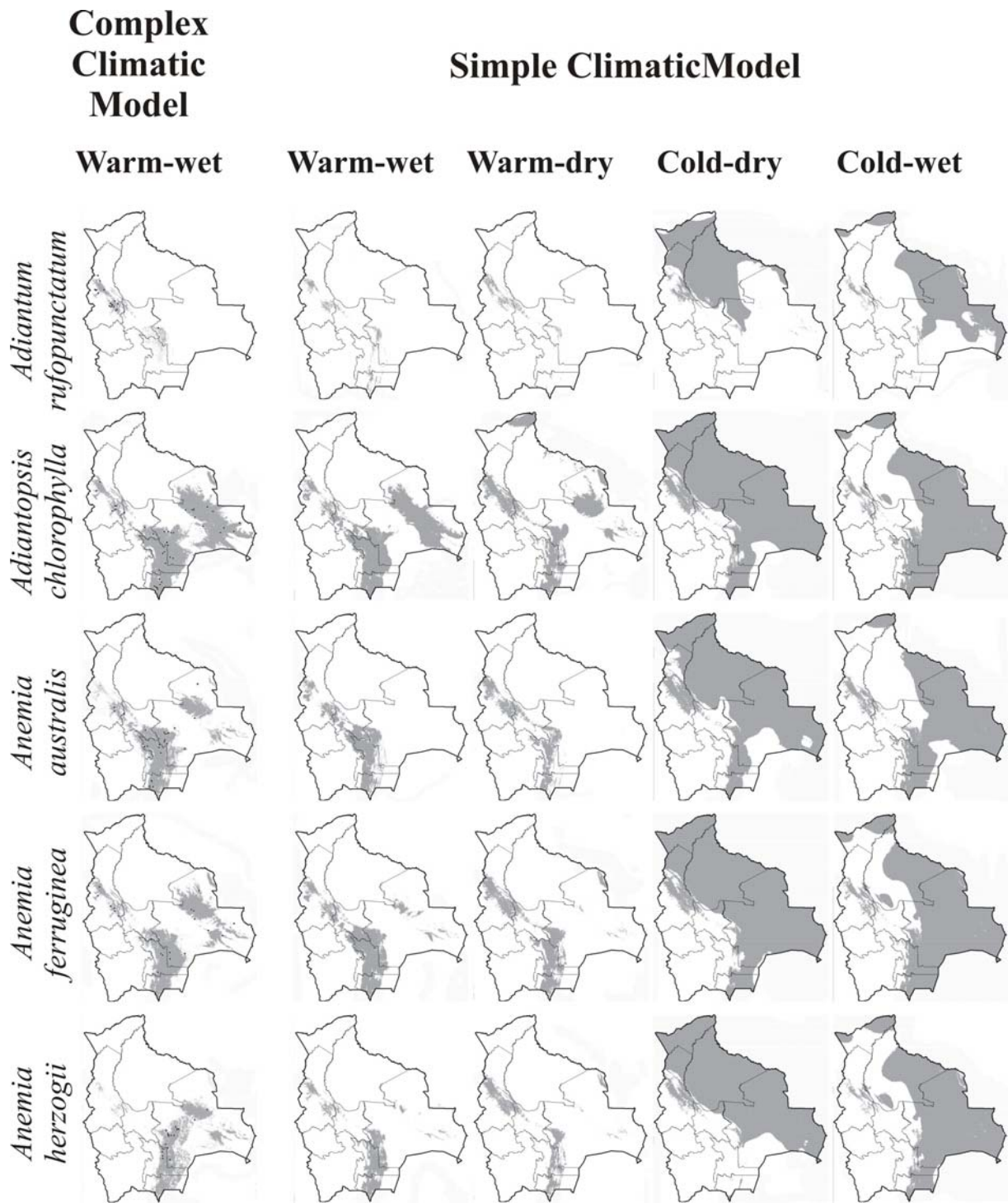
A4. Appendix 1 to chapter 5

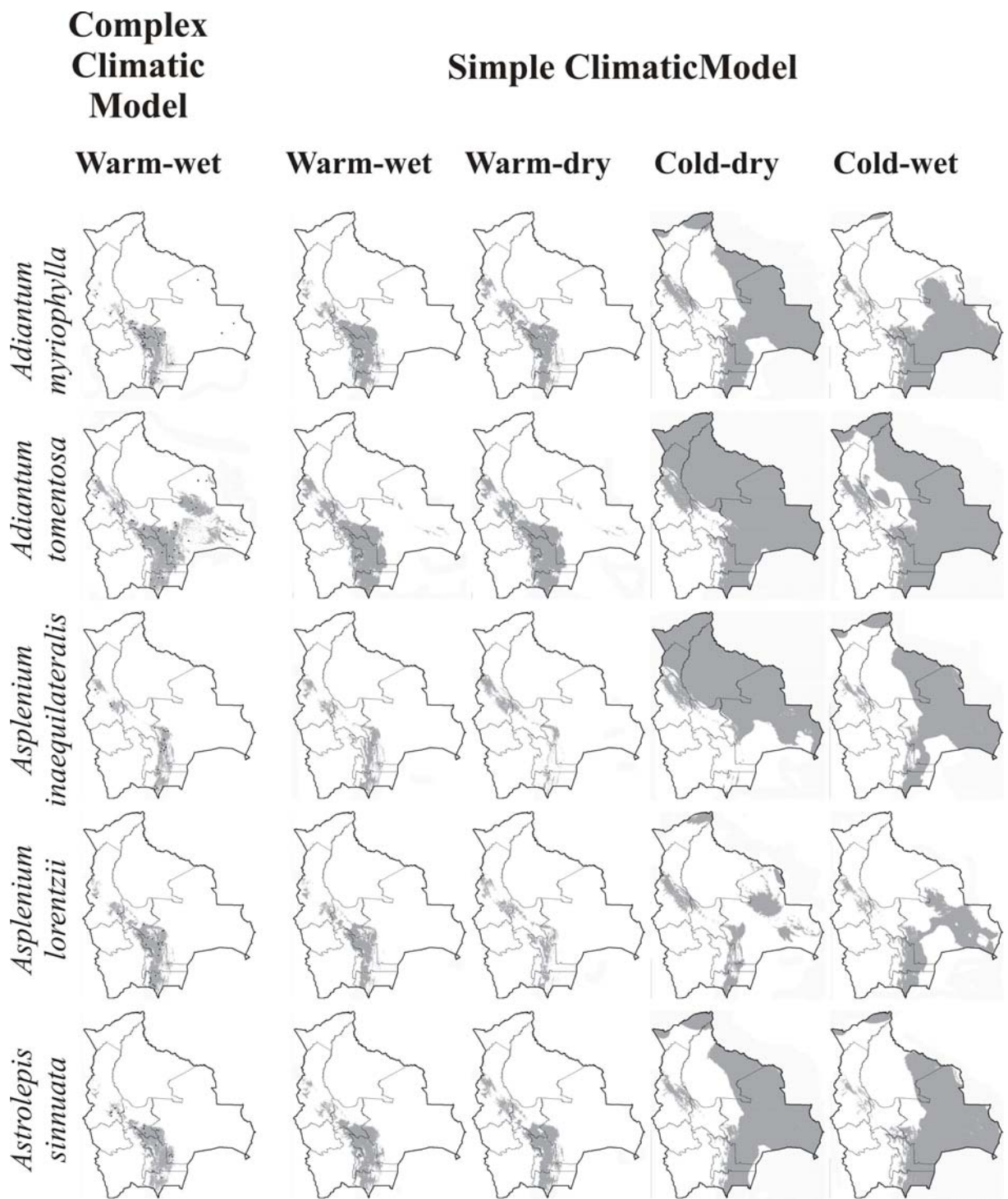
AUC values obtained when species ranges were modelled with the complex and simple climatic model.

