GÖTTINGER ZENTRUM
FÜR BIODIVERSITÄTSFORSCHUNG UND ÖKOLOGIE
– GÖTTINGEN CENTRE FOR BIODIVERSITY AND ECOLOGY –

Diversity and Ecological patterns of Bolivian deciduous forests

Dissertation zur Erlangung des Doktorgrades der
Mathematisch-Naturwissenschaftlichen Fakultäten der
Georg-August-Universität Göttingen

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Cusco, Peru

Göttingen, December, 2008

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Tag der mündlichen Prüfung:

Para Susana y Matti

*Three is a magic number,
Yes it is, it's a magic number.
Somewhere in the ancient, mystic trinity
You get three as a magic number.*

*The past and the present and the future.
Faith and Hope and Charity,
The heart and the brain and the body
Give you three as a magic number.*

*A man and a woman had a little baby,
Yes, they did.
And there were three in the family,
And that's a magic number.*

Bob Dorough

Abstract

This dissertation focuses on two aspects of tropical forests. In the first part I report patterns of plant diversity at local scales in a central Bolivian Andean foothill seasonal forest and evaluate the importance that different life-forms have on contributing to overall diversity. Total vascular plant species surveys from three 1-ha plots yielded species richness values from 297 species and 22360 individuals per hectare to 382 species and 31670 individuals per hectare. Epiphytes, and other non-woody life-forms, contributed to significant numbers of overall species richness and abundances. Comparing the observed patterns with other inventories in the Neotropics, showed that the studied Central Bolivian forest plots were similar in total species richness to other dry deciduous and humid montane forests, but less rich than most Amazonian forests. Nonetheless, species diversity of lianas, terrestrial herbs and especially epiphytes proved to be of equal or higher species richness than most other neotropical forest inventories from which data are available. These results highlight the significant contribution that non-woody life-forms in Andean forest ecosystems have toward overall species diversity and abundances, and show that we need an increased inventory effort of these life-forms in order to obtain accurate information useful for the characterization of vegetation types, for the mapping of diversity hotspots and ultimately for conservation purposes.

However, since woody species (especially trees above a certain diameter cut-off) are still extensively used to characterise tropical vegetation, I also present a detailed account of the tree inventories on the same three one-hectare plots in central Bolivia. Inter-plot comparisons showed remarkable variation eventhough the vegetation of the study area was assigned by a recent classification to one single vegetation unit.

Few species were shared among plots and most (between 34 % and 50 %) were locally rare, i.e., species with only one or two individuals per plot. The species richness values we found in this study were similar to other tree inventories in comparable seasonal forest ecosystems in Bolivia. Species and familial composition, however, were contrastingly different, except for the well-known fact that Leguminosae is the numerically most important family in seasonally dry neotropical forest ecosystems.

In the second part of this dissertation I focus on (meta-)community patterns and address questions about the processes and mechanisms that might have produced them. I first present results from a study at a large geographical scale, covering the whole of Bolivia. Using presence-absence data for species of Acanthaceae, Bromeliaceae, Cactaceae and Pteridophyta occurring in Bolivian Andean seasonally dry forest islands I explore patterns in the beta-diversity of these plant groups. Floristic comparisons among the islands showed that Acanthaceae and Bromeliaceae, showed coincident biogeographic patterns, suggesting two disjunct seasonally dry forest groups in Andean Bolivia: one including all small isolated northern dry valleys and another including all southern valleys with connections to the lowland seasonal forests in southern and western Bolivia. Furthermore, the analysis of the variation of the beta-diversity of each studied plant group suggested an important role of group-specific dispersal characteristic. Thus, plant groups with species that have seed dispersal restricted to short distances (a few tens of metres as in Acanthaceae and Bromeliaceae) were geographically structured. In contrast, groups with species without long-distance dispersal limitation and with a potentially ubiquitous distribution (as in pteridophyta, due to their wind-dispersal system), were rather more influenced by local environmental site conditions suggesting post-dispersal restricting mechanisms (e.g., during establishment).

In a second study, I used the information from the total vascular plant inventories in central Bolivian forest referred to above to evaluate if and to what extent a suite of environmental factors influenced plant species richness and community composition at the local scale. The results suggested a major role of selected above-

and below-ground environmental gradients in determining small scale patterns of species richness and community composition, of the whole forest community and also of each life-form group (terrestrial herbs, epiphytes, shrubs, lianas and trees). Different life-forms, however, were related to different combinations of these factors and the latter were not able to account for a significant fraction of the variation in the data. In conclusion, spatial and environmental factors (individually or acting together) can be invoked to explain species richness and community composition patterns in the tropical deciduous forests of Bolivia. The importance of each one appears to depend on the geographical scale at which the study is made and on the ecological characteristics of the study group. However, neither of them are able to explain all the variation in the data, and novel methods that include evolutionary information of each taxon need to be explored.

Acknowledgements

Foremost I would like to thank Michael Kessler, my advisor, who back in 2003, way before I officially embarked in this odyssey accepted to have me as a PhD student. He helped to write a research proposal which was successful in being funded by the German Academic Exchange Service. I thank him for giving me the freedom to pursue my own interests in this dissertation, for all his advice, time and friendship he has given me during this time.

I thank Professor Erwin Bergmeier and Professor Teja Tscharntke, for accepting to be members of my dissertation committee.

Whilst in Santa Cruz, Bolivia, I acknowledge logistical support from Sebastian Herzog, D. Soto for local advice and M. Saldias and F. Mamani (both of the Museo de Historia Natural Noel Kempff Mercado) for working space at the USZ herbarium.

Many people have contributed to the wealth of information that was obtained from the Los Volcanes plots, either by being directly involved in the establishment and surveying of the plots, by curating and identifying botanical specimens, by providing relevant data and literature, and a large etcetera. The production of vascular plant inventories is indeed a mammoth task! I would especially like to thank Sebastian Herzog (who together with Michael Kessler developed the idea of a research project at Los Volcanes), Jasmin Lendzion and Ernest Hennig for selflessly sharing unpublished data and information from their own research at Los Volcanes.

I wish to thank Professor W. Zucchini for encouraging me to keep on using R at a time when I was still struggling to understand it and for introducing me to writing this dissertation in L^AT_EX.

I acknowledge the financial support from the German Academic Exchange Service (DAAD) in form of a Scholarship during all my period in Göttingen. Especially Rosa Nagel, my personal contact in Bonn, for solving most of my personal and study-related inquiries and problems. A WWF Prince Bernhard Scholarship for Nature Conservation allowed me to successfully finish this dissertation.

This dissertation, however, has not only been an academic matter. Thus, on a personal note I would like to mention a few more people. Michael and Elke Kessler helped us so much during Susana's pregnancy and during our early months of parenthood! I do not know what would have been of our little family without your advice. A big thank you to both of you! And it has been a real pleasure to get to know the Gonzales-Toivonen family.

At the Institute I would like to thank my room-mates for great discussions (on topics ranging from generalized linear models, Akaike weights and neutral ecological theory to Half-Life, Käsebrötchen and Simón Bolívar) and a nice working atmosphere: Stefan, Jörn and Rodrigo.

Este viaje comenzó hace mucho tiempo gracias al apoyo, incentivos y sacrificios de mis padres Esther y Carlos. Gracias!

Finally, but most importantly, I have to thank my wife Susana and little Matti. These last years have been a tough test for all of us. I thanks both of you so much for all your patience and continuous encouragement. I love you!

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Chapter 1

Plant diversity and ecological patterns in the Neotropics - A general introduction

”The primeval forests of the equatorial zone are grand and overwhelming by their vastness, and by the display of a force of development and vigour of growth rarely or never witnessed in temperate climates. Among their best distinguishing features are the variety of forms and species which everywhere meet and grow side by side, and the extent to which parasites, epiphytes, and creepers fill up every available station with peculiar modes of life. If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions, and colours are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct. He may at length, perhaps, meet with a second specimen half a mile off, or may fail altogether, till on another occasion he stumbles on one by accident. (Alfred R. Wallace, *Tropical Nature, and other Essays*, 1878, p. 65)”

1.1 Research Focus 1: Neotropical and Bolivian plant diversity

The introductory quote from Alfred Russel Wallace (Wallace, 1878) is an excellent and short summary of the enormous plant diversity of tropical forests. Even after

so many years since he wrote the essay to which it belongs, we are still struggling to document tropical diversity patterns and to understand the processes that have caused them.

It is a well-known fact that the tropics contain an overwhelmingly large number of the world's living species. Prance (1977) and Raven (1988) estimated that approximately two-thirds of all species of flowering plants (angiosperms) are native to the tropics. In turn, Thomas (1999) estimated that approximately 90 000 species of flowering plants are present in the tropics of the Western Hemisphere (Neotropics), which include southern Mexico, Central America, most of South America, and the West Indies.

Nevertheless, plant diversity within the Neotropics is unevenly distributed. Major hotspots of diversity have been recognized in the Brazilian Atlantic forests, the Caribbean, the Tropical Andes and Amazonia (Myers *et al.*, 2000; Kier *et al.*, 2005). Traditionally, however, most public and academic attention has been towards tropical rain forests (Henderson *et al.*, 1991), resulting in a large body of research projects and findings. The other side of the coin is that little is known about the diversity patterns in the neglected regions. A recent study to find out the geographical distribution of ecological research in the tropics revealed that considerable scientific productivity has emerged from few biological field stations like the those of the Organization for Tropical Studies (OTS) in Costa Rica or the Smithsonian Tropical Research Institute (STRI) in Panama (Stocks *et al.*, 2008), all located in (Central American!) rain forests.

Bolivia, a landlocked country of ca. 1 million square kilometres located in central South America, is considered as one of the seventeen megadiverse countries of the world (i.e., rich in biological diversity and associated traditional knowledge) (Ibisch & Merida, 2003). But as recently as the late 1980s, knowledge of the Bolivian flora was considered depauperate (Solomon, 1989). The situation has changed considerably in recent years and much progress has been done in documenting plant diversity in Bolivia (Jørgensen *et al.*, 2006), with currently more than 12700 species of vascular

plants (including ferns) and 1500 species of bryophytes recorded. Nevertheless, much work still needs to be done and, as in so many other tropical countries of the world (e.g., Laurance & Peres, 2006), natural habitat fragmentation and destruction are major threats to the long-term conservation of the Bolivian forests (Killeen *et al.*, 2007).

Thus, two major issues arise from the preceding paragraphs. First, there is a need for additional basic information from plant inventories, especially in non-Amazonian ecosystems. Second, there is an urgent need for the rapid and accurate production of this information. In the first two chapters of this dissertation I address this issues by showing results from quantitative plant inventories in the semi-deciduous forests of the eastern Andean foothills of Santa Cruz department.

1.2 Research Focus 2: Community assembly in biodiverse tropical forests

The causes of extremely high species diversity in (apparently) homogeneous and small areas of tropical forests has been a debate dating several decades back. Alfred Russel Wallace commented on this subject in the second half of the 19th century by saying:

”In the equable equatorial zone there is no ... struggle against climate. Every form of vegetation has become alike adapted to its genial heat and ample moisture, which has probably changed little even throughout geological periods; and the never-ceasing struggle for existence between the various species in the same area has resulted in a nice balance of organic forces, which gives the advantage, now to one, now to another, species, and prevents any one type of vegetation from monopolising territory to the exclusion of the rest. The same general causes have led to the filling up of every place in nature with some specially adapted form. Thus we find a forest of smaller trees adapted to grow in the shade of greater trees. Thus we find every tree supporting numerous other forms of vegetation, and some so crowded with epiphytes of

various kinds that their forks and horizontal branches are veritable gardens. Creeping ferns and arums run up the smoothest trunks; an immense variety of climbers hang in tangled masses from the branches and mount over the highest tree-tops. Orchids, bromelias, arums, and ferns grow from every boss and crevice, and cover the fallen and decaying trunks with a graceful drape. Even these parasites have their own parasitical growth, their leaves often supporting an abundance of minute creeping mosses and hepaticae. But the uniformity of climate which has led to this rich luxuriance and endless variety of vegetation is also the cause of a monotony that in time becomes oppressive. (Alfred R. Wallace, *Tropical Nature, and other Essays*, 1878, p. 66-67)”

Since then, much has been written about determinants of species diversity (e.g., Huston, 1994; Rosenzweig, 1995). Brown & Lomolino (1998) stated that the restriction of a taxon to a particular geographic range is consequence of both historical events and ecological processes. Both can help to explain how the taxon became confined to its present range and, by using modern molecular tools, we are now able to make inferences about the geographic origin, spread and contraction of the studied taxon (e.g., Hughes & Eastwood, 2006; Saslis-Lagoudakis *et al.*, 2008). Likewise, we are now able to assess the relative influence of historical events such as the formation of barriers by drifting continents, changing sea levels, glaciation and mountain uplift, but also by other taxon-specific events, such as stochastic long-distance dispersal and extinction of small populations, going on at the same time. Further, geologic, climatic, and other environmental changes caused the expansion and contraction of the ranges of many different species, allowing new combinations of organisms to come into contact and to limit each others distributions through biotic interactions (Brown & Lomolino, 1998).

Willis & Whittaker (2002) noted that species diversity is scale-dependant (either in terms of geography or time) and that the processes that best account for patterns of biodiversity at one scale are not necessarily the same at another, smaller or greater scale (Table 1.1). At very large, global scales, plant species richness seems to be primarily determined by potential evapotranspiration, the number of wet days

per year, and measurements of topographical and habitat heterogeneity (Kreft & Jetz, 2007). At smaller, continental to regional scales annual rainfall and rainfall seasonality seem to be the most important variables for explaining woody plant species richness in Neotropical forests (Clinebell *et al.*, 1995). At much smaller and even local scales, soil properties (such as P availability, Al toxicity, drainage, water-holding capacity, and availability of K, Ca, and Mg) have been proposed as being most likely to influence the diversity of tropical forests (Sollins, 1998). Endemic species richness, on the other hand, is thought to be a product of either refugia from past extinctions or of high rates of ecological and allopatric speciation (Brown & Lomolino, 1998; Stattersfield *et al.*, 1998; Jetz & Rahbek, 2002; Orme *et al.*, 2005). One of the few studies examining patterns of endemic plant species found that, at a global scale, latitude and area were the strongest independent predictors (Cowling & Samways, 1995).

In a similar vein, much research has been done to identify the most important processes that shape community composition in exceptionally species-rich tropical forests (e.g., Gentry, 1988; Valencia *et al.*, 1994). Two diametrically opposite theories, each with several variants, are currently invoked as the main mechanisms driving the assembly of (meta-) communities: (i) niche theories and (ii) the recently re-postulated neutral theories. The classical Hutchinsonian niche theory proposes that the niche is the sum of all the environmental factors biologically relevant to a certain species (such as soil nutrients, light or water availability) and thus that a given species occupies a N-dimensional environmental hypervolume that represents the range of conditions where it could exist (i.e., Hutchinsonian niche concept = a species' environmental needs). The alternative niche theory of Elton proposed that the niche of a species represented its functional role within the food-chain (Eltonian niche concept = a species' impacts on the environment). A recent synthesis of niche theory by Chase & Leibold (2003), termed 'contemporary niche theory', unified both older niche concepts resulting in the following revised definition: "niche is the joint description of the environmental conditions that allow a species to satisfy

Table 1.1: A hierarchical framework for processes influencing biodiversity (Willis & Whittaker, 2002)

Spatial scale	Scale of species richness	Environmental variables predominantly responsible	Temporal scale at which processes occur
Local scale	Species richness within communities, within habitat patches	Fine-scale biotic and abiotic interactions, e.g., habitat structure, disturbance by fires, storms	Processes occurring on time scales of ~1-100 years
Landscape scale	Species richness between communities; turnover of species within a landscape	Soils, altitude, peninsula effect	Processes occurring on time scales of ~100-1000 years
Regional scale	Species richness of large geographical areas within continents	Radiation budget and water availability, area, latitude	Processes occurring over the last 10,000 years, i.e., since end of last glacial
Continental scale	Differences in species lineages and richness across continents	Aridification events, glacial/interglacial cycles of the Quaternary, mountain-building episodes, e.g., Tertiary uplift of the Andes	Processes occurring over the last 1-10 million years
Global scale	Differences reflected in the biogeographical realms, e.g., distribution of mammal families between continents	Continental plate movements, sea-level change	Processes occurring over the last 10-100 million years

its minimum requirements so that the birth rate of a local population is equal to or greater than its death rate along with the set of per capita effects of that species on these environmental conditions". Similar renewed and more complex visions of the classical niche concept that incorporate the effects of dispersal, competition and stochasticity have been offered by Tilman (2004) and Kneitel & Chase (2004).

Neutral community models (Bell, 2000; Hubbell, 2001; Chave *et al.*, 2002) have received increased attention after Hubbell's formulation of the '*Unified Neutral Theory of Biodiversity and Biogeography*' (Hubbell, 2001). In essence, Hubbell postulated that all individuals in a community are ecologically equivalent or neutral, i.e., "that trophically similar species are, at least to a first approximation, demographically identical on a per capita basis in terms of their vital rates, of birth, death, dispersal - and even speciation" (Hubbell, 2001). This theory invoked dispersal and stochastic demographic processes to explain coexistence and assembly in highly diverse tropical forests, but it was the concept of ecological equivalence, so contrary to our own perceptions and current understanding of the differential ecological requirements of species and individuals (Tilman, 1982), that sparked a multitude of studies (Holoak & Loreau, 2006). The bulk of these studies emphasized a major role of environmental heterogeneity at all spatial scales (Table 1.2), and in response to this, Hubbell and his colleagues redefined the equivalence concept a few times, going from treating initially all individuals in a community as completely equivalent in all requirements (Hubbell, 2001), to more restricted versions (Volkov *et al.*, 2003, 2005; Hubbell, 2005). It is in the last two years, however, that evidence for the non-equivalence of species in a community, and thus for a major role of niche-based processes, has been accumulating. Two recently published studies stand particularly out, as they used very different and novel approaches to test the niche-neutral community assembly mechanism. The first study by Kelly *et al.* (2008) paired woody species from the dry forests in Chamela, Mexico, based on evolutionary similarity. They used resolved terminal dichotomies and distinguished between congeneric pairs and non-congeneric pairs (within the same family) to analyse fractional abundance

patterns (cf. Sugihara *et al.*, 2003). They argued, that, if neutral processes are operating (and species are ecologically equivalent), then the fractional abundance patterns of congeneric and non-congeneric species pairs should be indistinguishable from that of pairs chosen at random from the Chamela community. What they found was in fact the opposite, and very much at odds with ecological equivalence assumptions, as there appears to be some regulation mechanism within populations of congeneric species pairs that is not present in randomly selected or non-congeneric pairs. The second study by Kraft *et al.* (2008) tested if tree distribution of 1089 woody species at the 0.04 ha scale in a 25 ha plot of tropical rain forest in Yasuni (Ecuador) were distributed randomly with respect to six critical functional traits (e.g., specific leaf area, seed mass) essential for woody plant strategy. They compared each trait's measures of central tendency (mean) and variability (range, standard deviation and variance) to a null model to infer the occurrence of either environmental filtering and/or classical niche differentiation and found strong evidence for both processes.

It follows from the previous paragraphs that much progress has been achieved in our understanding of community assembly in hyper-diverse tropical forests. Hubbell's theory has certainly been an important driver of novel ecological research, but nevertheless, many questions remain unanswered. For example, for logistical and practical reasons most of the studies have focused on few groups of plant species (Table 1.2), while none has used all plant species within a community. Are the mechanisms of community assembly that operate within one homogeneous forest community the same and of similar importance for different life-forms (e.g., trees, terrestrial herbs, epiphytes) or guilds? What happens at larger regional scales? Are metacommunity assembly mechanisms influenced by taxon-specific characteristics? Within this state-of-the-art of the mechanisms invoked to explain species coexistence and community assembly, I test the relative importance of niche and dispersal (neutral) processes in shaping metacommunities in dry forest islands of Andean Bolivia (Chapter 4). Further, I separately evaluate the relationships between environmental factors

and community composition for several life-forms at the hectare-scale to assess if gradients in the former influence the latter (Chapter 5).

1.3 Specific Research objectives

This dissertation is a compilation of three publications and one manuscript and divided into two major parts corresponding to the two research areas presented above. The first two chapters address issues of Neotropical and Bolivian plant diversity (Research Focus 1), while the latter two address community assembly mechanisms in Bolivian forests at large and local geographical scales (Research Focus 2):

- i To document and compare the total vascular plant diversity in three different central Bolivian sub-Andean forest types (deciduous, semi-deciduous and evergreen) (Chapter 2).
- ii To quantitatively assess the relative importance that different life-form groups and taxa (families, genera and species) have on species richness and community composition of a sub-Andean tropical forest (Chapter 2).
- iii To compare total vascular plant and life-form diversity in Central Bolivian forest plots with similar studies in the neotropical region (Chapters 2 & 3).
- iv To study the phytogeography of the tree flora of these Central Bolivian forest plots (Chapter 3).
- v To assess biogeographical patterns of seasonally dry forests in Andean Bolivia (Chapter 4).
- vi To explore the relative importance of environmental or neutral mechanisms to explain species coexistence in tropical forests at large regional and local spacial scales (Chapters 4 & 5).

Table 1.2: A selection of studies evaluating factors that influence community composition in Neotropical forests

Scale	Size of study area	Region	Study group	Number of plots or transects sampled	Variables nantly responsible	predomi-	Authors
Local	1 - 7 ha	Ecuador, Peru	Trees, pteridophytes, Melastomataceae	0.1 - 1 ha plots (trees), 5x500 m transects (pte, melast)	Soil Ca, Mg		Ruokolainen <i>et al.</i> (2007)
	1 ha	Peru	Palms, trees, Melastomataceae, pteridophytes	25 400 m ² plots	Soil type, drainage		Vormisto <i>et al.</i> (2000)
	1 ha	Ecuador	Pteridophytes, herbs, palms	20 100 m ² plots	Edaphic, topographic		Poulsen <i>et al.</i> (2006)
Small	25 ha	Brazil	Woody species	5 30x75 m plots	Canopy gaps, soil chemistry-topography		Oliveira-Filho <i>et al.</i> (1998)
	25 ha	Mexico	Trees	8 30x100 m transects	Water availability		Balvanera <i>et al.</i> (2002)
	25 and 50 ha	Panama	Woody species	1 50 ha, 2 25 ha plots	Edaphic		John <i>et al.</i> (2007)
	< 1 km ²	Mexico	Trees, tree seedlings and saplings	9 2x50 m transects	Gaps, slope, disturbance (trees), edaphic (seedlings and saplings)		Vargas-Rodriguez <i>et al.</i> (2005)
Landscape	5.73 km ²	Costa Rica	Trees, palms	1179 0.01 ha plots	Edaphic		Clark <i>et al.</i> (1999)
	5 km ²	Costa Rica	Pteridophytes	1042 0.01 ha plots	Soil chemistry, spatial structure		Jones <i>et al.</i> (2008)
	16 km ²	Panama	Herbs and woody plants	350 0.01 ha (herbs) and 0.09 ha (woody) plots	Spatial, environmental-historical factors		Svenning <i>et al.</i> (2004)
Regional	500 km ²	Panama, Ecuador, Peru	Trees	64 1 ha plots	Spatially structured environment		Duivenvoorden <i>et al.</i> (2002)
	> 1000 km ²	Peru	Trees, pteridophytes, Melastomataceae	8 0.125 - 0.16 ha plots	Soil chemistry		Ruokolainen <i>et al.</i> (1997)
	500 km ²	Ecuador	Pteridophytes, Melastomataceae	27 5x500 m transects	Soil chemistry		Tuomisto <i>et al.</i> (2003)

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Chapter 2

Non-woody life-form contribution to vascular plant species richness in a tropical American forest

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Plant Ecology (In press)

DOI: [dx.doi.org/10.1007/s11258-008-9505-z](https://doi.org/10.1007/s11258-008-9505-z)

Abstract

We provide total vascular plant species counts for three 1-ha plots in deciduous, semi-deciduous, and evergreen forests in central Bolivia. Species richness ranged from 297 species and 22360 individuals per hectare in the dry deciduous forest to 382 species and 31670 individuals per hectare in the evergreen forest. Orchidaceae, Pteridophyta and Leguminosae were among the most species-rich major plant groups in each plot and *Peperomia* (Piperaceae), *Pleurothallis* (Orchidaceae) and *Tillandsia* (Bromeliaceae), all epiphytes, were the most species-rich genera. This dominance of a few but very diverse and/or widespread taxa contrasted with the low compositional similarity between plots. In a neotropical context, these Central Bolivian forest plots are similar in total species richness to other dry deciduous and humid montane forests, but less rich than most Amazonian forests. Nevertheless, lianas, terrestrial herbs and especially epiphytes proved to be of equal or higher species richness than most other neotropical forest inventories from which data are available. We therefore highlight the importance of non-woody life-forms (especially epiphytes and terrestrial herbs) in Andean foothill forest ecosystems in terms of species richness and numbers of individuals, representing in some cases nearly 50% of the species and more than 75% of the individuals. These figures stress the need for an increased inventory effort on non-woody plant groups in order to accurately direct conservation actions.

Keywords: alpha diversity, Andean foothills forest ecosystem, life-form diversity, non-woody plants, total species inventory

2.1 Introduction

Statements about the diversity of plant species in forest ecosystems are usually based on results from vegetation inventories that are mostly restricted to a certain plant subgroup. Woody species, usually trees and shrubs with diameter at breast

height of ≥ 1 cm (e.g., the STRI 50 ha plots, Condit 1995), ≥ 2.5 cm (e.g., 0.1 ha transects, Gentry 1982) and ≥ 10 cm (e.g., Gentry 1988; Valencia *et al.* 1994; Smith & Killeen 1998), are the most commonly studied plant groups. In contrast, herbs (e.g., Poulsen & Balslev 1991; Poulsen & Nielsen 1995), lianas (Perez-Salicrup *et al.*, 2001; Mascaro *et al.*, 2004) and epiphytes (Ingram *et al.*, 1996; Arévalo & Betancur, 2004; Benavides *et al.*, 2005; Krömer *et al.*, 2005) are less commonly used to characterize the diversity of vegetation types. These non-woody life-forms, however, have been shown to be of importance in the few assessments of tropical plant alpha diversity in which all vascular plants were counted (Whitmore *et al.*, 1985; Gentry & Dodson, 1987; Duivenvoorden, 1994; Balslev *et al.*, 1998; Galeano *et al.*, 1998; Langenberger *et al.*, 2006). The scarcity of such studies can be attributed to the difficulties associated with identification of more (and usually less well-known) plant groups (restricting inventories to some life-form groups in the tropics is already a huge identification task) and the difficulty of collecting epiphyte specimens from the forest canopy. Whitmore and colleagues have undertaken the most comprehensive study of vascular plants to date in a Costa Rican rain forest. To accomplish their task of inventorying all species (including non-vascular plants), destructive sampling of a 10 m x 10 m plot was required (Whitmore *et al.*, 1985). The few full tropical plant inventories performed to date have focused on a single and homogeneous vegetation type, usually tropical lowland rain forests. Although some of these studies (e.g., Duivenvoorden 1994; Langenberger *et al.* 2006) inventoried plots and transects along edaphic and physiographic gradients, only two have inventoried and compared different vegetation types using a uniform sampling methodology throughout. (Alvarez, 2003) reported total vascular plant counts in three 0.1 ha plots in Amazonian, Chocoan and Andean forests in Colombia. This study, however, was not published formally and epiphytes in the Amazonian plot were not sampled, restricting the total vascular plant count to the Chocó and Andean forest only. The other study by (Gentry & Dodson, 1987) compared three 0.1-ha plots in wet, moist and dry forests in Ecuador. The lack of standardized inventory methods hampers the quantitative

comparison between both of these studies. The use of florulas could be an option to compare different forests (e.g., Gentry 1990), but the size of the areas studied and collection intensities are not uniform (Tobler *et al.*, 2007). We chose Central Bolivia, a region where four major biomes occur in close proximity to each other (humid and moist vegetation from Amazonia, seasonal subtropical lowland vegetation from the Chaco, subtropical highland vegetation from the Andes and seasonal vegetation of the Chiquitanía (Ibisch *et al.*, 2003)) as our study region. We established within this complex biogeographic setting three permanent 1-ha plots. We used a uniform methodology along a humidity gradient from deciduous to evergreen forest, inventorying all vascular plants present. Our main objective was to quantitatively assess the relative importance of different life-form groups and taxa within the different vegetation types we surveyed and to compare our results with similar studies in the neotropical region.

2.2 Methods

2.2.1 Study area

The study was carried out at the Refugio Los Volcanes in Santa Cruz, Bolivia. Los Volcanes is a private reserve of approximately 300 ha. It is located about 18°06' S and 63°36' E and is adjacent to the southern border of Amboró National Park, directly on the transition from the humid inner tropics to the seasonally dry subtropics (Fig.2.1a). The substrate of the study area consists primarily of red sandstone and locally of loamy sedimentary rocks (lutite). These red sandstones form cliffs several hundred meters high and are intersected by narrow valleys providing the area with dramatic scenery. Annual precipitation is about 1200-1500 mm, with most of the rainfall from October/November to March/April, but with high temporal variability. The general vegetation of the area has been classified as 'subhumid to humid deciduous forest of southeastern Amboró'(Navarro *et al.*, 1996), and is usually found at 900-1100 masl. Among the dominant tree species are *Aspidosperma cylindrocarpon*

Figure 2.1: Main vegetation types and plot shape and location in the study area. (a) Aerial photograph of the Refugio Los Volcanes area in central Bolivia, inset showing map of Bolivia and location of study area, (b) schematic representation of the major vegetation types and geographical characteristics of the area, showing plot locations and orientation (ss: sandstone, ca: cleared area, LV Station: Los Volcanes Research Station), and (c) shape of inventory plots, where numbers denote subplots.

(Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela lilloi* (Meliaceae), *Gallesia integrifolia* (Phytolaccaceae), *Pachystroma longifolium* (Euphorbiaceae), *Pogonopus tubulosus* (Rubiaceae) and *Tabebuia lapacho* (Bignoniaceae) (Navarro *et al.*, 1996). Locally, however, vegetation types are determined by differences in topography, aspect, and precipitation regime that lead to ecologically relevant differences in water availability within the study area. Consequently, the dominant zonal vegetation is semi-deciduous forest (about 30-50% deciduous trees) mainly found on shaded south-facing slopes. Steep, sunny and north-facing slopes are occupied by deciduous forest (70-90% deciduous trees), whereas flat, shaded valleys with groundwater supply support evergreen forest (10-20% deciduous trees) (Fig.2.1b).

2.2.2 Vegetation sampling

A permanent plot of 1 ha was established in each forest type (deciduous, semi-deciduous and evergreen) between 2002-2003. Each plot was subdivided into 25 adjacent 20 m x 20 m subplots. Plots were laid out in such a way as to include

only the forest type under study, avoiding other forest types, young secondary vegetation, and non-forest vegetation (e.g., rock outcrops). Thus, our plots are not the traditional square 100 m x 100 m inventory plots, but have rather irregular shapes (Fig.2.1b). All vascular plants in each plot were inventoried between 2002 and 2004, mainly in the season following the summer rains (i.e., May to August). J. Lendzion inventoried herbs, shrub and tree seedlings, E.I. Hennig epiphytes, D. Hoffmann lianas and V. Cardona, D. Soto and S.K. Herzog woody plants. For the herb inventories, we recorded all species with stem diameter below 1 cm. Additionally, we recorded all Cactaceae, Bromeliaceae and Costaceae below 1 m height and epiphytes on fallen branches. For lianas, we recorded all individuals, including Araceae, with a diameter of > 1 cm at 1.3 m above soil level. All epiphytes were observed and counted. Collections of epiphytes were made either with a clipper pole or with the help of rope climbing techniques. Binoculars were used to aid identification when they were too inaccessible to collect. Finally, we recorded all woody plants, excluding lianas, with diameter at breast height (dbh) of > 1 cm. Voucher specimens of all species were collected for later determination and are deposited at USZ (Santa Cruz) and LPB (La Paz), with a small subset of samples at the Göttingen Herbarium (GOET) (herbarium acronyms follow Holmgren & Holmgren, 1998). Several sterile specimens could not be fully identified and were sorted into morphospecies. The final stage of data production was completed at USZ (by R. Linares-Palomino) by cross-checking all collected vouchers in order to unify morphospecies delimitations.

2.2.3 Data Analysis

We used a conservative approach in calculating species numbers by lumping highly similar morphospecies into one group instead of considering them as several distinct species. The herb inventory, which included life-forms other than herbaceous plants, was split into terrestrial herbs, tree seedlings, shrub seedlings and epiphytes. Thus, terrestrial herbs formed a life-form group by itself in subsequent analyses. The other three subgroups were cross-referenced with the tree, shrub

and epiphyte inventories, and merged accordingly. We follow the TROPICOS and Flora of Bolivia online databases for nomenclatural purposes (both available at <http://mobot.mobot.org/W3T/Search/vast.html> and <http://www.efloras.org/>, respectively). Despite much progress in the understanding of the phylogeny of extant ferns, familial composition and relationships are still unsatisfactorily solved (Smith *et al.*, 2006; Schüttpelz & Pryer, 2007). We therefore refrained from assigning our collections to families and treated all ferns and fern allies as a single taxon Pteridophyta. We computed species accumulation curves based on the 20 m x 20 m subplots using EstimateS (Colwell, 2005). Similarity between forest plots was evaluated by subtracting the Bray-Curtis distance between two forest plots from unity. Pair-wise Bray-Curtis distances (DBC) were calculated in the vegan package for R (Oksanen *et al.*, 2008; R Development Core Team, 2008) using presence/absence data by $DBC = 2a/(2a+b+c)$, where a: total number of species present in both forest plots, b: number of species present only in the first forest plot, c: number of species present only in the second forest plot (Magurran, 2004). In order to compare the species richness of the Los Volcanes plots with that of other forests in the Neotropics, we searched for other published full plant, epiphyte, liana, terrestrial herb and tree/woody plant inventories (Appendix 1) and plotted species accumulation curves for each forest type at Los Volcanes against the species richness data of the other studies.

2.3 Results

2.3.1 Taxonomic Diversity

We recorded 80352 individual plants belonging to 670 species (including morphospecies) on the three plots (Appendix 2). We were able to completely identify 52% of our collections to species level (341 species), an additional 25% could be assigned to genus (172 morphospecies) and 14% to family (95 morphospecies). Nine percent (62 morphospecies) could not be assigned to a family or lower taxon. The most

Table 2.1: Number of families, genera and species of three 1-ha plots in Santa Cruz, Central Bolivia (A: angiosperm, P: pteridophytes). Life-form composition values show the number of species assigned to each plant group.

	Total from the three forest plots			Deciduous forest plot			Semi-deciduous forest plot			Evergreen forest plot		
	A	P	Total	A	P	Total	A	P	Total	A	P	Total
Families	80	12	92	55	5	60	64	8	72	65	10	75
Genera	245	28	273	149	13	162	168	17	185	166	24	190
Species	617	53	670	279	18	297	353	29	382	337	44	381
life-form												
Epiphyte	142			67			80			109		
Hemiepiphyte	9			1			4			8		
Liana	153			64			86			44		
Shrub	97			45			49			57		
Tree, liana	1			1			-			1		
Tree, shrub	39			17			16			20		
Terrestrial herb	79			30			42			57		
Tree	148			71			105			84		
Other	1			-			-			1		
Parasite	1			1			-			-		

species-rich plots were in the evergreen and semi-deciduous forest, both of which had an almost identical number of species (381 and 382, respectively). The deciduous forest had 297 species. Of the 273 genera, most were recorded in the evergreen and semi-deciduous forest (190 and 185, respectively) compared to 162 genera in the deciduous forest. Of the 92 families, 75 were found in the evergreen, 72 in the semi-deciduous and 60 in the deciduous forest. The contribution of ferns and lycophytes ("pteridophytes") to species richness was higher in the evergreen forest than in the two other forest types (Table 2.1).

Of the ten most species-rich families, seven were shared between all three plots, although with different ranking within each plot (Table 2.2). Taking all three plots together, the most species-rich families were Orchidaceae, pteridophytes, Leguminosae and Bignoniaceae. Orchidaceae, a family containing mostly epiphytic species, was by far the most species-rich in all plots. Pteridophytes, composed mostly of ground herbs, ranked second in the evergreen and semi-deciduous, and fourth in the deciduous forest. Leguminosae, which was mainly composed of woody species in our plots, decreased in importance from the deciduous (second) to the evergreen forest (fourth). Absolute species numbers were similar in the evergreen forest and higher in the semi-deciduous forest as compared to the deciduous forest. Bignoniaceae (a family including liana, shrub and tree species), the third most important family in the

deciduous forest, was the fourth most important family in the semi-deciduous forest (again with a higher species number), but was ranked only eighth in the evergreen forest. Only two other families were important in terms of species numbers and these were shared by two forest types: Apocynaceae (mostly trees) present in the deciduous and semi-deciduous forest and Rubiaceae (shrubs and trees) present in the semi-deciduous and evergreen forest. In contrast to families, only five species-rich genera were common to all three forest plots (*Peperomia*, *Pleurothallis*, *Tillandsia*, *Acalypha* and *Eugenia*). Of these, the three most species-rich genera were *Peperomia*, *Tillandsia* and *Pleurothallis*, although ranking varied between forests plots (Table 2.2).

Two species of *Tillandsia* had the highest numbers of individuals on all three plots (Table 2.2): *T. bryoides* had highest numbers in the deciduous forest, whereas *T. tenuifolia* had most individuals in the semi-deciduous and evergreen forests. The ten species with highest number of individuals in the deciduous forest included epiphytes and terrestrial herbs (three species each) and shrubs and trees (two species each). The contribution of non-woody plants increased in the semi-deciduous forest, including epiphytes (four species), terrestrial herbs (three species) and one species each of shrubs, trees and lianas. Non-woody plant contribution was highest in the evergreen forest with six species of epiphyte, two species of terrestrial herb and one hemiepiphyte species dominating. Only one shrub species was included among the top ten.

Table 2.2: Most species-rich families and genera (number of species in parentheses) and most abundant species (number of individuals in parentheses). The dominant life-form is indicated for families and individual species (e=epiphytic, h=terrestrial herb, s=shrub, t=tree, l=liana). Nomenclature follows TROPICOS and the Flora of Bolivia online databases (mobot.mobot.org/W3T/Search/vast.html and www.efloras.org/, respectively).