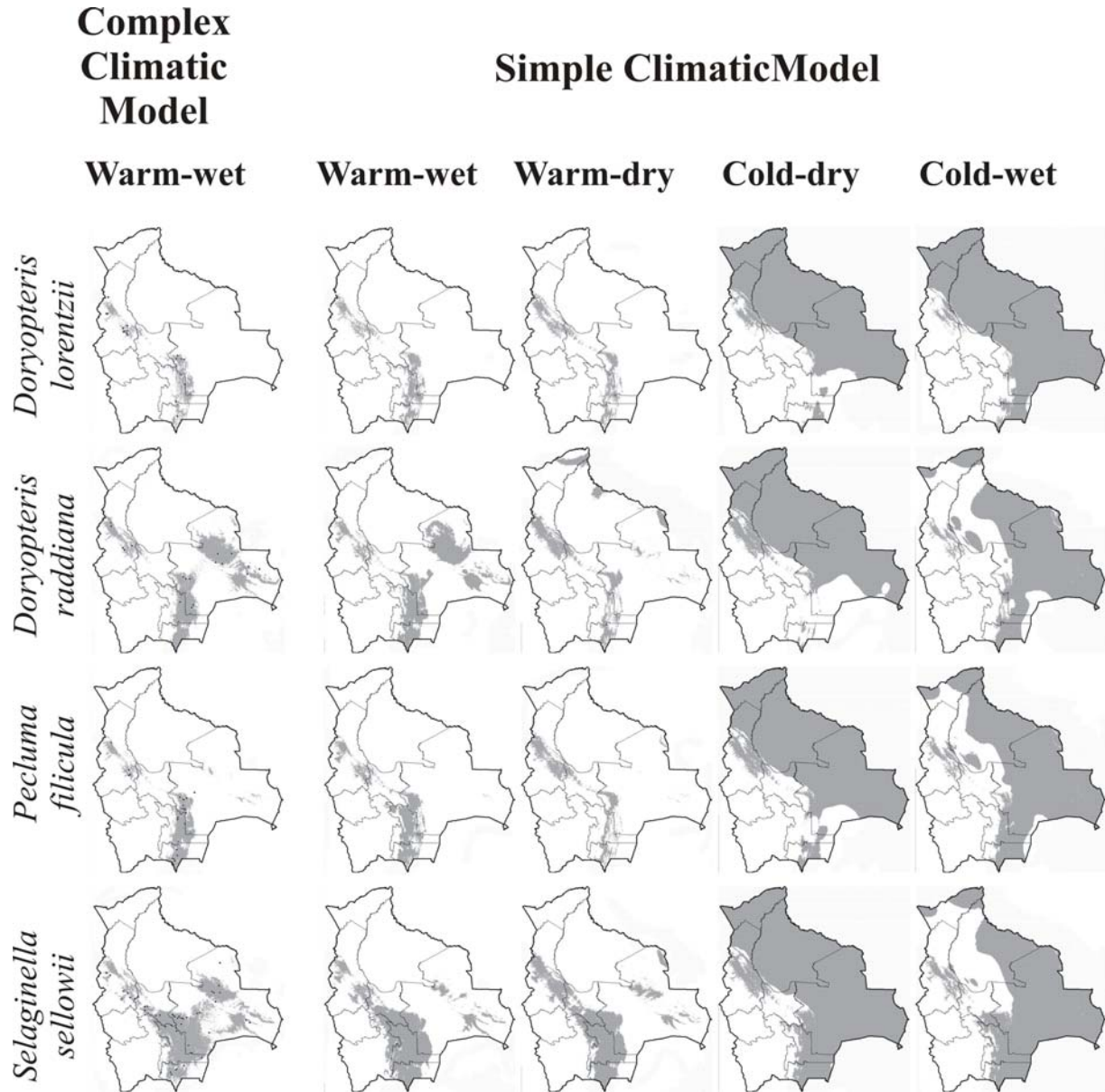
		Complex climatic model	Simple climatic model	Difference
		Warm-Wet	Warm-Wet	
Species				
	Birds			
<i>Arremon flavirostris</i>		0.951	0.895	0.056
<i>Cranioleuca henricae</i>		0.993	0.992	0.001
<i>Cranioleuca pyrrhophia</i>		0.954	0.919	0.034
<i>Formicivora melanoleuca</i>		0.935	0.831	0.103
<i>Myiopsitta luchsii</i>		0.996	0.996	0.000
<i>Myiopsitta monachus</i>		0.961	0.930	0.031
<i>Nystalus maculatus</i>		0.931	0.863	0.068
<i>Polioptila dumicola</i>		0.919	0.879	0.039
<i>Poospiza boliviana</i>		0.990	0.986	0.004
<i>Serpophaga munda</i>		0.940	0.865	0.076
<i>Stigmara budyoides</i>		0.963	0.935	0.028
<i>Suiriri suiriri</i>		0.891	0.836	0.055
<i>Synallaxis scutata</i>		0.953	0.895	0.058
	Ferns			
<i>Adiantum rufopunctatum</i>		0.998	0.995	0.003
<i>Adiantopsis chlorophylla</i>		0.968	0.974	-0.005
<i>Anemia australis</i>		0.977	0.972	0.005
<i>Anemia ferruginea</i>		0.963	0.968	-0.005
<i>Anemia herzogii</i>		0.989	0.981	0.008
<i>Anemia myriophylla</i>		0.966	0.966	0.000
<i>Anemia tomentosa</i>		0.936	0.942	-0.006
<i>Asplenium inaequillateralis</i>		0.992	0.995	-0.003
<i>Asplenium lorentzii</i>		0.991	0.994	-0.003
<i>Astrolepis sinuata</i>		0.989	0.989	0.000
<i>Doryopteris lorentzii</i>		0.996	0.995	0.001
<i>Doryopteris raddiana</i>		0.962	0.968	-0.006
<i>Pecluma filicula</i>		0.987	0.991	-0.004
<i>Selaginella sellowii</i>		0.960	0.966	-0.006
Mean				0.020

A5. Appendix 2 to chapter 5

Maps of fern species estimated with the complex climatic model (warm-wet) and the simple climatic model (under the four climatic scenarios: warm-wet, warm-dry, cold-dry and cold-wet).







Maps of bird species estimated with the complex climatic model (warm-wet) and the simple climatic model (under the four climatic scenarios: warm-wet, warm-dry, cold-dry and cold-wet)