Deciduous	Semi-deciduous	Evergreen	Total
Families (Pteridophyta is considered as one family)			
Orchidaceae (34, e)	Orchidaceae (45, e)	Orchidaceae (60, e)	Orchidaceae (85, e)
Leguminosae (20, t)	Pteridophyta (29, h)	Pteridophyta (44, h)	Pteridophyta (53, h)
Bignoniaceae (19)	Leguminosae (26, t)	Bromeliaceae (20, e)	Leguminosae (39, t)
Pteridophyta (18, h)	Bignoniaceae (23)	Leguminosae (20, t)	Bignoniaceae (35)
Bromeliaceae (16, e)	Rubiaceae (16)	Piperaceae (16)	Bromeliaceae (26, e)
Euphorbiaceae (13, s,t)	Bromeliaceae (15, e)	Rubiaceae (14)	Rubiaceae (23)
Piperaceae (12)	Sapindaceae (13)	Euphorbiaceae (12, s,t)	Euphorbiaceae (21, s,t)
Acanthaceae (12, h)	Euphorbiaceae (12, s,t)	Araceae (9, e)	Acanthaceae (20, h)
Apocynaceae (10, t)	Myrtaceae (9, s,t)	Moraceae (9, t)	Apocynaceae (18, t)
Myrtaceae (9, s,t)	Piperaceae (11)	Asteraceae (8)	Piperaceae (18)
Cactaceae (9)		Bignoniaceae (8)	
		Lauraceae (8, t)	
		Melastomataceae (8)	
Genera			
<i>Peperomia</i> (9)	<i>Tillandsia</i> (11)	<i>Tillandsia</i> (13)	<i>Tillandsia</i> (15)
<i>Pleurothallis</i> (8)	<i>Peperomia</i> (8)	<i>Pleurothallis</i> (10)	<i>Pleurothallis</i> (14)
<i>Tillandsia</i> (7)	<i>Pleurothallis</i> (8)	<i>Peperomia</i> (9)	<i>Peperomia</i> (11)
<i>Acalypha</i> (6)	<i>Forsteronia</i> (6)	<i>Epidendrum</i> (8)	<i>Acalypha</i> (10)
<i>Forsteronia</i> (6)	<i>Acalypha</i> (5)	<i>Acalypha</i> (7)	<i>Epidendrum</i> (9)
<i>Acacia</i> (5)	<i>Eugenia</i> (5)	<i>Begonia</i> (7)	<i>Forsteronia</i> (9)
<i>Eugenia</i> (5)	<i>Machaerium</i> (5)	<i>Piper</i> (7)	<i>Begonia</i> (8)
<i>Machaerium</i> (4)	<i>Philodendron</i> (5)	<i>Eugenia</i> (6)	<i>Eugenia</i> (7)
<i>Epidendrum</i> (4)	<i>Psychotria</i> (5)	<i>Ficus</i> (6)	<i>Ficus</i> (7)
<i>Philodendron</i> (4)	<i>Randia</i> (5)	<i>Thelypteris</i> (6)	<i>Piper</i> (7)
<i>Ruellia</i> (4)	<i>Thelypteris</i> (5)		
Species (number of individuals)			
<i>Tillandsia bryoides</i> (2410, e)	<i>Tillandsia tenuifolia</i> (2008, e)	<i>Tillandsia tenuifolia</i> (5576, e)	<i>Tillandsia tenuifolia</i> (8059, e)
<i>Peperomia comarapana</i> (1654, h)	<i>Piper callosum</i> (1132, s)	<i>Racinaea parviflora</i> (1879, e)	<i>Peperomia tetragona</i> (2549, e)
<i>Rinorea ovalifolia</i> (1534, s)	<i>Paspalum humboldtianum</i> (972, h)	<i>Vriesia mazontiana</i> (1745, e)	<i>Racinaea parviflora</i> (2426, e)
<i>Peltiveria alliacea</i> (1056, s)	<i>Olyra fasciculata</i> (932, h)	<i>Blechnum occidentale</i> (1058, h)	<i>Tillandsia bryoides</i> (2410, e)
<i>Peperomia tetragona</i> (1012, e)	<i>Peperomia tetraphylla</i> (925, e)	<i>Philodendron campoportianum</i> (837, e)	<i>Piper callosum</i> (2156, s)
<i>Olyra fasciculata</i> (986, h)	<i>Adiantum tetraphyllum</i> (800, h)	<i>Thelypteris dentata</i> (803, h)	<i>Vriesia mazontiana</i> (2120, e)
<i>Acacia polyphylla</i> (802, t)	<i>Peperomia tetragona</i> (789, e)	<i>Peperomia tetragona</i> (748, e)	<i>Olyra fasciculata</i> (2012, h)
<i>Commelina erecta</i> (777, h)	<i>Philodendron campoportianum</i> (745, e)	<i>Lomagramma guianensis</i> (741)	<i>Philodendron campoportianum</i> (2007, e)
<i>Tillandsia streptocarpa</i> (755, e)	<i>Piper amalago</i> (681, t)	<i>Peperomia acrona</i> (735, e)	<i>Peperomia comarapana</i> (1678, h)
<i>Coursetia brachyrhachis</i> (522, t)	<i>Herreria montevidensis</i> (521, l)	<i>Piper callosum</i> (692, s)	<i>Commelina erecta</i> (1574, h)

2.3.2 Life-form composition

In the deciduous forest, trees, epiphytes and lianas contributed similar species numbers (22-24% of the total (Table 2.1). In the semi-deciduous forest, trees were slightly more species-rich than other life-forms (28%), followed by lianas (23%) and epiphytes (21%). The most species-rich life-form in the evergreen forest was epiphytes (29%), followed by trees (22%), shrubs (15%), and ground herbs (15%) (Table 2.1). Woody plants (including lianas and shrubs) contributed to approximately 66%, 57% and 54% of total species richness in the deciduous, semi-deciduous and evergreen forest plots, respectively. There was a highly significant statistical difference between the proportions of life-forms in the three studied forest types (G-test, $G = 28.34$, $p = 0.0004$, $df = 8$). Pearson correlation analyses among life-form richness patterns within each forest plot showed that tree species richness patterns were positively and significantly correlated with total plant species richness: deciduous forest $r = 0.67$ ($p = 0.0002$), semi-deciduous forest $r = 0.54$ ($p = 0.0049$), evergreen forest $r = 0.59$ ($p = 0.0021$). No other significant correlation could be detected between trees and other life-forms, except with shrubs in the semi-deciduous forest ($r = 0.51$, $p = 0.01$) and with lianas in the evergreen forest ($r = 0.53$, $p = 0.0064$). Apart from trees, lianas were the only other life-form that showed similar levels of positive and significant correlations with total plant species richness across the three plots: deciduous forest $r = 0.63$ ($p = 0.0007$), semi-deciduous forest $r = 0.66$ ($p = 0.0003$), evergreen forest $r = 0.54$ ($p = 0.0051$). Other positive significant correlations were detected in the evergreen forest plot between total plant species richness and epiphytes ($r = 0.60$, $p = 0.0017$) and terrestrial herbs ($r = 0.69$, $p = 0.0001$).

2.3.3 Similarity among plots

Similarity among plots was 0.46 between deciduous and semi-deciduous (155 species shared), 0.37 between deciduous and evergreen (125 species shared) and 0.57 between semi-deciduous and evergreen (216 species shared). We recorded 106 species

occurring in all three plots. 123 species were recorded only in the deciduous plot, 117 only in the semi deciduous plot and 146 only in the evergreen forest plot.

2.4 Discussion

2.4.1 Plot shape and its influence on species richness estimations

Spatial distribution patterns of plant species in tropical forests are influenced by niche assembly and/or random dispersal assembly processes acting at both local and landscape scales (Chave, 2004; Gaston & Chown, 2005; John *et al.*, 2007), resulting in mostly clumped distributions (e.g., Condit *et al.*, 2000). Within this scenario, plot shape has been documented to influence estimates of species richness, i.e., longer and narrower rectangular plots are prone to capture more species than square plots of similar area (Condit *et al.*, 1996; Laurance *et al.*, 1998). The differences, however, were found to be small and statistically non-significant in a study comparing tree species richness in 100 m x 100 m square plots versus 40 m x 250 m rectangular plots in Central Amazonia (Laurance *et al.*, 1998). Given the patchy and fragmented nature of the deciduous and evergreen forests in our study area, it was impossible to survey the vegetation types in traditional square or rectangular plots. Rather, we tried to survey as environmentally homogeneous an area as possible, leading to our irregular plot shape design. There is little doubt that plot shape has influenced our results, especially those of the evergreen forest plot. The extent of this influence, however, seems to be small, since the species accumulation curves for all vascular plants together and for individual life-forms significantly decrease or level off when the hectare is completely surveyed, suggesting that sampling was representative in all three forest types.

2.4.2 Alpha diversity and plant density at Los Volcanes

Additional plant surveys across the entire Los Volcanes reserve (aprox. 300 ha) have documented 65 species of pteridophytes (M. Kessler, unpub. data), of which

53 (82%) were recorded in the plots. The corresponding figures are 83% for Acanthaceae, 90% for Araceae, 84% for Bromeliaceae, and 92% for Cactaceae. If these groups are considered to be representative of the total flora, then our plots contain roughly 80% - 90% of the vascular plant flora of Los Volcanes reserve, which would then be estimated to be around 740 - 840 species, corresponding to about 6.4% - 7.2% of the Bolivian vascular plant flora (estimated at 11600 species, Jørgensen *et al.*, 2006). Species that were not encountered in the plots are either forest species that are patchily distributed, or non-forest species occurring on sandstone walls of the area, secondary vegetation on landslides, rock falls, or along streams. The impressive number of individuals of *T. tenuifolia* and *T. bryoides* in the Los Volcanes plots is not unique to these forests. Both have been documented as the characteristic and dominant species of some seasonal forests of Central and Southern Bolivia (Navarro, 2001). Likewise, Bonnet (2006) and Bonnet *et al.* (2008) reported high densities and wide regional distribution for *T. tenuifolia* in Paraná, Brazil. They attributed the success of this species in humid and seasonal semi-deciduous forests to its small size (ca. 25 cm long, Smith & Downs, 1977), the presence of plumose wind-dispersed diaspores, CAM metabolism, its atmospheric nutrient acquisition strategy (i.e., species that have no form of absorptive root system, in which the tank habit is lacking and where epidermal trichomes cover the whole shoot system and are entirely responsible for nutrient and water uptake, cf. Griffiths & Smith, 1983) and to the fact that this species usually forms dense monospecific associations with no explicit preference for some position on the phorophyte. Most of these factors are also true for *T. bryoides*, in particular the small size of the plants (usually no longer than 5 cm), their plumose diaspores (Smith & Downs, 1977) and the formation of dense monospecific populations (Navarro, 2001).

2.4.3 Los Volcanes plots in a neotropical context

To our knowledge, there is only one other study (Balslev *et al.*, 1998) that includes an inventory of all vascular plants in one hectare of tropical forest and is therefore

directly comparable to our study (although the mentioned study inventoried trees and shrubs of 1-5 cm dbh only in a 0.49-ha subplot). In the Amazonian terra firme rain forest of Cuyabeno, Ecuador, a perhumid area with 3555 mm of annual rainfall and no dry season, Balslev *et al.* (1998) found 942 species of vascular plants in 88 families. Our plots contained between 297-382 species in 60-75 families per hectare for the three forest types studied. This is clearly much lower than the Cuyabeno plot, but lower rainfall and strong seasonality set the forests at Los Volcanes apart from the Amazonian site. There were further differences in the relative contribution of different life-forms to overall species richness at both sites. At Cuyabeno, trees (which made up 50% of species) were clearly the most species-rich group, distantly followed by epiphytes (making up 18% of species) and shrubs and lianas (both making up 11% of species). At Los Volcanes, trees were the most species-rich life-form in the deciduous and semi-deciduous forest, but contributed only 32% of all species. Epiphytes (including hemiepiphytes) and lianas (23% and 22% in the deciduous forest, 22% and 23% in the semi-deciduous forest, respectively) followed them closely. Shrubs were less important in these forests, contributing 13% and 15% of all species in the deciduous and semi-deciduous forest, respectively, and having percentages only slightly higher than terrestrial herbs (ca. 10%). The most striking difference is in the evergreen forest in which epiphytes (31%) were more species-rich than trees (27%). For a more representative comparison of the Los Volcanes data with other neotropical sites, we constructed species-accumulation curves for Los Volcanes that allowed comparisons with other surveys with plot sizes of up to 1 ha (Fig.2.2). As Los Volcanes is found in a biogeographical transition zone and has high moisture variability between plots, our study plots cannot be easily assigned to any of the usual broad categories used for neotropical forests (lowland humid, montane humid, lowland dry, etc.). We therefore compared our richness counts with data from a wide range of other neotropical forest habitats.

Most inventories in lowland humid forests (mostly in Amazonia) have higher vascular plant, epiphyte, liana, and terrestrial herb counts than any of the plots at

Figure 2.2: Species accumulation curves (sac) for each forest type at Los Volcanes (*D*=deciduous, *SD*= semi-deciduous, *E*=evergreen) against species richness data of: a) vascular plant counts, b) epiphyte inventories, c) liana inventories, d) terrestrial herb inventories and e) woody plant inventories in the Neotropics. Symbols described in the legend apply to the entire figure. Note the different scales of the x and y axes. (Values for individual sites are provided in Appendix 1).

Los Volcanes (Fig.2.2). In contrast, plots inventoried in dry deciduous or humid montane forests have similar levels of species richness (Fig.2.2). For example, vascular plant counts at Los Volcanes are similar to those in the humid mountains of the Carrasco National Park (Ibisch, 1996) and those in the deciduous forest of Capeira and moist forest of Jauneche in Ecuador (Gentry & Dodson, 1987), at least at small plot sizes (Fig.2.2a). Epiphytes are perhaps the best represented group at Los Volcanes. They are more diverse here than a humid forest plot in Ecuador (Jauneche, Gentry & Dodson, 1987)) and at least as diverse as the humid forest plots in French Guyana (Sinamary, Bordenave *et al.*, 1998)), Venezuela (Surumoni, Nieder *et al.*, 2000)) and interestingly also as the Chocoan forests in Caquetá (Colombia, Duivenvoorden, 1994)). They also have higher species richness than other deciduous forests and similar species richness as montane forests (Fig.2.2b). Lianas have similar levels of species richness to several humid forests in Ecuador (Yasuní, Nabe-Nielsen, 2001; Burnham, 2004)), Colombia (Nuqui and Coqui, Galeano *et al.*, 1998)) and Bolivia (Oquiriquia, Perez-Salicrup *et al.*, 2001)). In contrast, the deciduous forest of Capeira in coastal Ecuador (Gentry & Dodson, 1987) has a much higher species richness of lianas in smaller plots (Fig.2.2c). Terrestrial herb counts are similar to other humid forests from Costa Rica (Whitmore *et al.*, 1985), Panama (Royo & Carson, 2005), French Guyana (Bordenave *et al.*, 1998), Colombia (Galeano *et al.*, 1998), Ecuador (Gentry & Dodson, 1987; Poulsen & Balslev, 1991) and Brazil (Costa, 2004). The deciduous forest in Capeira (Gentry & Dodson, 1987) again has a higher count of terrestrial herbs than any plot at Los Volcanes (Fig.2.2d). Tree species richness at Los Volcanes is similar to several other forest types in the Neotropics. If only trees with dbh > 10 cm are considered, the plots at Los Volcanes are similar to other deciduous forests in Bolivia and reach the lower end of species richness of 1-ha plots in humid and montane forests (Fig.2.3). If we compare the overall richness of trees on the Los Volcanes plots (including those with dbh ≤ 10 cm) with several forest types inventoried by A. Gentry (0.1-ha transects using the exploded quadrat method, available at <http://www.mobot.org/MOBOT/research/gentry/transect.shtml>), the

Figure 2.3: Species richness values of woody plants and trees at Los Volcanes (LV) with $dbh \geq 10$ cm compared against species richness data of other woody plant inventories (1 hectare, $dbh \geq 10$ cm) in Bolivia (filled symbols), and all trees inventoried at Los Volcanes compared to species richness data of woody plant inventories (0.1 hectare, $dbh \geq 2.5$ cm) in the Neotropics (empty symbols).

studied plots have higher species richness values than most dry deciduous forests in the Neotropics. They have also values similar to the average species richness of humid montane forests, but only reach the lower end of the species richness values of humid lowland forest (Fig.2.3).

2.4.4 Contribution of non-woody plant groups to overall plant species richness

Non-woody plants, and specifically epiphytes, have been highlighted by Gentry & Dodson (1987) as the most important plant group in terms of species richness and individual numbers in wet tropical rain forests in Ecuador, whereas tree species

with $\text{dbh} \geq 10$ cm were more or less equally well represented in dry, moist and wet forest. In the wet forest sampled by them, 35% of the species and 49% of the individuals were epiphytes. At Los Volcanes, epiphytes (including hemiepiphytes) included ca. 30% of the species and nearly 60% of the individuals in the evergreen forest plot. If terrestrial herbs are included, non-woody life-forms represent 45% of the species and more than 76% of the individuals. In the semi-deciduous and deciduous forest plots, figures are somewhat lower but still impressive. Epiphytes (including hemiepiphytes) comprised 22% and 23% of the species and 36% and 31% of the individuals on the semi-deciduous and deciduous forest plots, respectively. If terrestrial herbs are included, the figures are ca. 32% of the species in both forests and 58% and 52% of the individuals, respectively. Non-woody life-forms showed a consistent pattern across the different forest types and represented an important component of neotropical forests. This is certainly overlooked when plots are only sampled for trees. In contrast, trees with $\text{dbh} \geq 10$ cm represented only 14%, 18% and 16% of the species and 2.4%, 2.5% and 1.7% of the individuals on our deciduous, semi-deciduous and evergreen forest plot, respectively. Despite these facts, species richness and floristic data arising from tree inventories are often used (for want of better and more complete, but also usually more work-intensive, information) to characterise all the surrounding vegetation because they are the major structural element (e.g., ter Steege *et al.*, 2000a; La Torre-Cuadros *et al.*, 2007). While this may be enough to identify the major forest types, and indeed some studies in tropical forests do confirmed a positive correlation between the richness of the woody component of a forests and its accompanying non-woody component (e.g., Webb *et al.*, 1967), there is also evidence that this is not a consistent pattern (Duivenvoorden & Lips, 1995 in Colombia; ter Steege *et al.*, 2000b in Guyana; Williams-Linera *et al.*, 2005 in Mexico; Tchouto *et al.*, 2006 in Cameroon). Our own data indicate that that there is no consistent correlation between tree species richness and the other life-forms studied at Los Volcanes. The comparisons of inventories across the Neotropics discussed above also show that forests with higher tree species

richness do not necessarily contain higher species richness in non-woody life-forms. In a neotropical context, the forests at Los Volcanes may be poor in terms of tree species richness, but they do show remarkable species richness of lianas, terrestrial herbs and, especially, epiphytes, challenging even those of the most diverse forests of the continent, the Colombian Chocó. We have shown that tree species richness alone does not always correlate with species richness patterns in other life-forms (although it consistently did so with total species richness across the three forest types studied, as did the species richness patterns of lianas). We thus advocate that more effort be put into non-woody plant inventories in order to better assess the biodiversity of an area and to allow more informed conservation decisions to be made.

2.5 Acknowledgements

We thank three anonymous reviewers who provided helpful critiques of and insightful suggestions to the manuscript. We thank P. Wilkie for his suggestions and for correcting the English of the manuscript. We also thank the owner of Los Volcanes, A. Schwiening, for allowing us to work on his land. SKH and MK are indebted to the Colección Boliviana de Fauna and the Dirección General de Biodiversidad for research permits. We thank the curators of the Herbario Nacional de Bolivia (LPB) and Herbario del Oriente Boliviano (USZ) for providing us with working facilities and allowing access to their collections. Several botanists aided in species identification (S. Beck, T. Krömer, J.F. Morales, M. Nee, C. Taylor, R. Vasquez). We are grateful to C. Hamel and M. Valverde for help in the field. Financial support is acknowledged from the Deutsche Forschungsgemeinschaft (DFG) and the German Academic Exchange Service (DAAD).

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Chapter 3

Tree community patterns along a deciduous to evergreen forest gradient in central Bolivia

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2008

Ecología en Bolivia 43(2):1-20.

Abstract

We studied trees with a diameter at breast height ≥ 10 cm on three one-hectare plots in the Refugio Los Volcanes seasonal forests (1000-1400 m altitude), located in the Andean foothills of central Bolivia. The plots included local variants of deciduous, semi-deciduous and evergreen forest vegetation. We recorded a total of 115 species and 43 families. The most diverse plot was the semi-deciduous forest plot with 70 species, 56 genera and 31 families, whereas the evergreen forest plot had slightly lower richness values (63 species, 49 genera, 31 families). The deciduous forest plot had much lower numbers (44 species, 38 genera and 21 families) and shared only 19 and 15 species with the semi-deciduous and evergreen forest plots, respectively. Between 34% and 50% of the species in the study plots were locally rare species, i.e., species with only one or two individuals per plot. On the other hand, a high percentage of the total number of individuals and basal area was contributed by a few dominant species in each plot. *Pachystroma longifolium* (Nees) I.M. Johnst. (Euphorbiaceae) was the only species among the three most important species in each of the three plots. Leguminosae was the most important family in the deciduous and semi-deciduous plots. The evergreen forest plot contained different dominant families compared to the other two plots. The species richness values we found in this study were similar to other tree inventories in comparable seasonal forest ecosystems in Bolivia. Species and familial composition, however, were contrastingly different, except for the well-known fact that Leguminosae is the numerically most important family in seasonally dry neotropical forest ecosystems. Phytogeographically, the tree flora of Los Volcanes is heterogeneous, being composed of elements belonging to seasonal forests as well as to humid tropical forests.

Key-words: Amboró National Park, seasonal forest, tree density, tree dominance, tree inventory

3.1 Introduction

The Amboró National Park located in Santa Cruz department (Bolivia) must be one of the most biodiverse protected areas in the world with vegetation types such as lowland humid evergreen forests, inter-Andean dry forests, high altitude cloud forests and puna vegetation from which more than 3000 plant species have been reported to date (Nee, 2004). The southeastern part of the national park is mainly composed of deciduous vegetation and previous classifications have tended to include it in single broad categories. Navarro *et al.* (1996) for example, included this area in the 'subhumid to humid deciduous forest of southeastern Amboró', a vegetation type usually found between 900-1100 m and where the dominant tree species are *Aspidosperma cylindrocarpum* (Apocynaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela lilloi* (Meliaceae), *Gallesia integrifolia* (Phytolaccaceae), *Pachystroma longifolium* (Euphorbiaceae), *Pogonopus tubulosus* (Rubiaceae) and *Tabebuia lapacho* (Bignoniaceae). More recently, Navarro & Maldonado (2002) assigned the vegetation in this area to the 'Upper central subandean Cerrado semideciduous forest', found between 1000-1900 m and with *P. longifolium* and *C. estrellensis* dominating the 1000-1300 m range. Based on visual inspections of the area, however, we observed substantial variations of the vegetation within these broad categories. During the course of a multidisciplinary study on the ecology of animals and plants at the Refugio Los Volcanes (hereafter LV), an area adjacent to the south of Amboró National Park, we observed that the dominant zonal vegetation in the area was indeed semi-deciduous forest (about 30-50% deciduous trees), mainly found on the shaded south-facing slopes. Local differences in topography and aspect, however, seemed to lead to ecologically relevant differences in water availability. Consequently, steep, sunny and north-facing slopes were occupied by deciduous forest (70-90% deciduous), whereas the flat, shaded valleys with groundwater supply supported evergreen forest (10-20% deciduous). In order to test these visual observations we established three permanent one-hectare plots along the deciduous to evergreen seasonal forests vegetation gradient of LV. Our aims were to characterise the forest types within the

LV area, to understand the relationship between these distinct types using quantitative tree inventories and to investigate the wider biogeographic affinities (within Bolivia and beyond) of the LV forest.

3.2 Study area

The study was carried out at the Refugio Los Volcanes (1000-1400 m altitude) in Santa Cruz, Bolivia. LV is located at about 18°06' S and 63°36' W, adjacent to the southern border of Amboró National Park, on the transition from the humid inner tropics to the seasonally dry subtropics (Fig.3.1). The geological substrate of the study area consists primarily of red sandstone and locally of loamy sedimentary rocks (lutite). Annual precipitation is about 1200-1400 mm, with a three month dry season from July to October. The deciduous forest plot (18° 06' 48"S, 63° 36' 10"W) was located at an average altitude of 1150 m on a sunny north-facing slope. The semi-deciduous forest plot (18° 06' 13"S, 63° 35' 44"W, 1300 m northeast of the deciduous forest plot) was located at an average altitude of 1070 m on a south-facing slope shaded by a rock-wall toward the southeast. The evergreen forest plot (18° 06' 03"S, 63° 35' 58"W, 500 m northwest of the semi-deciduous forest plot) was located at an average altitude of 1100 m in a ravine with loose soils and permanent groundwater supply provided by a small watercourse that divided the plot into two parts with steep slopes on both sides of the creek.

3.3 Methods

We established one permanent plot of 1 ha in each forest type in 2002-2003. We subdivided each plot into 25 adjacent 20 m x 20 m subplots, which were laid out in such a way as to include only a homogeneous representation of the forest type under study (i.e., avoiding secondary vegetation or other forest types). Thus, our plots are not the traditional square 100 m x 100 m inventory plots, but have rather irregular shapes (Fig. 3.1). We recorded diameter at breast height (dbh) for each tree

Figure 3.1: Study area in Refugio Los Volcanes, Santa Cruz (inset shows location within Bolivia). Plot shape and approximate location are given by D (deciduous forest), SD (semi-deciduous forest) and E (evergreen forest).

with a diameter of 10 cm or more. Voucher specimens of all species were collected for later determination and are deposited at USZ (Santa Cruz) and LPB (La Paz) (herbarium acronyms following Holmgren & Holmgren, 1998). Identification of the most common species was done directly in the field whenever possible. Vouchered specimens were identified at USZ and LPB using local (e.g., Jardim *et al.*, 2003) and national tree floras (Killeen *et al.*, 1993), as well as by comparison with reference collections and expert identification from local and visiting botanists at the mentioned herbaria. Sterile specimens that could not be completely identified were sorted into morphospecies. We calculated relative density, relative dominance (using basal area)

and relative frequency for each species in order to estimate the importance value index (IVI) following Curtis & McIntosh (1951). To calculate the family value index (FVI) we followed Mori *et al.* (1983) and used relative density, relative dominance and relative diversity (number of species per family). We constructed smoothed individual based species accumulation curves by randomly adding individuals to the species accumulation curve. This procedure was repeated 100 times and we used the mean and 1.96 standard deviations to plot the curve and 95% confidence intervals (Magurran, 2004).

3.4 Results

3.4.1 Diversity and density

We recorded 115 tree species from 43 families on the three 1-ha plots (Appendix 1A.3). The semi-deciduous and evergreen forest plots were the most species-rich (Table 3.1). In contrast, density values were much higher on the deciduous forest plot, where multi-stemmed trees were about twice as common as on the other two plots. A higher percentage of species represented by a single individual (singleton) and by two individuals (doubletons) was found in the semi-deciduous and evergreen forest plots (Table 3.1). Overall, locally rare species represented by one or two individuals accounted for 34-50% of the species on our study plots. We found no lianas or hemi-epiphytes with a dbh ≥ 10 cm on the deciduous forest plot. The semi-deciduous forest plot contained five individuals of hemi-epiphytes (*Ficus* sp., *F. obtusifolia* Kunth in Humb., Bonpl. & Kunth and *F. trigona* L. f., all Moraceae) and two of lianas (*Machaerium* cf. *punctatum* (Poir.) Pers. (Leguminosae) and *Celtis iguanaea* (Jacq.) Sarg. (Ulmaceae)). The evergreen forest plot contained eight individuals of hemi-epiphytes (*Ficus* cf. *eximia* Schott in Spreng., *F. maxima* Mill., *F. obtusifolia* Kunth in Humb., Bonpl. & Kunth, *F. pertusa* L. f. and *F. trigona* L. f., all Moraceae) and no lianas. Individual based species accumulation curves showed that when up to ca. 180 individuals are sampled randomly from each plot,

Table 3.1: General diversity and structural characteristics of three one-hectare plots in Central Bolivia.

	Deciduous	Semi-deciduous	Evergreen
Species	44	70	63
Genera	38	56	49
Families	21	31	31
# Ind	640	572	537
# steems	706	612	569
% multistemmed trees	9.5%	4.9%	5.6%
Singletons	10 (23%)	24 (34%)	20 (32%)
Doubletons	5 (11%)	11 (16%)	10 (16%)

confidence intervals of the estimated species richness values overlap, indicating that the observed differences could have arisen by chance (Fig. 3.2). Increased random sampling of individuals, however, revealed clear differences between the deciduous forest plot and the two other forest plots. Nevertheless, irrespective of increased sampling these two latter forest types showed very similar estimated species richness values up to the total individuals sampled.

3.4.2 Diameter distribution in size classes

The range of dbh values increased from the deciduous forest plot (10-83 cm) to the evergreen forest plot (10-162 cm), with intermediate values on the semi-deciduous forest plot (10-125 cm). Basal area was highest on the semi-deciduous and deciduous forest plots with 27.7 m² and 27.5 m², respectively. The evergreen forest plot had a somewhat lower basal area with 24.2 m². All three plots showed a left-skewed "inverted J" distribution of the number of individuals per dbh size class (Fig. 3.3). Nevertheless, there were differences in the dbh size class that contributed most to total basal area (Fig. 3.3). Dbh size classes from 10-50 cm contributed most on the deciduous forest plot (with 11.4% to 14.9% of total basal area per size class). On the semi-deciduous forest plot, the 30-40 cm dbh size class contributed with 22.6% of total basal area. On the evergreen forest plot low dbh size classes, as well as high dbh classes, were responsible for most of the total basal area (dbh size classes 10-15

Figure 3.2: Individual based species accumulation curves of the deciduous (black), semi-deciduous (red) and evergreen (green) forest plots. Lines indicate estimated species richness values by given number of individuals, polygons indicate a 95% confidence interval.

cm and 15-20 cm contributed with 12.1% and 11.4% of total basal area, respectively. The dbh size class of 100 cm or more contributed with 13.1%).

3.4.3 Dominant species and families

The deciduous forest plot (Table 3.2) was dominated by *Parapiptadenia excelsa* (Griseb.) Burkart (Leguminosae) and *Trichilia claussenii* C. DC. (Meliaceae). Both had the highest number of individuals (97 and 98, respectively) and together contributed to more than 30% of the total number of individuals on the plots and to 24% of total basal area (8% and 16%, respectively). Other important and dominant species were *Aspidosperma cylindrocarpon* Mull. Arg. (Apocynaceae), *Schinopsis hankeana* Engl. (Anacardiaceae), *Pachystroma longifolium* (Nees) I.M. Johnst. (Euphorbiaceae) and *Anadenanthera colubrina* (Vell.) Brenan (Leguminosae). They

Figure 3.3: Number of individuals (bars) and percentage contribution of total basal area (lines) per diameter size class on three 1-hectare forest plots in central Bolivia. Note different scales of the ordinates for each graph.

contributed 24% of the total number of individuals and 41% of total basal area. Together these six species represented 54% of all individuals and 62% of total basal area. The most important family was Leguminosae with 32% of the individuals, 12 species and 39% of the basal area, followed by Meliaceae and Euphorbiaceae. These three families contributed 58% of the number of individuals, 54% of basal area and 40% of species richness (Table 3.3). The semi-deciduous forest plot (Table 3.4) was dominated by *Pachystroma longifolium* and *Myrciantes* cf. *pseudomato* (Legrand) Mc. Vough. (Myrtaceae). *Pachystroma longifolium* had the highest number of individuals (118, 21% of the total), and both species had the highest basal area, comprising 38% of total basal area. Other important species in terms of density were *Chomelia* cf. *sessilis* Mull. Arg. (Rubiaceae) and *Chrysophyllum gonocarpum* (Mart. & Gichl.) Engl. (Sapotaceae). The most important family was Euphorbiaceae, in which only two species contributed 25% of the individuals and 21% of basal area, followed by Sapotaceae and Myrtaceae. These three families comprised 47% of the number of individuals, 55% of basal area and 13% of species richness (Table 3.5). The evergreen forest plot (Table 3.6) was dominated by *Aniba* sp. (Lauraceae), with 76 individuals (14% of the total) and 8% of total basal area. *Drypetes amazonica* Steyerm. (Euphorbiaceae), *Pachystroma longifolium* and *Clarisia biflora* Ruiz & Pav. (Moraceae) were also important. These four species contributed 40% of the total number of individuals and 26% of total basal area. The most important family was Moraceae with 74 individuals (14% of the total), 25% of total basal area and eight species, followed by Lauraceae, Sapotaceae and Euphorbiaceae. These four families represented 66% of the individuals, 70% of basal area and 35% of species richness (Table 3.7).

Table 3.2: Ten most dominant woody plants with dbh ≥ 10 cm in the deciduous forest plot according to importance value indices (species are ranked by descending importance value index). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, F: frequency, rF: relative frequency, IVI: importance value indices).

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
LEG	<i>Parapiptadenia excelsa</i> (Griseb.) Burkart	97	15.16	3.71	13.48	20	7.33	35.96
MEL	<i>Trichilia clausenii</i> C. DC.	98	15.31	2.13	7.73	19	6.96	30.01
APO	<i>Aspidosperma cylindrocarpon</i> Mull. Arg.	43	6.72	2.55	9.27	17	6.23	22.22
ANA	<i>Schinopsis hankeana</i> Engl.	17	2.66	4.30	15.63	10	3.66	21.95
EUP	<i>Pachystroma longifolium</i> (Nees) I.M. Johnst.	57	8.91	1.99	7.23	15	5.49	21.63
LEG	<i>Anadenanthera colubrina</i> (Vell.) Brenan	35	5.47	2.39	8.69	12	4.40	18.56
NYC	<i>Neea</i> sp.	30	4.69	0.70	2.53	15	5.49	12.71
URT	<i>Pouzolzia</i> sp.	32	5.00	0.46	1.66	15	5.49	12.16
LEG	<i>Tipuana tipu</i> (Benth.) Kuntze	11	1.72	1.98	7.19	5	1.83	10.74
LEG	<i>Piptadenia buchtienii</i> Barneby	21	3.28	0.84	3.05	12	4.40	10.73

Table 3.3: Ten most dominant families of woody plants with dbh ≥ 10 cm in the deciduous forest plot according to family value indices (families are ranked by descending family importance value). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, Div: species diversity, rDiv: relative diversity, FIV: family importance value).

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Leguminosae	208	32.50	10.70	38.89	12	27.27	98.66
Meliaceae	99	15.47	2.28	8.29	2	4.55	28.30
Euphorbiaceae	66	10.31	2.12	7.71	4	9.09	27.11
Anacardiaceae	23	3.59	4.48	16.28	2	4.55	24.42
Apocynaceae	47	7.34	2.63	9.56	2	4.55	21.45
Nyctaginaceae	33	5.16	0.78	2.83	3	6.82	14.81
Capparidaceae	26	4.06	0.67	2.44	2	4.55	11.04
Sapotaceae	25	3.91	0.42	1.53	2	4.55	9.98
Urticaceae	32	5.00	0.46	1.67	1	2.27	8.94
Myrtaceae	5	0.78	0.10	0.36	3	6.82	7.96

Table 3.4: Ten most dominant woody plants with dbh ≥ 10 cm in the semi-deciduous forest plot according to importance value indices (species are ranked by descending importance value index). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, F: frequency, rF: relative frequency, IVI: importance value indices).

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
EUP	<i>Pachystroma longifolium</i> (Nees) I.M. Johnst.	118	20.59	5.43	19.63	23	7.42	47.64
MYRT	<i>Myrciantes</i> cf. <i>pseudomato</i> (Legrand) Mc. Vough.	38	6.63	5.01	18.11	17	5.48	30.23
RUB	<i>Chomelia</i> cf. <i>sessilis</i> Mull. Arg.	40	6.98	2.11	7.63	15	4.84	19.45
SAPO	<i>Chrysophyllum gonocarpum</i> (Mart. & Gichl.) Engl.	32	5.58	1.61	5.82	17	5.48	16.89
SAPO	<i>Sarcaulus</i> sp.	35	6.11	0.44	1.59	15	4.84	12.54
EUP	<i>Drypetes amazonica</i> Steyerm.	28	4.89	0.48	1.74	16	5.16	11.78
APO	<i>Aspidosperma rigidum</i> Rusby	25	4.36	0.48	1.74	12	3.87	9.97
MOR	<i>Sorocea guilleminiana</i> Gaudich.	22	3.84	0.23	0.83	16	5.16	9.83
SAPO	<i>Chrysophyllum venezuelanense</i> (Pierre) T.D. Penn.	11	1.92	1.29	4.66	8	2.58	9.16
PHY	<i>Gallesia integrifolia</i> (Sprengel) Harms	6	1.05	1.74	6.29	5	1.61	8.95

Table 3.5: Ten most dominant families of woody plants with dbh ≥ 10 cm in the semi-deciduous forest plot according to family value indices (families are ranked by descending family importance value). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, Div: species diversity, rDiv: relative diversity, FIV: family importance value).

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Euphorbiaceae	146	25.48	5.91	21.37	2	2.50	49.35
Sapotaceae	80	13.96	4.08	14.75	4	5.00	33.71
Myrtaceae	42	7.33	5.15	18.62	3	3.75	29.70
Leguminosae	33	5.76	1.66	6.00	9	11.25	23.01
Rubiaceae	46	8.03	2.2	7.95	3	3.75	19.73
Lauraceae	38	6.63	0.98	3.54	6	8.75	18.92
Apocynaceae	49	8.55	1.43	5.17	4	5.00	18.72
Moraceae	35	6.11	0.69	2.49	6	7.50	16.10
Tiliaceae	3	0.52	0.12	0.43	11	13.75	14.71
Meliaceae	22	3.84	0.36	1.30	4	5.00	10.14

Table 3.6: Ten most dominant woody plants with dbh ≥ 10 cm in the evergreen forest plot according to importance value indices (species are ranked by descending importance value index). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, F: frequency, rF: relative frequency, IVI: importance value indices).

Family	Species	# Ind	rDe	BA	rDo	F	rF	IVI
LAU	<i>Aniba</i> sp.	76	14.18	1.95	8.05	23	7.42	29.65
EUP	<i>Drypetes amazonica</i> Steyerm.	60	11.19	0.91	3.76	22	7.10	22.05
EUP	<i>Pachystroma longifolium</i> (Nees) I.M. Johnst.	43	8.02	1.81	7.47	17	5.48	20.98
MOR	<i>Clarisia biflora</i> Ruiz & Pav.	38	7.09	1.53	6.31	19	6.13	19.53
SAPO	<i>Pouteria nemorosa</i> Baehni	11	2.05	2.64	10.90	10	3.23	16.17
URT	<i>Myriocarpa stipitata</i> Benth.	35	6.53	0.78	3.22	10	3.23	12.97
SAPO	<i>Chrysophyllum gonocarpum</i> (Mart. & Gichl.) Engl.	21	3.92	0.69	2.85	14	4.52	11.28
MOR	<i>Ficus</i> cf. <i>eximia</i> Schott in Spreng.	3	0.56	2.26	9.33	3	0.97	10.85
NYC	<i>Guapira</i> aff. <i>olfersiana</i> (Link et al) Standl.	17	3.17	0.79	3.26	11	3.55	9.98
MOR	<i>Sorocea guilleminiana</i> Gaudich.	22	4.10	0.25	1.03	15	4.84	9.97

Table 3.7: Ten most dominant families of woody plants with dbh ≥ 10 cm in the evergreen forest plot according to family value indices (families are ranked by descending family importance value). (# Ind: no. of individuals, rDe: relative density, BA: basal area, rDo: relative dominance, Div: species diversity, rDiv: relative diversity, FIV: family importance value).

Family	# Ind	rDe	BA	rDo	Div	rDiv	FIV
Moraceae	74	13.81	6.04	24.93	8	12.90	51.64
Lauraceae	118	22.01	3.21	13.25	6	9.68	44.94
Sapotaceae	56	10.45	4.69	19.36	5	8.06	37.87
Euphorbiaceae	104	19.40	2.87	11.84	3	4.84	36.09
Urticaceae	40	7.46	0.88	3.63	2	3.23	14.32
Leguminosae	7	1.31	0.63	2.60	4	6.45	10.36
Rubiaceae	12	2.24	0.58	2.39	3	4.84	9.47
Araliaceae	13	2.43	0.7	2.89	2	3.23	8.54
Meliaceae	16	2.99	0.17	0.70	3	4.84	8.53
Apocynaceae	15	2.80	0.6	2.48	2	3.23	8.50

3.5 Discussion

3.5.1 Effect of plot shape on species richness and community composition estimations

Spatial distribution patterns of plant species in tropical forests have been reported to show mostly clumped distributions (e.g., Condit *et al.*, 2000). Within this scenario, longer and narrower rectangular plots are prone to capture more species than square plots of similar area, because the former could include a potentially more heterogeneous area (Condit *et al.*, 1996; Laurance *et al.*, 1998). Nevertheless, small and statistically non-significant differences were found in a study comparing tree diversity in square plots versus rectangular plots in Central Amazonia (Laurance *et al.*, 1998). Given the patchy and fragmented nature of the deciduous and evergreen forests in our study area, it was impossible to survey all vegetation types in regular square or rectangular plots. Rather, we tried to survey as environmentally homogeneous an area as possible, leading to our irregular plot shape design. We acknowledge that plot shape has influenced our results, especially those of the transect-like evergreen forest plot. The extent of this influence, however, seems to be variable, as

can be seen from the species accumulation curves. It significantly decreased in the irregularly shaped deciduous forest plot when the hectare was completely surveyed, suggesting that sampling was representative. In contrast, the species accumulation curves did not level off in the more-or-less regularly shaped semi-deciduous plot and in the long and transect-like evergreen forest plot, suggesting, that sampling, irrespective of plot shape, was incomplete.

3.5.2 Local variation of tree diversity, dominance and structure at Los Volcanes

There were obvious differences in the diversity and floristic composition between the deciduous forest plot and the two other plots, which were rather similar in diversity and structure. Not only was the deciduous forest plot poorer in terms of generic and familial diversity, it also shared fewer species with the semi-deciduous and the evergreen forest plot. The deciduous forest plot shared 19 species with the semi-deciduous and 15 with the evergreen forest plot, whereas the latter two shared 39 species. Eleven species were present in all three plots and represented a selection of the tree species characteristic of the Amboró region like *Aspidosperma cylindrocarpum*, *Gallesia integrifolia* and *Pachystroma longifolium* (Navarro *et al.*, 1996). Of these species, few were dominant and abundant on each of the plots, like *Chrysophyllum gonocarpum*. On the contrary, most were locally rare species, at least at the hectare-scale, with abundances of one individual per hectare (e.g., *Cariniana estrellensis* (Raddi) Kuntze, *Swartzia jorori* Harms, *Eugenia* sp.). Differences in diversity and composition between the three plots, especially between the deciduous forest plot and the two other, was mirrored by several environmental factors. For example, soil humidity and pH increased from the deciduous forest plot to the evergreen forest plot (Lendzion, 2003). Therefore, even though there is a dominant regional flora, small-scale environmental variations produce significant differences in the composition and dominance of the local tree flora. This fact has already been shown for terrestrial herbs at LV (Lendzion, 2003) and for woody species in seasonal

forests elsewhere (Oliveira-Filho *et al.*, 1998; Balvanera *et al.*, 2002). Lianas have been considered important components of tropical forests (Medina, 1995), constituting in some cases 20% or more of the local flora (Gentry, 1995; Schnitzer & Bongers, 2002). In this study, however, we were not able to record lianas with a dbh ≥ 10 cm in the deciduous and evergreen forest plots. Only the semi-deciduous forest plot contained two individuals belonging to two tree species (*Machaerium* cf. *punctatum* and *Celtis iguanaea*), which occasionally also grow as lianas, with a dbh ≥ 10 cm. This agrees with another study in Bolivian deciduous forests that found similar low levels of liana diversity and density using the same sampling methodology (Cayola *et al.*, 2005). Nonetheless, this does not mean that the LV forests are devoid of vines and climbers. In fact, most of the liana diversity and abundance in each of the studied forest plots is found in dbh classes below 10 cm (Hoffmann, 2004), so that our results have to be interpreted as a sampling artefact. In mountainous areas, with forest growing on steep slopes, one of the factors that can influence and produce low basal area values are landslides (Chazdon, 2003). Since the humid forest plot was located on steeper slopes than the other two plots and additionally had rather loose soils, we suggest that an increased frequency of localized landslides could have produced the lower basal area as compared to the other two plots.

3.5.3 The Los Volcanes forests in a Bolivian context

Our inventory on the deciduous forest plot contained species richness and densities of trees with dbh ≥ 10 cm within the range of other inventories in Bolivian seasonal forests (Table 3.8). It was much richer and denser than that of the Santa Cruz Botanical Garden (inventoried by Uslar *et al.*, 2004), which is located in a slightly drier lowland area (350 m). Our plots in the semi-deciduous and evergreen forest variants, although much more species-rich, were less dense than the San Rafael (1500 m, Vargas, 1995) and Río Tuichi (880 m, Cayola *et al.*, 2005) plots. The dominant and most diverse family in seasonal deciduous forests in the Neotropics is usually Leguminosae (Gentry, 1995; Pennington *et al.*, 2006). There is, however,

ample variation as to which are the next most diverse and dominant families. This is confirmed by several other inventories in Bolivian deciduous forests (Killeen *et al.*, 1998; Kessler & Helme, 1999; Fuentes *et al.*, 2004) and by our study, where we had six different families following Leguminosae in importance. In nearby Santa Cruz (Uslar *et al.*, 2004) Leguminosae was the overwhelmingly dominant family (seven species), all other families with only one or two species (Table 3.8). In the adjacent Amboró National Park (Vargas, 1995), they were Lauraceae and Myrtaceae. Finally, the Tuichi valley dry forests inventory in La Paz department (Cayola *et al.*, 2005) reported also Myrtaceae and Bombacaceae as important. The dominant families on the evergreen forest plot in LV showed contrasting results with Moraceae, Lauraceae and Sapotaceae as the most diverse families (Table 3.8). The diversity of Moraceae, whose members are prominent components of tropical rain forests, already suggests the prevalence of different local environmental conditions on this plot. In contrast, species composition and densities of trees with dbh ≥ 10 cm on the LV plots differed from other tree inventories in Bolivia with similar annual rainfall and similar seasonal vegetation. For instance, the Santa Cruz plot in the deciduous Chiquitanía forests (Uslar *et al.*, 2004) reported *Aspidospermum cylindrocarpon* (Apocynaceae), *Myrciaria cauliflora* (Myrtaceae) and *Phyllostylon rhamnoides* (Ulmaceae) as the most abundant species (Table 3.8). The Río San Rafael plot in Amboró contained *Nectandra* sp. (Lauraceae), *Casearia* sp. (Flacourtiaceae) and *Chrysophyllum* cf. *gonocarpum* (Sapotaceae) as the most frequent species (Vargas, 1995). The three most common species in the Tuichi plot were *Phyllostylon rhamnoides* (Ulmaceae), *Trichilia catigua* (Meliaceae) and *Anadenanthera colubrina* (Leguminosae) (Cayola *et al.*, 2005). At LV, the most abundant species were *Trichilia clausenii*, *Parapiptadenia excelsa* and *Pachystroma longifolium* on the deciduous forest plot, *Pachystroma longifolium*, *Chomelia* cf. *sessilis* and *Myrciantes* cf. *pseudo-mato* on the semi-deciduous forest plot, and *Aniba* sp., *Drypetes amazonica* and *Pachystroma longifolium* on the evergreen forest plot (Table 3.8). In terms of basal area, our deciduous and semi-deciduous forest inventories reached similar values of around 27

m², which is comparable to other seasonal forest inventories in Bolivia, except for the Tuichi plot in La Paz (20 m²) and our evergreen forest plot in LV (24.2 m²). Murphy & Lugo (1986) stated that seasonal forests were less complex structurally than wet tropical forests, with basal area values in the range from 17 m² to 40 m². Several other studies have reaffirmed this statement (e.g., Reis Lopes *et al.*, 2008). Basal area values of the LV plots, however, were also within the range of other tree inventories in several vegetation types in South America, using the same diameter cut-off, and particularly within Bolivia. For instance, basal area values of several 1-ha inventories in humid tropical forests ranged between 21.4 m² (Beni, Bolivia) and 39.2 m² (Amboró, Bolivia) (Smith & Killeen, 1998).

3.5.4 Phytogeography of the Los Volcanes species

Based on the distribution of over 70 plant taxa, Prado & Gibbs (1993) proposed the existence of a Pleistocenic Arc of seasonal forest formations. The extant fragments of this arc are mainly located in three nuclei: the Caatinga nucleus in northeastern Brazil; the Misiones nucleus comprising the area from the Bolivia-Brazil border in Corumbá southward to the Paraguay-Paraná river confluence and eastward to Santa Catarina in Brazil; and the Piedmont nucleus extending from Santa Cruz de la Sierra in Bolivia southward to Tucumán and the sierras of Catamarca in Argentina. Because our study area is located within the area of the Piedmont nucleus (cf. Prado, 2000), we examined the distribution patterns of the 115 species found at LV. We recorded *Anadenanthera colubrina*, *Myracrodruon urundeuva* Allemão and *Celtis iguanaea* in our plots, all of which have been reported as characteristic to the wider Pleistocenic Arc formation (Prado & Gibbs, 1993). We also found *Diatenopteryx sorbifolia* Radlk., classified as a restricted Arc species since it only occurs in the Misiones and Piedmont nuclei. Navarro & Maldonado (2002), who considered the area around LV as transitional between the Brazilian-Paraná biogeographic region and the Bolivian-Tucumán biogeographic province, also noted this affinity with the seasonal vegetation in the Misiones and Piedmont nuclei. In total, we identified

Table 3.8: Seasonal forest inventories in Bolivia. Diameter cut-off: 10cm. (Ind.: No. of individuals, BA: basal area, Alt. altitude, dry: seas: length of the dry season, NA: data not available).

Plot (Reference)	Species	3 most dense species	Families	3 most diverse families	Ind.	BA (m ²)	Plot shape	Alt. (m)	Rainfall (mm/year)	dry: seas (months)
Jardin Botánico Santa Cruz (Uslar et al. 2004)	28	<i>Aspidospermum cylindrocarpon</i> (99) <i>Myrciaria cauliflora</i> (91) <i>Phyllostylon rhamnoides</i> (79)	18	Leguminosae	503	27	100x100	375	1122	6
Río San Rafael (Vargas 1995)	50	<i>Nectandra</i> sp. (158) <i>Casearia</i> sp. (117) <i>Chrysophyllum</i> cf. <i>gonocarpum</i> (74)	33	Lauraceae (6), Leguminosae (4), Myrtaceae (3)	713	27.7	irregular	1500	1500	NA
Tuichi (Cayola et al. 2005)	51	<i>Phyllostylon rhamnoides</i> (197) <i>Trichilia catigua</i> (96) <i>Anadenanthera colubrina</i> (48)	24	Leguminosae (10), Myrtaceae (4), Bombacaceae, Cactaceae, Flacourtiaceae, Meliaceae, Polygonaceae (3)	697	20	NA	880	1300	3
IV Deciduous (This study)	44	<i>Trichilia clausenii</i> (98) <i>Parapiptadenia excelsa</i> (97) <i>Pachystroma longifolium</i> (57)	21	Leguminosae (12), Euphorbiaceae (4), Nyctaginaceae and Myrtaceae (3)	640	27.5	irregular	1055	1600	3
IV Semi-deciduous (This study)	70	<i>Pachystroma longifolium</i> (118) <i>Chomelia</i> cf. <i>sessilis</i> (40) <i>Myciartes</i> cf. <i>pseudo-mato</i> (38)	32	Leguminosae (9), Lauraceae (6), Moraceae (6)	572	27.7	irregular	1073	1600	3
IV Evergreen (This study)	63	<i>Aniba</i> sp. (76) <i>Drypetes amazonica</i> (60) <i>Pachystroma longifolium</i> (43)	31	Moraceae (8), Lauraceae (6), Sapotaceae (5)	537	24.2	irregular	1104	1600	3

21 species as typical of Bolivian seasonal forest formations. More complex and widespread distribution patterns are attributed to *Cordia alliodora* (Ruiz & Pav.) Cham. and *Ximenia americana* L., the later occurring in diverse vegetation types throughout the Neotropics. On a local scale, the forests at LV shared only 21% (24 species) of all recorded tree species with the inventories in Santa Cruz, San Rafael and Tuichi. As expected, the deciduous forest plot shared most species (10 species, 23%) with the nearby (65 km) deciduous forests in the Santa Cruz Botanical Garden and less than 12% with the other two inventories (43 km to San Rafael, 660 km to Tuichi). In contrast, the semi-deciduous forest plot shared only 13% of its species with the inventory in the Santa Cruz Botanical Garden, and less than 10% of its species were also present in the other two inventories. The evergreen forest shared even fewer species with any of the other seasonal forest inventories (less than 11%). Low percentages of shared species between seasonal forest inventories, irrespective of geographical distance, have also been reported for the seasonally dry forest in Mexico and attributed to the existence of processes of high local diversification, possibly due to particular historical processes (Trejo & Dirzo, 2002). Indeed, the complex vegetational arrangement of the area, a region, where four major biomes come into contact: the humid vegetation from Amazonia, the seasonal subtropical lowland vegetation from the Chaco, the subtropical highland vegetation from the Andes and the seasonal vegetation of the Chiquitanía (Ibisch *et al.*, 2003), would have provided an optimal setting for the extraordinary floristic diversification in the Santa Cruz region. Thus, even though we are comparing seasonal forest with similar rainfall, dry season length or at similar altitude, their low floristic similarity seems to be strongly influenced by the biome they are closest to. The San Rafael plot in Amboró National Park will be more likely influenced by the Andean biome, the Tuichi plot by the northern Bolivian Andes and Amazonia and Santa Cruz Botanical Garden by the Chiquitanía and the Chaco. In similar fashion, the different vegetation types reported at LV have probably been influenced by all these major biomes, and it is the varied local environmental characteristics that have allowed

the co-existence of species with differing ecological requirements.

3.6 Acknowledgements

We thank the reviewers and the handling editor for suggestions and critique that improved the original manuscript. We thank the owner of Los Volcanes, A. Schwiening, for allowing us to work on his land. SKH and MK are indebted to the Colección Boliviana de Fauna and the Dirección General de Biodiversidad for research permits. We thank the curators of the Herbario Nacional de Bolivia (LPB) and Herbario del Oriente Boliviano (USZ) for providing us with working facilities and allowing access to their collections. We are grateful to C. Hamel and M. Valverde for help in the field and to J. Lenzion for providing unpublished soil and environmental data from the plots. Financial support was provided by the Deutsche Forschungsgemeinschaft (DFG) and the German Academic Exchange Service (DAAD).

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Chapter 4

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

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Journal of Biogeography (In press)

DOI:10.1111/j.1365-2699.2008.02028.x

Abstract

Aim: To assess biogeographic patterns of Acanthaceae, Bromeliaceae, Cactaceae and Pteridophyta in Bolivian Andean seasonally dry forest islands and to explain current floristic differences between these islands by means of extrinsic (precipitation, elevation) and intrinsic (dispersal ability) factors.

Location: Ten isolated and disjunct seasonally dry forest areas in the Bolivian Andes and the adjacent seasonal forest areas of the Chiquitanía and Chaco regions.

Methods: We collated species data from recently updated and revised taxonomic treatments and herbarium collections for Acanthaceae, Bromeliaceae, Cactaceae and Pteridophyta, constructed floristic distance matrices to estimate beta diversity at the study sites, and subjected them to Mantel correlation analyses. Multiple regressions on distance matrices allowed us to test the influence of geographical distance and environmental (elevation and precipitation) differences on floristic differentiation.

Results: Acanthaceae and Bromeliaceae, and to a lesser extent Cactaceae, showed coincident biogeographic patterns and suggested the presence of two seasonally dry forest groups in Andean Bolivia: one including all small isolated northern dry valleys and another including all southern valleys with connections to the lowland seasonal forests of the Chiquitanía and the Chaco. Most of the variation in the floristic distance matrices in these plant groups, with seed dispersal typically restricted to short distances, was explained by spatial separation between habitat islands. In contrast, pteridophytes showed a different biogeographic pattern. Their floristic differences between sites were determined by the environmental variables. The anemochorous and spore-based dispersal system of this plant group seems to be a highly effective mechanism allowing pteridophytes to easily reach even the isolated dry valleys in inter-Andean Bolivia.

Main conclusions: Current biogeographic patterns in dry Andean habitat islands can provide insights into the factors that control processes of community assembly. We show that differences in community composition of phylogenetically distant

plant groups in the understorey of seasonally dry forest islands can be explained by a combination of the habitat characteristics where the group is present (either precipitation, elevation, or both) and, more interestingly, by group specific dispersal limitation (as inferred by geographical distance between island habitats).

Keywords: Andes, Bolivia, dispersal limitation, environmental factors, floristic dissimilarity, island biogeography, plant geography, seasonal forest island

4.1 Introduction

Plant dispersal is a central theme in plant community ecology (Bullock & Nathan, 2008). The fact that most plant species cannot disperse their seeds over distances beyond a few metres implies that they are effectively dispersal limited (van Oudtshoorn & van Rooyen, 1999; Cain *et al.*, 2000). Within these shorter spatial scales, diaspore dispersal is an important process influencing the structure of communities. At larger geographical scales, rare long distance dispersal events of diaspores are considered an important factor for shaping and maintaining metacommunities (Holoak *et al.*, 2005). This is because these diaspores, aided by vectors such as vertebrates (especially birds), wind and water (Cain *et al.*, 2000; Willson & Traveset, 2000; Nathan, 2006), have the potential to reach sites that are separated from the source populations by great distances, physical barriers or surrounded by an adverse habitat matrix (Levin *et al.*, 2003; Nathan, 2006; Soons & Bullock, 2008).

Seed dispersal and life history processes occurring after it (such as germination and seedling establishment), depend heavily on the environmental conditions prevailing in the newly colonized habitat (van Oudtshoorn & van Rooyen, 1999). These environmental conditions act as filters, removing all species lacking a specified combination of traits (Keddy, 1992). Thus, ecological communities appear to be mainly structured by two important albeit contrasting processes: dispersal and niche related environmental factors, known as the dispersal assembly and niche assembly view, respectively (Ozinga *et al.*, 2005; Gravel *et al.*, 2006; Leibold & McPeck, 2006;

Thompson & Townsend, 2006; Chase, 2007). Consequently, observed differences in beta diversity between communities may be due to dissimilar environments, may reflect spatial patterns of dispersal, or may be the result of both. Much empirical evidence supports the view that environmental heterogeneity, especially soil factors, contributes to differences in present day plant distribution and community composition patterns at very local to landscape scales (e.g., Clark *et al.*, 1999; Condit *et al.*, 2000; Tuomisto *et al.*, 2003b; John *et al.*, 2007; Jones *et al.*, 2008). There is also some evidence in support of dispersal (as measured by degree of isolation or distance between two communities) as an important factor (e.g., Kadmon & Pulliam, 1993; Gilbert & Lechowicz, 2004), but the bulk of studies point to a coupled influence of both processes (e.g., Balvanera *et al.*, 2002; Duivenvoorden *et al.*, 2002; Cottenie, 2005).

Biogeographic "island" systems with spatially discrete entities such as oceanic islands, mountains, or valley systems, have long played a central role in biogeographic research (MacArthur & Wilson, 1967; Prance, 1996; Lomolino *et al.*, 2005). Seasonally dry forests, a tree-dominated ecosystem in which grasses are a minor element (Mooney *et al.*, 1995), occur in disjunct areas throughout the Neotropics (Pennington *et al.*, 2000). The smallest and most isolated of these areas occur in the rain-shadowed Andean valleys from Colombia to Bolivia (Pennington *et al.*, 2006b) where they are currently isolated by more humid vegetation types and can consequently be considered as island-like habitats (Herzog & Kessler, 2002). This situation provides a superb opportunity to explore the biogeography of an Andean vegetation island system. Following the distance decay biogeographical rule (Nekola & White, 1999), we would expect valleys that are geographically and environmentally close to each other (or which are connected by other nearby valley systems) to show similar faunal and floral characteristics, whereas valleys separated by greater geographic or environmental distances should be inhabited by distinct faunal and floral assemblages. Partial evidence in support of this for some Andean valleys comes from ornithological (Herzog & Kessler, 2002) and botanical data (Killeen *et al.*, 1998;

Kessler & Helme, 1999; Fuentes *et al.*, 2004; Cayola *et al.*, 2005). Vegetation model simulations provide further evidence (Mayle, 2004).

In recent years, some plant groups occurring in Bolivia have been taxonomically revised based on extensive and intensive fieldwork (e.g., Wasshausen & Wood, 2004), providing up-to-date distribution data and taxonomically uniform treatments suitable for regional scale biogeographic analyses. Of these, we selected four phylogenetically distant and ecologically distinct plant groups (Acanthaceae, Bromeliaceae, Cactaceae, Pteridophyta) conspicuously present in the understorey of Bolivian seasonally dry forests. Our aims in this study were to assess to what degree the distribution and community composition patterns of these plant groups in the isolated seasonally dry forests in Bolivia coincide and whether these patterns can be attributed to environmental determinants such as current local rainfall conditions and topography (as inferred by altitudinal distribution), to dispersal limitation (as inferred by current geographical separation between isolated seasonally dry forest areas), or to a combination of both.

4.2 Methods

4.2.1 Study area and data collation

We identified 12 seasonal vegetation areas in Bolivia with sizes ranging from 30 km² to 140000 km², the smallest being located in the northern inter-Andean valleys (Fig.4.1a, Table 4.1). Eleven were true seasonally dry forests (SDFs) as defined by (Mooney *et al.*, 1995). Of these seven are discrete, isolated SDF areas, occurring in narrow inter-Andean dry valleys in the departments of La Paz, Cochabamba and Potosí. The rest of the SDF areas have no sharp boundaries separating them from adjacent vegetation formations and we used topographical data and an unpublished vegetation map of Bolivia by M. Kessler to delimit them. Three occur in more extended river catchments originating in the Andes and opening out into the southern lowlands, whilst the Chiquitanía region constitutes one of the most extensive sea-

Table 4.1: Seasonal vegetation areas defined for the biogeographical analysis of selected plant groups in Bolivia.

Area	Departamento	Elevation range (m a.s.l.)	Rainfall range (mm year ⁻¹)	Area (km ²)
Río Tuichi	La Paz	700-1300	1200-1600	700
Camata valley	La Paz	1150-1500	1200-1600	30
Consata valley	La Paz	1100-1500	1200-1600	50
Coroico valley	La Paz	700-1300	1400-1600	100
Río La Paz	La Paz	800-3000	800-1600	400
Río Cotacajes	Cochabamba, La Paz	1500-2300	1100-1600	200
Río Caine	Cochabamba, Potosí	2000-3300	550-900	5000
Río Grande	Santa Cruz	500-2000	900-1600	10000
Río Parapetí	Chuquisaca	500-1800	800-1600	10000
Río Pilcomayo	Chuquisaca, Tarija	500-3000	500-1600	10000
Chiquitanía	Santa Cruz	200-1200	900-1600	140000
Chaco	Santa Cruz	250-500	400-900	100000

sonal forest areas in south-western Bolivia. In addition, we included the adjacent seasonal lowland forests of the Bolivian Chaco, comprising the northernmost section of the Chaco *sensu stricto* as delimited by (Prado, 1993). Despite being considered a different vegetation unit, inclusion of the Chaco is justified because several herbaceous to woody plant species show consistent distribution patterns pointing to a strong link with the seasonal forests in southern Bolivia (López, 2003; Killeen *et al.*, 2006; Wood, 2006).

We collated species lists for four relatively well known and recently taxonomically revised plant groups for each seasonal forest area: Bromeliaceae (Krömer *et al.*, 1999; B. Steudel *et al.*, unpub. data), Acanthaceae (Ezcurra, 2002; Wasshausen & Wood, 2004; M. Kessler, unpub. data), Pteridophyta (M. Kessler & A.R. Smith, in prep.) and Cactaceae (Navarro, 1996 used as baseline data and modified according to Ritter, 1980 and Ibisch *et al.*, 2000, updated following Hunt *et al.*, 2006). Synonymies were checked and records modified (merged or split) accordingly. To limit our data to species naturally occurring in seasonally dry forest vegetation we excluded species showing exclusive occurrences above 3000 m, as well as introduced and cultivated

Figure 4.1: a. Seasonally dry forest (SDF) areas studied in Bolivia. Northern SDF: 1. Río Tuichi, 2. Camata, 3. Consata, 4. Coroico, 5. Río La Paz, 6. Río Cotacajes. Southern SDF: 7. Río Caine, 10. Río Grande, 11. Río Parapetí, 12. Río Pilcomayo. Sørensen similarity relationships among areas: b. All Plant Groups (ALL), c. Acanthaceae, d. Bromeliaceae, e. Cactaceae, f. Pteridophyta. Thin lines show similarities above 0.5, thick lines show similarities above 0.7. Numbers follow those in the map, and additionally: 8. Chiquitanía, 9. Chaco.

species. Our choice of these four groups had practical reasons. First, there are only incomplete vascular plant checklists (or any subgroup of these, e.g., woody plants or trees) for few of the studied seasonally dry forest areas (e.g., the trees and shrubs guide for the Chiquitanía region by Jardim *et al.*, 2003), whilst most of the smaller and isolated areas have none. Second, including more groups would have required a broader taxonomic expertise and the taxonomic treatment of individual groups, between taxa and between areas, would not have been uniform.

4.2.2 Data analyses

All species were coded as present (1) or absent (0) in the 12 seasonal vegetation areas. We produced separate data matrices for each plant group plus an additional matrix containing all four groups (henceforth called "ALL").

In an initial step, to assess if diversity among the plant groups was similar or not, we calculated all possible pairwise Pearson's product-moment correlations of their species richness at the 12 seasonal forest areas. In a second step, we estimated beta diversity by constructing Sørensen dissimilarity matrices for each individual plant group. We used the Sørensen (Bray-Curtis) distance index D because this index is simple to calculate for presence-absence data and easy to interpret (Vellend, 2001; Magurran, 2004), and has been used repeatedly in similar studies (e.g., Vormisto *et al.*, 2000; Tuomisto *et al.*, 2003b). To assess whether the plant groups performed similarly in reflecting biogeographic relationships among the sites we calculated Mantel correlation coefficients between all possible pairwise combinations of floristic dissimilarity matrices. When we used similarity values (S), we calculated them with the formula: Sørensen similarity (S) = 1 - D . We used a normalised Mantel statistic, r_M , and evaluated its statistical significance through 10000 permutations (Manly, 1997).

We estimated dispersal limitation by constructing a matrix of log-transformed nearest horizontal geographical distances among the studied areas using geographical coordinates of each area, as dispersal limitation is expected to cause distance decay

(Condit *et al.*, 2002). In case they were adjoining, we considered a distance of zero. We also constructed an altitudinal, a precipitation and a combined elevation-precipitation environment distance matrix as follows. We coded the presence or absence of each seasonal forest area in a table summarizing the total elevation (200-3300 m a.s.l.) and precipitation (400-1600 mm) ranges of the study area in 100 m and 100 mm increments, respectively (e.g., the Consata SDF area ranging from 1100-1500 m a.s.l. would be only present in the 1100 to 1500 columns). Based on these tables, we calculated Sørensen distance matrices summarizing altitudinal and precipitation differences, or both combined. We used the Sørensen coefficient because it is an asymmetric index that measures overlap over the average range of values and excludes double-zero matches, preventing sites with many zeros being considered as similar. We then calculated all possible pairwise correlations of each environmental distance matrix with each of the floristic distance matrices using a simple Mantel test and evaluated statistical significance as in the floristic matrix comparisons. We then performed a Mantel test to evaluate whether there was a correlation between the geographical and all other floristic matrices. We evaluated this correlation with $\alpha = 0.05$ (1000 permutations).

We then used a multiple regression on distance matrices procedure to evaluate which of all possible combinations of the two sets of matrices (dispersal/space and environment) best explained total variation in the floristic matrices. To quantify the proportion of variation in floristic distances between SDF areas explained uniquely by dispersal limitation (as horizontal geographical distance) we subtracted the variation produced by environmental factors (combined matrix) from the total variation produced by both environmental factors and dispersal/space. To quantify the proportion of variation in floristic distances between SDF areas explained uniquely by environmental factors we subtracted the variation produced by dispersal/space from the total variation produced by both environmental factors and dispersal/space (Tuomisto *et al.*, 2003a; Lichstein, 2007). We evaluated the statistical significance of each regression by performing 10000 permutations. We did all calculations with the

R software (R Development Core Team, 2008) and package Vegan (Oksanen *et al.*, 2008).

4.3 Results

4.3.1 Species richness

Our complete database included 411 species of which 137 (33.3%) were recorded in a single area, whilst only three species occurred in all areas (*Tillandsia recurvata* (L.) L., *T. streptocarpa* Baker and *T. tricholepis* Baker, all Bromeliaceae). The number of species per seasonal forest area varied between 83 (Chaco) and 176 (Río Grande) (mean 122, Table 4.2). Of the 411 species, 116 (28%) were classified as endemic to Bolivia. 71 (52%) of the 137 species recorded in one single area have been recognised as endemic to Bolivia (either from a single collection as in several locally rare Cactaceae, or from several collections as in the case of the locally abundant *Justicia kessleri* Wassh. & J.R.I. Wood). With the exceptions of species richness and endemism values of Bromeliaceae, which decreased significantly with increasing seasonal forest area (Pearson's product-moment correlation: $r = -0.82$, $P = 0.001$ and $r = -0.75$, $P = 0.005$, respectively), we found no correlation between species richness or endemism and total area of each seasonal forest.

Acanthaceae contributed 72 species to the total (17.5%), of which 18 were endemic to Bolivia. The number of species per area varied between 4 (Río Camata) and 35 (Río Grande) (mean 20). Bromeliaceae had 132 species (32.1%; 55 endemic), varying between 15 (Chaco) and 53 (Río Tuichi) species per area (mean 37). Cactaceae had 88 species (21.4%; 42 endemic), varying between 1 (Río Tuichi) and 40 (Río Pilcomayo) species per area (mean 14). Pteridophytes had 119 species (29%; 1 endemic), varying between 15 (Chaco) and 76 (Chiquitanía) species per area (mean 51) (Table 4.2).

Pearson's product-moment correlations between species richness among the four vascular plant groups at the 12 seasonal forest areas were positive and statistically

Table 4.2: Number of species/endemics per seasonally dry forest area and plant group (ACA = Acanthaceae, BRO = Bromeliaceae, CAC = Cactaceae, PTE = Pteridophyta, ALL = all plant groups).

	ACA	BRO	CAC	PTE	ALL
Río Tuichi	14/3	53/11	1/0	39/0	107/14
Camata	4/1	39/4	5/0	51/0	99/5
Consata	9/4	39/7	3/1	47/0	98/13
Coroico	19/4	43/8	4/1	47/0	113/13
Río La Paz	20/5	43/10	14/6	69/0	146/23
Río Cotacajes	19/6	31/8	15/8	50/0	115/25
Río Caine	7/2	42/12	10/7	48/0	107/21
Chiquitanía	29/1	17/1	14/3	76/0	136/5
Chaco	24/2	15/1	29/8	15/1	83/12
Río Grande	35/6	46/11	32/16	63/1	176/36
Río Parapetí	29/4	44/5	6/1	42/0	121/10
Río Pilcomayo	34/6	30/8	40/13	61/0	165/29
Total	72/18	132/55	88/42	119/1	411/116

Table 4.3: Pearson Correlation coefficients between species richness values of 12 seasonally dry forest areas (P -values are given in parentheses; significance levels: * $P < 0.05$, ** $P < 0.01$; ACA = Acanthaceae, BRO = Bromeliaceae, CAC = Cactaceae, PTE = Pteridophyta, ALL = all plant groups).

	ACA	BRO	CAC	PTE
BRO	-0.29			
CAC	0.71**	-0.46		
PTE	0.27	0.07	0.12	
ALL	0.72**	0.13	0.59*	0.74**

significant only for the combinations ALL with Acanthaceae, Cactaceae or Pteridophytes, as well as between Acanthaceae and Cactaceae (Table 4.3).

4.3.2 Floristic similarity analysis

Pairwise similarity values calculated between the seasonal forest areas ranged from 0.15 to 0.69 (mean = 0.43 ± 0.13) when all plant groups were considered (see Table A.4 in Supplementary Material). Values for individual plant groups were between 0.06 and 0.88 (mean = 0.33 ± 0.22) for Acanthaceae, between 0.21 and 0.82 (mean = 0.46 ± 0.16) for Bromeliaceae, between 0.0 and 0.73 (mean = 0.18 ± 0.18) for

Cactaceae and between 0.15 and 0.78 (mean = 0.49 ± 0.16) for pteridophytes. Two of the four plant groups (Acanthaceae and Bromeliaceae) and the combined matrix ALL showed similar floristic patterns (Fig.4.1b-f) consisting mainly of two groups of SDF areas: one included all small isolated northern dry valleys and the other included all southern valleys with connections to the lowland seasonal forests of the Chiquitanía and the Chaco. The two clusters in Cactaceae separated some of the northern inter-Andean SDF from those in the south and the lowlands, but the northern inter-Andean SDF cluster included the Río Parapetí SDF located well in the south of Bolivia (Fig.4.1e). Pteridophyta on the other hand, produced a nearly unresolved cluster network with no clear biogeographical structure (Fig.4.1f). The Río Caine SDF functions as a link between the northern SDFs and the southern SDFs, showing stronger affinities with either one or the other cluster depending on the plant group used as the basis of the analysis.

4.3.3 Beta diversity

Mantel correlations between estimates of beta-diversity for each of the vascular plant groups were positive and statistically significant to very highly significant for all pairwise community composition distances, except for the Cactaceae vs Pteridophyta (Table 4.4). The highest correlations were found between ALL and Bromeliaceae ($r_M = 0.78$, $P = 0.0001$), and between ALL and Pteridophyta ($r_M = 0.78$, $P = 0.0001$). The lowest statistically significant value was between Acanthaceae and Pteridophyta ($r_M = 0.26$, $P = 0.047$). All Mantel correlations between floristic differences and geographical distance were significant at $\alpha = 0.05$, except for Pteridophyta (Table 4.4).

Mantel correlations between floristic differences and altitudinal differences were significant to highly significant for all plant groups (Table 4.4). Mantel correlations between floristic differences and precipitation differences were highly significant for Pteridophyta and ALL, showing high correlation values. Mantel correlations between floristic differences and a combined environmental matrix showed significant

Table 4.4: Mantel correlations between floristic differences of 12 seasonally dry forest areas based on four different plant groups in Bolivia, and between plant groups and environmental factors and dispersal limitation (as horizontal geographic distance). Distance matrices for plant groups and environmental factors were based on the Sørensen distance index. Significance was evaluated by performing 10000 permutations for an alpha of * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Mantel correlations between floristic differences and dispersal limitation were evaluated on significance tests based on 1000 permutations for an α of * $P < 0.05$.

	ALL	ACA	BRO	CAC	PTE
ACA	0.66***				
BRO	0.78***	0.49***			
CAC	0.43**	0.32*	0.38**		
PTE	0.78***	0.26*	0.37*	0.20	
Geographical distance	0.42*	0.66*	0.39*	0.27*	0.05
Altitudinal distance	0.58***	0.29*	0.40**	0.30*	0.62***
Precipitation distance	0.55***	0.25	0.23	0.17	0.63***
Environmental distance	0.63***	0.29*	0.37*	0.26	0.70***

to highly significant correlations for all plant groups, except for Cactaceae.

4.3.4 Multiple matrix regression

Total statistically significant variation in floristic distances explained by environmental differences (either as a single combined matrix or as individual precipitation and elevation matrices), geographical distances, or both, per plant group ranged from 6% in Acanthaceae to 55% in the combined ALL matrix (Table 4.5). There were, however, differences among plant groups in the combinations of distance matrices that best explained this variation. The combination precipitation/geographical distance best explained the variation in Acanthaceae (49%). In Bromeliaceae and Cactaceae it was elevation-geographical distance (28% and 15%, respectively), in Pteridophyta elevation-precipitation (50%) and the combination elevation-precipitation-geographical distance in ALL (Table 4.5). The unique contribution of each of the factors changed significantly for each plant group. In Acanthaceae, dispersal limitation alone (i.e. spatial separation) explained 40% of the total variation, whereas pure environment explained only 7%. In Bromeliaceae and Cactaceae both pure dispersal limitation and pure environment explained similar levels of variation (12% and

Table 4.5: Coefficients of multiple determination (R^2) of the multiple regressions on distance matrices performed on four different plant groups in Bolivia. Floristic and environmental distance matrices were based on the Sørensen distance index. Significance values were based on 10000 permutations for an alpha of * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. [Abbreviations of plant groups follow those in 4.3; sp = floristic distance matrix, pp = precipitation distance matrix, ele = elevation distance matrix, geo = geographical distance matrix (dispersal limitation), env = environmental distance matrix].

	ALL	ACA	BRO	CAC	PTE
sp.geo	0.17***	0.43***	0.15**	0.07*	0.00
sp.pp	0.30***	0.06*	0.05	0.03	0.40***
sp.(pp.geo)	0.47***	0.49***	0.21**	0.10*	0.41***
sp.ele	0.34***	0.08*	0.16**	0.09*	0.39***
sp.(ele.geo)	0.46***	0.48***	0.28***	0.15**	0.39***
sp.(ele.pp)	0.40***	0.09*	0.16**	0.09	0.50***
sp.env	0.40***	0.09*	0.14**	0.07	0.49***
sp.(ele.pp.geo)	0.55***	0.50***	0.28***	0.15*	0.50***
sp.(env.geo)	0.54***	0.49***	0.27***	0.13*	0.49***

13%, and 6% and 8%, respectively). All the variation in Pteridophyta was purely explained by the environmental variables (whether these were or not combined into a single matrix).

4.4 Discussion

Species presence-absence data of Acanthaceae, Bromeliaceae, and to a lesser extent Cactaceae, from 12 seasonal forest areas in Bolivia showed roughly congruent biogeographic relationships. The resolution of these relationships varied somewhat between taxa. Nevertheless, all three plant groups suggested the existence of two main groups of seasonally dry forests in Bolivia: the seasonally dry forest sites in the northern Bolivian Andes, and the seasonally dry forests in the southern Bolivian Andes, which have stronger links to the adjoining Chaco and Chiquitania seasonal forests. The same pattern was also evident when all four plant groups were combined and analysed together (ALL matrix). Significant to very highly significant Mantel correlations run between each plant group and a matrix containing all other plant groups (data not shown) further supported this congruence. In contrast,

pteridophytes showed only weakly resolved patterns in all analyses. The extent to which these results can be extrapolated to the whole flora or to other plant groups present in the studied seasonal forest remains to be explored as different patterns can be expected from different plant groups. Thus, generalizations will be difficult, as the Bolivian inter-Andean dry valleys are in a complex biogeographical position, adjacent to and influenced by other major biomes (Wood, 2006; Linares-Palomino *et al.*, in press).

Current biogeographic vegetation patterns in the Neotropics are the result of complex historical and biological processes (Burnham & Graham, 1999). The Andes had already reached about half of their modern elevation by 10 Ma (million years ago) (Gregory-Wodzicki, 2000). A rain-shadow effect, causing semi-arid to arid climates in the Central Andes, has probably been influencing the region since 15 Ma, as shown by geological and palaeobotanical data and models, and it prevailed until 4 Ma (Hartley, 2003). (Hughes & Eastwood, 2006) have recently argued that Andean uplift is probably one of the most important factors that shaped current plant diversity and vegetation patterns in the region: Andean uplift presented the extant organisms with a large area subjected to repeated vegetation fragmentations due to altitudinal shifts, glacial fluctuations and a dissected topography, promoting geographical isolation. This generated habitat and environmental heterogeneity and provided new ecological opportunities. Dated phylogenies for SDF representative taxa (e.g., *Coursetia*, Leguminosae) show geographically structured evolutionary radiations well within the Andean uplift timeframe (Pennington *et al.*, 2004) and it has been argued that SDF might have had a long history of discontinuous distributions and relative floristic stability of at least 5-7 Ma (Lavin, 2006). Indeed, molecular phylogenies for some of our study groups suggest radiations congruent with the rise of the Andes and the formation of new seasonal vegetation areas to colonise, thus favouring speciation. Much of the current diversity in Andean Bromeliaceae (Givnish *et al.*, 2004; Barfuss *et al.*, 2005) and Cactaceae (Ritz *et al.*, 2007) appears to have originated during and/or after the major uplift of the

Andes. In addition, there is evidence that at least one genus in the pteridophytes has primarily radiated during Andean uplift (e.g., Lehnert *et al.*, in press). Current phylogenetic resolution in Acanthaceae is still too poor to elucidate Neotropical biogeographic patterns (McDade *et al.*, 2005; Daniel *et al.*, 2008). However, their mostly Andean distribution (Gentry, 1982) and the significant amount of species and endemics in dry Andean environments (Wood, 2006) hint of a comparable dynamic and explosive speciation phase during the rise of the Andes, as in the above mentioned vascular plant groups. Such shared historic factors may be hypothesised to be partly the cause of the repeated and consistent floristic patterns found in Acanthaceae and Bromeliaceae (and to a lesser extent in Cactaceae), and reflected in analyses of all plant groups combined.

In addition, Acanthaceae, Bromeliaceae and Cactaceae seem to be little influenced by environmental factors such as elevation and precipitation. Instead, spatial separation mostly accounts for differences in floristic composition among these groups, as they are restricted to specific sites due to by their limited dispersal ability. Indeed, Acanthaceae have autochorous ballistic seed dispersal that takes place on the order of less than a metre to a few metres (Ridley, 1930; Wasshausen, 2004) and Bromeliaceae have anemochorous and zoochorous seed dispersal that strongly influences the range sizes of the species (Kessler, 2002). Especially in subfamily Tillandsioideae, which has wind-dispersed seeds, bromeliads have dispersal distances beyond the range of those of Acanthaceae, but there still appears to be marked dispersal limitation (Kessler, 2002; Mondragon & Calvo-Irabien L., 2006). The zoochorous Bromeliaceae, as well as Cactaceae, which also have zoochorous seed dispersal syndromes, are mainly dispersed by birds and partly by mammals. Although quantitative data on dispersal distances for these taxa is lacking, the isolated position of Andean seasonally dry forests, separated from each other by high mountain ranges clothed in humid montane forest, strongly suggests that dispersal of these taxa between the individual seasonally dry forest regions might be rare. Acanthaceae, Bromeliaceae, and Cactaceae all show high levels of endemism for most of the stud-

ied areas and several of these endemics are rare and of narrow distribution (e.g., *Aphelandra kolobantha* Lindau, a very rare endemic species of scrubfilled gullies in relatively dry Andean valleys, only collected three times; (Wasshausen & Wood, 2004).

Pteridophytes, on the contrary, are more influenced by environmental variables than by spatial separation. The difference in geographical resolution seen between pteridophytes and the three other study groups may reflect the overall wider distribution of the individual pteridophyte species. In fact, all the pteridophyte species had geographical ranges spanning at least 5 degrees latitude, with 92% of the species having ranges extending over at least 10 degrees latitude. If we consider that some of the northern inter-Andean valleys in La Paz cover areas of less than 100 km², then the distributional amplitude of the pteridophyte species explains the low resolution in our biogeographical analyses. This is also evident in the lack of pteridophyte endemics restricted to these valleys, the only endemic species being *Elaphoglossum cruziense* M. Kessler & Mickel, restricted to the Chaco and the adjacent Río Grande. It is probable that the highly effective spore-based anemochorous dispersal system of pteridophytes (Barrington, 1993), possibly aided by anisotropic (direction-dependent) transport along "wind highways" (Muñoz *et al.*, 2004), has contributed many widely dispersed species to these isolated valleys and lowland SDF areas. On the other hand, pteridophytes are well known to be highly dependent on humidity in their distribution (Kessler, 2001) and our analyses reflect this relationship accordingly. Apparently, the geographical separation of SDF sites is less than the maximum distance typically dispersed by spores of most of the pteridophyte species we studied, enabling pteridophytes to colonise most climatically suitable sites, independently of their location. Clearly, at the spatial resolution of our analysis, pteridophytes are not suitable for historic biogeographic analyses.

In conclusion, we found that dispersal efficiency, in combination with spatial separation and differences in environmental conditions, leads to distinct biogeographic patterns in phylogenetically distant plant groups in the island-like SDF system of the

Bolivian inter-Andean valleys. Lower dispersal ability results in a stronger spatial signal in the resulting biogeographic pattern, whereas high dispersal ability leads to a stronger environmental signal. These conclusions are based, however, on a coarse environmental model, which does not necessarily reflect subtle climatic, soil or geological differences. The inclusion of information on e.g., dry season length, minimum and maximum temperatures, soil nutrient composition or human modifications of the habitat (as yet not available uniformly and accurately for each of our studied areas, and in fact for much of the Neotropics) might reveal that some of the studied plant groups are not as dispersal limited as they appear, and that they instead respond to subtle environmental differences. Dated molecular phylogenies on global as well as on more local and recent timescales (Pennington *et al.*, 2006a) and population genetic studies of species characteristic of seasonal forests (e.g., Caetano *et al.*, 2008) should provide additional information on the timing and intensity of dispersal events and, consequently, on the assembly of these communities.

4.5 Acknowledgements

S. Bridgewater and M. Jones provided comments and suggestions on an early version of this paper. Constructive critique and suggestions by two anonymous reviewers and the editor greatly improved the paper. J. Oksanen advised on the use of similarity indices, J. Wood and D. Wasshausen clarified Acanthaceae distribution data. RLP acknowledges financial support from the German Academic Exchange Service (DAAD).

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Chapter 5

Small-scale variation of vascular plant species richness and community composition in a tropical American forest: the role of selective niche partitioning processes

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Summary

1 Using information from total vascular plant inventories in a central Bolivian semi-deciduous forest, we evaluated the relationships that a suite of edaphic, topographic, light and forest structural factors had with plant species richness and community composition of selected plant groups.

2 Our sample, which included 75 0.04-ha square plots located in three adjacent forest types and a total of 670 species of vascular plant and 80352 individuals, was partitioned into the following life-form groups: terrestrial herbs (including pteridophytes), epiphytes, shrubs, lianas and trees.

3 A principal coordinates of neighbor matrices procedure (PCNM) indicated little spatial structure of species richness and abundances of the whole forest community and also of each life-form group.

4 Of 36 Regression and Redundancy Analysis models that we tested for association of species richness and community composition with spatial and environmental factors, four models of species richness patterns could neither be explained by spatial nor by environmental variables. Only one model included spatial structure as the only variable (species richness of herbs in one of the forest types) and two models included the combined effects of spatial and environmental variables. In contrast, 29 models (either species richness or community composition) were explained solely by environmental variables.

5 Although environmental factors were detected as more important than spatial variables, total explained variation for the models was moderate to low (R^2_{adj} for species richness: mean = 0.40, range = 0.20–72; R^2_{adj} for community composition: mean = 0.22, range = 0.04–45).

Synthesis. Our results suggest a major role of above- and below-ground environmental gradients in determining small scale patterns of species richness and community composition of several life-form groups in homogeneous tropical semi-deciduous forest types. Different life-forms, however, were related to different combinations of these factors. And although it is clear that environmental variables (especially

edaphic) play a significant role in species co-existence and community assembly processes at the local scale, other additional factors (such as phylogenetic diversity within the studied communities) must be invoked as well if we are to better understand these processes.

Key-words: Andes, Bolivia, niche-assembly, edaphic factors

5.1 Introduction

The traditional view in community ecology is that the niche is partitioned among competing species, and it is their relative fitness within this niche that determines their abundances (Tilman, 1982, 1988; Chase & Leibold, 2003; Silvertown, 2004). Theoretical models in which stochastic demography and dispersal are more important than niche-related factors, widely known as neutral community models (Hubbell, 2001; Bell, 2000; Chave *et al.*, 2002), have challenged this view by supplying tools and possible answers to the same question: how can so many species co-exist in apparently uniform places like tropical forests and coral reefs. Recent evidence from the very same tropical forests that inspired the development of modern neutral theories is suggesting a much more important role of niche-related processes than advocated by the proponents of neutral theories.

The past years, especially since the publication of Hubbell's *Unified Neutral Theory of Biodiversity and Biogeography* (Hubbell, 2001), have seen an upsurge of theoretical and empirical tests of neutral community models at all spatial scales. Studies trying to find evidence for an environmental control of species richness or community composition in tropical forests have principally focused on soils and woody species, mostly trees (e.g., Jha & Singh, 1990; Oliveira-Filho *et al.*, 1998, 2001; Sollins, 1998). Few other studies analysed the effect of other environmental variables. Clinebell *et al.* (1995); Kreft & Jetz (2007), for example, found that some measure of water availability, topography and habitat heterogeneity (and not soil chemistry) was particularly relevant in predicting richness patterns of woody species

at large geographical scales ($> 1\text{km}^2$), whereas studies on much smaller scales ($< 1\text{km}^2$) showed relationships with light and past disturbances (e.g., Vargas-Rodriguez *et al.*, 2005).

There are also few studies that have focused on other life-forms within homogeneous vegetation (e.g., Poulsen *et al.*, 2006; Tuomisto *et al.*, 2003; Svenning *et al.*, 2004; Tuomisto & Ruokolainen, 2005; Ruokolainen *et al.*, 2007; Jones *et al.*, 2008). For studies assessing the complete plant community we would have to look outside the tropics for additional examples (Gilbert & Lechowicz, 2004).

In this paper, we use detailed quantitative inventory data from an entire vascular plant community in a central Bolivian forest to explore the extent to which different environmental niche gradients (e.g., soil nutrients, light, forest structure) might have influenced the species richness and abundances of the major life-form groups (terrestrial herbs, shrubs, trees, lianas and epiphytes) at local spatial scales.

5.2 Methods

5.2.1 Study area and forest types

The Refugio Los Volcanes is situated in Santa Cruz, Central Bolivia, on the transition from the humid inner tropics to the seasonally dry subtropics. Annual precipitation is about 1200–1400 mm, with high intra-annual variability, although usually with a dry season from April to September/October, where temperatures average 18 °C. The rainy season is slightly warmer with 21 °C (S.K. Herzog, unpublished data).

The vegetation in the region has been broadly classified as subhumid to humid deciduous forests of southeastern Amboró (Navarro *et al.* 1996). Although much of the study area is covered by semi-deciduous forest, the dominant zonal vegetation mainly found on the shaded south-facing slopes, local differences in topography and aspect lead to the presence of deciduous forest (on the steep, sunny and north-facing slopes) and to evergreen forest (in the flat, shaded valleys with groundwater supply).

Within this vegetation matrix, we inventoried 25 adjacent 20 m x 20 m subplots in each forest type (deciduous, semi-deciduous and evergreen) and recorded all vascular plants (terrestrial herbs, epiphytes, lianas, shrubs and trees), yielding 80352 vascular plant individuals belonging to 670 species, including morphospecies. The most species-rich plots were those in the evergreen and semi-deciduous forest with similar numbers of species (381 and 382, respectively), whilst the deciduous forest plot had 297 species. In terms of the number of individuals, the highest density was recorded in the evergreen forest plot (31674 individuals), followed by the deciduous forest plot (26333 individuals) and the semi-deciduous forest plot (22360 individuals). An outstanding aspect of our inventories in these forests was that non-woody life-forms (epiphytes and terrestrial herbs) contributed important proportions to total vascular plant species richness and total abundance. For detailed sampling methodology and complete results of the inventories (including a complete species list), the reader is referred to Linares-Palomino *et al.* (in press).

5.2.2 Environmental data

Soil samples were obtained from each 20 m x 20 m subplot based on three random subsamples taken from 0–20 cm depth. Subsamples were pooled to form one single soil sample per subplot, for a total of 25 samples for the entire hectare, air-dried and sent for analysis to the Department of Plant Ecology and Ecosystems Research, University of Göttingen, Germany. The concentration of salt-extractable soil cations was determined by percolating 2.5 g of soil with 100 ml of 1 M BaCl₂ solution for 6 hours. The concentrations of Mg, Ca, Mn, Al and Fe were analyzed by atomic absorption spectroscopy. Iron was assumed to be Fe²⁺. Phosphorus was measured after percolation by photometric absorption of a phosphate-molybdate-complex. The C and N contents were measured with an elemental analyser (Elementar, Hanau, Germany). pH was measured for the litter layer and each soil horizon (Oh/Of horizon, Ah horizon and B horizon) in the middle of the subplot with a glass electrode in a 1:2.5 water solution and with KCl.

Soil moisture was estimated in each subplot following the Ad-hoc-Arbeitsgruppe Boden (1996). The percentage of tree, shrub and herb cover, as well as the percentage of the subplot covered by rocks and stones and dead wood was estimated visually. Slope of each subplot was estimated in percentage. Tree height was calculated based on the woody plant inventory of each subplot (Linares-Palomino *et al.*, 2008).

Hemispheric photos taken in the centre of each subunit at 1 m above the ground were used to assess light levels on the forest floor. The images were analysed in Adobe Photoshop and the percentage of light intensity reaching the forest floor was then estimated as the proportion of sky (bright areas) to the proportion of area covered by vegetation (darker areas).

5.2.3 Data analysis

We analysed species richness and community composition (abundance) patterns separately for the complete inventory and for each life-form (terrestrial herbs, epiphytes, lianas, shrubs and trees). Species abundance data were Hellinger-transformed to represent proportionate abundances prior to any analysis (Legendre & Gallagher, 2001). All calculations were performed in the R software environment (R Development Core Team, 2008).

We assessed the assumption of a normal distribution for each untransformed environmental variable graphically. Next, we compared each environmental variable among forest type with an analysis of variance. A significant difference among forest type was further assessed with a Tukey Honest Significant Difference test. Next we transformed the environmental variables, except pH which is already a logarithmically transformed value. Soil nutrients were log-transformed to model the responses of organisms to soil nutrient concentration (ter Braak, 1987). Data represented as percentages were arcsin-sqrt transformed (Zar, 1999), whilst categorical variables were split into separate binary variables.

Since we analysed several different life-forms, we produced different sets of ex-

plicative environmental variables for each one (not all measured variables were equally applicable to all studied life-forms). We used all variables for the complete dataset including all life-forms and for terrestrial herbs. For epiphytes, we excluded shrub cover, herb cover, percentage of stones and death wood. For lianas, we excluded herb and shrub cover; for shrubs, shrub and herb cover; and for trees, tree, shrub and herb cover.

We checked for spatial structure in the species richness and community composition data with a principal coordinates of neighbor matrices analysis (PCNM) and used the coordinates of the centre of each subplot to calculate the spatial variables. We used the quickPCNM function (version 7.7, developed by D. Borcard, available at www.bio.umontreal.ca/legendre/indexEn.html) to automatically carry out all steps of the PCNM spatial analysis.

Next we checked the influence of the environmental variables on species richness and community composition with a forward selection analysis by permutation under a reduced model (we used the packfor 0.0-7 package by Dray *et al.* (2007), available at <http://biomserv.univ-lyon1.fr/~dray/software.php>), selecting those variables with a significant ($p = 0.05$ after 999 random permutations) contribution to explaining variation in floristic composition (Blanchet *et al.*, 2008). Only selected variables of soil factors (mineral macro- and micronutrients, pH, soil humidity), topography, vegetation structure (vegetation cover and forest height), and/or habitat variables (light, death wood, stones), in addition to the previously selected spatial PCNM variables, were used to partition the variation of species richness and community composition using multiple regression and redundancy analysis (RDA), respectively, with function varpart in package vegan (Oksanen *et al.*, 2008). This procedure allowed us to quantify the individual and combined contribution of each selected variable. Thus, we were able to assess the partial contributions of spatial structure alone, environmental variables alone, that of spatially structured environmental variables and finally, to quantify the amount of variation left unexplained by our models (Borcard & Legendre, 1994; Legendre & Legendre, 1998).

5.3 Results

5.3.1 Environmental variability

The ANOVAs indicated no significant differences between forest types for three edaphic (Ca, Mn and Al), two structural (shrub cover and tree height) and one environmental variable (light). All other variables showed significant differences between at least one of the forest types and the other two (Table 5.1). Half of all the variables showed either increasing or decreasing values along the deciduous – semi-deciduous – evergreen humidity gradient. It is especially the micro- and macronutrients that showed decreasing values with increasing humidity, whilst pH, tree and herb cover increased with decreasing deciduousness.

High concentrations of C were accompanied by high concentrations in N and Ca in all three forest types (Appendix A.5). Soil humidity decreased with increasing slope in the deciduous forest plot and acted negatively on Fe levels and litter pH. In the semi-deciduous plot, moderate increases in P levels were paralleled by increasing C, N or Ca concentrations. Soil Humidity, however, which also decreased with increasing slope as in the deciduous plot, had moderate to strong negative effects on C, N, P, Ca, litter pH levels.

5.3.2 Spatial and regression analyses

The PCNM analyses detected statistically significant spatial structure in only three cases, all involving terrestrial herbs. In the deciduous forest the analysis detected spatial structure both in species richness and in community composition patterns, whilst in the semi-deciduous only community composition was detected to possess spatial structure. It is only for these combinations of life-form and forest type that we incorporated spatial structure into forward selection analyses (see below).

We tested 36 models by forward selection to find factors potentially influencing species richness and community composition (Table 5.2). Of these, four models of species richness patterns in the deciduous (all vascular plants and lianas) and semi-

Table 5.1: Edaphic, structural and environmental variables in the 75 20 m x 20 m subplots classified by forest type. Figures are means $\pm$ standard errors. In forest types where ANOVAs rejected the null hypothesis of no difference between the means, means followed by different bold letters indicate significant differences detected by a Tukey test ($p < 0.05$).

Variable	Forest type		
	Deciduous N = 25	Semi-deciduous N = 25	Evergreen N = 25
C (mmol/g)	3.03 $\pm$ 1.45 a	1.71 $\pm$ 0.29 b	1.49 $\pm$ 0.80 b
N (mmol/g)	0.26 $\pm$ 0.11 a	0.15 $\pm$ 0.02 b	0.13 $\pm$ 0.06 b
P (μ mol/g TB)	11.55 $\pm$ 8.46 a	6.35 $\pm$ 2.00 b	7.59 $\pm$ 6.49 ab
K (μ mol μ eq/g)	0.18 $\pm$ 0.09 a	0.11 $\pm$ 0.04 b	0.10 $\pm$ 0.05 b
Ca (μ mol μ eq/g)	131.56 $\pm$ 68.46	116.38 $\pm$ 58.94	144.73 $\pm$ 162.15
Mg (μ mol μ eq/g)	51.21 $\pm$ 10.77 a	9.65 $\pm$ 4.53 b	12.30 $\pm$ 6.13 b
Mn (μ mol μ eq/g)	0.17 $\pm$ 0.09	0.16 $\pm$ 0.08	0.12 $\pm$ 0.05
Fe (μ mol μ eq/g)	0.29 $\pm$ 0.22 a	0.20 $\pm$ 0.26 ab	0.09 $\pm$ 0.17 b
Al (μ mol μ eq/g)	3.83 $\pm$ 5.60	2.12 $\pm$ 3.18	3.23 $\pm$ 5.62
pH soil litter (pHL)	6.48 $\pm$ 0.33 a	6.71 $\pm$ 0.66 a	7.25 $\pm$ 0.29 b
pH organic matter (pHO)	6.38 $\pm$ 0.39 a	6.61 $\pm$ 0.40 a	7.08 $\pm$ 0.23 b
pH A horizon (pHA)	6.03 $\pm$ 0.60 a	5.97 $\pm$ 0.61 a	6.64 $\pm$ 0.41 b
pH B horizon (pHB)	5.16 $\pm$ 0.88 a	5.25 $\pm$ 0.68 a	6.09 $\pm$ 0.33 b
Soil Humidity (SH)	NA	NA	NA
Tree cover (%) (TC)	52.40 $\pm$ 17.68 a	63 $\pm$ 11.27 b	68.60 $\pm$ 13.35 b
Shrub cover (%) (SC)	52.80 $\pm$ 25.25	43.48 $\pm$ 17.27	42.88 $\pm$ 10.76
Herb cover (%) (HC)	62.80 $\pm$ 8.91 a	70.60 $\pm$ 9.17 b	75.20 $\pm$ 13.27 b
Slope (%) (Sl)	42.00 $\pm$ 12.08 a	30.80 $\pm$ 11.52 b	41.60 $\pm$ 16.18 a
Stone (%) (St)	13.00 $\pm$ 12.50 a	2.40 $\pm$ 2.93 b	13.00 $\pm$ 10.41 a
Dead wood (%) (DW)	15.20 $\pm$ 4.67 a	27.52 $\pm$ 10.27 b	21.00 $\pm$ 12.99 ab
Light (%) (L)	13.80 $\pm$ 5.51	11.73 $\pm$ 4.70	13.82 $\pm$ 4.72
Tree height (m) (TH)	10.23 $\pm$ 1.48	11.13 $\pm$ 1.92	10.71 $\pm$ 1.55

deciduous forest plots (epiphytes and shrubs) could neither be explained by spatial nor by environmental variables. Species richness of herbs in the deciduous forest was the only model that included spatial structure as the only variable (six PCNM vectors, $R^2_{adj} = 0.72$). In contrast, 29 models (either species richness or community composition) could be explained solely by environmental variables (depending on the plant group and forest type, one to six variables were included). Two models, community composition of herbs in the deciduous and semi-deciduous forest, were explained by both selected environmental variables ($R^2_{adj} = 0.37$ and $R^2_{adj} = 0.14$, respectively) and spatial structure ($R^2_{adj} = 0.02$ and $R^2_{adj} = 0.10$, respectively). A higher variance was always explained in species richness models than in the corresponding community composition models.

Of the environmental variables, the variables that entered most models were soil Mg, soil Ca and soil humidity. In the deciduous forest plot, soil humidity, P and Mg were the variables responsible for explaining most community variation. In the semi-deciduous plot, it was mainly Ca, in the evergreen plot they were soil humidity and Mg.

All vascular plants (Table 5.2): we found no combination of spatial or environmental variables to adequately explain species richness in the deciduous forest. Different variables were found to explain species richness in the semi-deciduous and evergreen forest plots and the highest predictive power was attained in the evergreen forest ($R^2_{adj} = 0.43$). Total community composition was also predicted by a different set of variables in each forest type. Soil humidity was the only variable included in all forest types. Other variables entered the models at most in two different forests (Mg, tree height and shrub cover).

Terrestrial herbs (Table 5.2): the spatial configuration of the plants seemed to be an important factor in herb species richness, less so in community composition. In the deciduous forest, space alone explained most of the variation ($R^2_{adj} = 0.72$), with no additional environmental variables included in the models. In contrast, variation in species richness patterns in the semi-deciduous and evergreen forest plots was

Table 5.2: Results of the forward selection analyses of different life forms in three tropical forest types. Adjusted R-square values for the complete model are given in parentheses, except for models where both spatial and environmental variables were selected. In the later case, adjusted R-square values for individual spatial and environmental variables are given. Life forms: all=all life forms, epi=epiphytes, her= terrestrial herbs, lia=lianas and vines, shr=shrubs, tre=trees. Variables: SH=soil humidity

	Richness		Community composition	
	Space	Environment	Space	Environment
			Deciduous Forest	
all	X	X	X	SH 1, Tree Height, Mg, Shrub Cover, P, Al (0.30)
epi	X	Mg (0.24)	X	Tree Height, P (0.21)
her	6 PCNM variables (0.72)	X	1 PCNM variable (0.02)	SH 1, Mg, Shrub Cover, K (0.37)
lia	X	X	X	Stones (0.04)
shr	X	pH A (0.20)	X	SH 1, Slope, P, Mg (0.29)
tre	X	Death Wood (0.39)	X	SH 1, P, Al, Slope, Mg (0.28)
			Semi-deciduous Forest	
all	X	pH L (0.25)	X	Ca, Shrub Cover, SH 3, Mg (0.16)
epi	X	X	X	Ca, SH 3 (0.11)
her	X	Death Wood, pH B (0.27)	3 PCNM variables (0.10)	Shrub Cover, pH L (0.14)
lia	X	Ca (0.40)	X	Mg, pH L, K, pH O (0.21)
shr	X	X	X	Ca, Light (0.15)
tre	X	SH 3 (0.28)	X	SH 3, Ca (0.11)
			Evergreen Forest	
all	X	SH 4, Al (0.43)	X	SH 4, Mn, Tree Height, pH L (0.25)
epi	X	Mn, SH 3, Mg (0.51)	X	SH 4, Mn, Tree Height, pH L, Ca (0.27)
her	X	SH 4 (0.53)	X	SH 4, Slope, Ca, Al, Herb Cover, Tree Height (0.45)
lia	X	Mg, Stones (0.37)	X	Light, Mg (0.10)
shr	X	Ca, P, pH B, K (0.60)	X	SH 4, Mn, Light (0.17)
tre	X	Stones, Al (0.36)	X	SH 4, SH 3, Stones, Mn (0.19)

related to the environment. Community composition patterns were mostly related to soil variables and overall forest structure, and no single variable was repeated in all forest types.

Epiphytes (Table 5.2): soil magnesium content seemed to be an important factor influencing species richness patterns in the deciduous and evergreen forest plots. It was in the latter where we found a higher explained variance with the combination of Mg, Mn and soil humidity ($R^2_{adj} = 0.51$). Several and different variables were related to the composition of epiphyte communities. It was again in the evergreen forest that the variables explained most of the variation, although including five variables, whereas in the other two plots only two variables were selected. Soil calcium and soil humidity seemed to be important in the more humid forests.

Lianas (Table 5.2): specie richness of lianas in the semi-deciduous and evergreen forest plots was related to few soil characteristics that explained a relatively high amount of variance ($R^2_{adj} = 0.40$ and $R^2_{adj} = 0.37$, respectively). Community composition of lianas, in contrast, was related to several different variables explaining little variance in the models (R^2_{adj} values from 0.04 to 0.21), and none was included in models of all three forest types. Neither spatial nor environmental variables explaining a substantial amount of the variation of specie richness and composition patterns in the deciduous forest could be detected.

Shrubs and trees (Table 5.2): species richness patterns were related to several and different soil characteristics explaining a substantial amount of variation (R^2_{adj} values from 0.20 to 0.60). Soil Ca, P, K and pH B explained 60% of the variation in species richness of shrubs in the evergreen forest plot. Within the same plot, there was a high coincidence in both the variables that best explained community composition patterns and the amount of variance explained. Between forest types, however, different sets of variables best explained community composition patterns. Soil humidity was the exception, being included in the models for all three forest types.

5.4 Discussion

Within homogeneous forest types, the patterns of species richness and community composition of several life-form groups seemed to be primarily determined by gradients in above- and below-ground environmental factors. Different life-forms, however, were related to different suites of these factors. This is the main conclusion suggested by our results. The strength and nature of these relationships (as inferred from explained variation and the combination of the several environmental factors, respectively), varies as well, and is higher when analysing species richness than when looking at species abundances. In order to better visualize these results we calculated Pearson correlations for species richness and Mantel correlations for abundances with all environmental factors and performed a PCA of the latter with each one of the correlation coefficients (Fig. 5.1a,b). The graphical representation of these relationships confirms our previous assertions.

These results agree with the observation of Gilbert & Lechowicz (2004) who noted that even though environmental factors were consistently important in determining the distribution of vascular plants in a Canadian temperate forest, different plant groups were not affected equally by the various environmental gradients. We also show, that neither species richness nor community composition patterns had significant spatial structure, if any at all. In fact, only species richness patterns of terrestrial herbs showed some degree of spatial structure that explained part of their total variation. A similar conclusion was reached in a study looking at relationships between floristic and edaphic variation in the lowland rain forests of Amazonian Ecuador (Poulsen *et al.*, 2006) and Peru (Ruokolainen *et al.*, 2007). These studies found that the strongest predictors of floristic variation in angiosperm ground herbs, pteridophytes, palms and trees were topography and selected soil cations (Na and Ca in the Ecuador study, Ca and Mg in the Peru study). The contribution of spatial distance between sampling units was in contrast little or negligible (see also Phillips *et al.*, 2003; Potts *et al.*, 2002, for equivalent results at the landscape and regional spatial scales). The novel methodological addition from our work is

(a) Species richness

(b) Community composition

Figure 5.1: Behaviour of Pearson (a) and Mantel (b) correlation values between environmental variables and plant groups in three different forest types. Abbreviations of the variables follow those in Table 5.1

that we included additional environmental factors, and the floristic composition of several life-forms in the Los Volcanes forest plots was significantly correlated with edaphic and topographic variables, but also with structural characteristics of the forests, presence of stone outcrops, death wood and light incidence. Several of these last factors have been shown to contribute to explain variation of community composition at the local to small scale, especially in trees. For instance, Balvanera *et al.* (2002); Vargas-Rodriguez *et al.* (2005); Oliveira-Filho *et al.* (1998); Webb & Peart (2001) report several measures of light (e.g., measured as gaps in the canopy or at lower levels, or solar radiation interception in the canopy) as an important predictor of tree distributions (including their seedlings and saplings), together with soil and topographical variables.

It is notable, that the explained variation of species richness or community composition included such an extensive range of values (R^2_{adj} values from 0.20 to 0.72 in species richness models and from 0.04 to 0.45 in community composition models, respectively). Most of the times, however, unexplained variation constituted the greater value. What is more, some of the data from Los Volcanes could not be predicted at all by any combination of our suite of variables (spatial nor environmental). Bell *et al.* (1993) showed that environmental factors have a strong spatial structure, even at scales below the metre. Since our sampling units were composed of 20 m x 20 m square plots, this could have been too coarse a scale and a possible reason for some of our models not being adequately predicted by our data. But even finer grained studies (e.g., Jones *et al.*, 2008) failed to explain much of the variation in their data, and it is more probable that important factors such as phylogenetic information and regional scale population dynamics of the species present in the Los Volcanes communities were left out. The inclusion of phylogenetic information of the species that compose a community as an additional explanatory factor in the search for species co-existence and assembly mechanisms is a promising new research area (Webb, 2000; Webb *et al.*, 2002; Graham & Fine, 2008; Kelly *et al.*, 2008; Lavin & Beyra-Matos, 2008). Similarly, since local species

assemblages are not isolated entities (neither in time nor in space), but interact constantly with neighbouring communities (i.e., the metacommunity concept, Hubbell, 2001; Holyoak *et al.*, 2005), inclusion of regional population dynamics and ranges of the species that compose the community have a great potential to add to our understanding of these mechanisms (Harrison & Cornell, 2008; Ricklefs, 2008).

5.5 Acknowledgements

RLP acknowledges financial support from the German Academic Exchange Service (DAAD).

5.6 References

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Chapter 6

General conclusions

6.1 A summary of major Findings

- **Vascular plant diversity in central Bolivian sub-Andean forest types.**

The complete vascular plant inventory of three 1-ha plots in a central Bolivian forest contained an estimated 6–7% of all the currently known Bolivian plants, with 670 species and 80352 individuals. Orchidaceae, Pteridophyta and Leguminosae were among the most species-rich major plant groups in each plot and *Peperomia* (Piperaceae), *Pleurothallis* (Orchidaceae) and *Tillandsia* (Bromeliaceae), all epiphytes, were the most species-rich genera. Despite these commonalities, species turnover between the deciduous, semi-deciduous and evergreen forest plots was relatively high with less than 60% similarity. More importantly though was the fact that the non-woody life-forms in these Andean foothill forest ecosystems were outstanding in terms of species richness and numbers of individuals, representing roughly 30–50% of the species and between 50–75% of the individuals in the community. This was especially true for epiphytes and terrestrial herbs and in stark contrast with the levels of diversity and abundance found for woody life-forms and especially for trees with a dbh ≥ 10 cm.

Together, these data show that these Central Bolivian forest plots are similar in total and individual life-form species richness to other dry deciduous and humid montane forests in the neotropics, but less rich than most Amazonian

forests.

- **The phytogeography of the tree flora of a central Bolivian forest.**

Of the 115 tree species found at Los Volcanes, eleven that were present in all three plots represented a selection of the tree species characteristic of the Amboró region like *Aspidosperma cylindrocarpum*, *Gallesia integrifolia* and *Pachystroma longifolium*. Interestingly, however, few of these species were dominant and abundant on each of the plots, with most being locally rare species (at least at the hectare-scale) and with abundances of one individual per hectare.

Although the general vegetation of the region is characterised as semi-deciduous (Navarro & Maldonado, 2002), a comparison with other similar vegetation types in Bolivia showed surprisingly little similarity. This might have been caused by the complex vegetational arrangement of the study area (Ibisch & Merida, 2003), composed of the adjacent humid vegetation from Amazonia, seasonal subtropical lowland vegetation from the Chaco, subtropical highland vegetation from the Andes and seasonal vegetation of the Chiquitanía. This setting suggests an answer for the high turnover of species in the Los Volcanes plots and their low resemblance to other similar vegetation types in Bolivia.

On a wider geographical context, and considering that Los Volcanes is located within the dry forest Pleistocenic Arc formation in the Neotropics (Prado & Gibbs, 1993; Prado, 2000), we found some species in our plots that have been considered as characteristic (*Anadenanthera colubrina*, *Myracrodruon urundeuva* and *Celtis iguanaea*) and restricted to certain areas (*Diatenopteryx sorbifolia*) of this arc. Together with other species said to belong to this arc, although with more complex distribution patterns, we found a total of 21 species as typical of Bolivian seasonal forest formations.

- **Biogeographical patterns of seasonally dry forests in Andean Bolivia.** Separate floristic analyses of presence-absence data obtained for species

of Acanthaceae, Bromeliaceae, Cactaceae and Pteridophyta found in 12 seasonal forest areas in Bolivia showed incongruent biogeographic relationships. Only Acanthaceae and Bromeliaceae, and partly Cactaceae, showed coincident patterns, suggesting the existence of two main groups of seasonally dry forests in Bolivia. A first group would be composed of the northern sites and characterized by small areas isolated in the inter-Andean dry valleys and heavily affected by anthropogenic activities. The second group includes the seasonally dry forests in the southern Bolivian Andes and lowlands, characterized by covering greater expanses of land and with strong links to the adjoining Chaco and Chiquitanía seasonal forests. They are, nevertheless, also seriously under constant threat from land conversion, fragmentation and similar anthropogenic activities. Pteridophytes on the other hand proved to be of little use in revealing biogeographic patterns among the studied areas. Their ubiquitous presence in most of the dry forest sites, facilitated by their spore-based dispersal mechanism, hindered the recognition of clear patterns, with most sites having similar levels of similarity.

- **The relative importance of environmental or neutral mechanisms to explain species coexistence in tropical forests at large regional and local spatial scales.** The large scale study in the seasonally dry forest islands of Andean Bolivia showed that, depending on the dispersal characteristics of the studied plant group, either environmental factors or the distance between suitable areas were more important in explaining current community composition in these forests. Most of the variation in the beta-diversity of the plant groups with seed dispersal typically restricted to short distances (Acanthaceae: ballistichory, and Bromeliaceae: anemochory and zoochory) was explained by spatial separation between habitat islands, suggesting dispersal limitation and an inadequacy to reach even adjacent areas suitable for colonization. In contrast, the floristic differences between dry forest sites using pteridophyte data were primarily determined by the environmental variables (total annual rain-

fall and altitudinal range of the sites). The spore-based dispersal system of this plant group, easily transported by wind over large distances, seems to be a highly effective mechanism for the colonization of even the most isolated dry valleys in inter-Andean Bolivia. Successful establishment of these spores is then finally dependent on the environmental conditions of each reached area. Accordingly, at the large scale it seems that both niche-related mechanism and spatial dispersal processes structure the dry forest metacommunities in the Bolivian Andes. The relative importance of each one, however, seems to depend ultimately on dispersal traits specific to each taxon.

The local scale study at Los Volcanes showed that gradients in several above- and below-ground environmental variables were the best predictors of the observed patterns in species richness and community composition. They also showed little support for space (dispersal) related variables having any influence on species richness and community composition patterns of the whole plant assemblage nor of individual life-form groups. A notable exception was species richness of terrestrial herbs (and to a lesser extent their abundances), showing strong spatial structure. Although soil variables (such as soil Mg, soil Ca and soil humidity) entered most models, there were ample differences in the combination of factors determining each pattern in each life-form group.

Finally, a substantial portion of the variation in the data of the local (Los Volcanes) and large scale (Bolivia) study could not be explained by the chosen variables, indicating a need for the inclusion of additional, especially historical (i.e., temporal) and phylogenetic factors.

6.2 Implications of the Findings

Total vascular plant inventories in tropical forests are logistically difficult and time-consuming tasks and surely the reason why there are so few of them. However, they provide extremely relevant information. In addition to giving basic information about species diversity, vegetation structure and floristic relationships, the whole-

plant survey from Los Volcanes reported in Chapter 2, showed that non-woody life-forms contribute to a major part of the species richness and community abundances in these central Bolivian forests. This information is of utmost relevance to tropical forest characterization and conservation because tree inventories are still being used extensively as a major source of information to define vegetation types. Although trees are the major structural element of these forests, the present results also showed that there is not always a strong correlation between them and other life-forms. Thus, forests characterized by high species richness and/or abundances of trees and woody species are not necessarily equally rich and abundant in other life-forms. As a result, we might be missing an important component of the forest diversity. These findings point to a necessary change in the way conservation decisions are made: we also need to take into account the non-woody component of the forest to make more informed decisions.

The phytogeography of the seasonally dry forests in Andean Bolivia is interesting because of the uplift history of the Andes, considered to be major cause of biogeographical barriers in the region (Sarmiento, 1975). Separate biogeographical analyses of plant groups differing in ecological characteristics and phylogenetic relationships, as those performed in Chapter 3, can lead to diametrically opposite scenarios. This hinders the extrapolation of the results to the whole flora in the seasonally dry forests in Andean Bolivia. Thus, a definitive answer as to the true biogeographical relationships and subdivisions of the seasonally dry forests in Andean Bolivia must necessarily take into account information from other plant groups present in the studied seasonal forests.

The findings presented in this dissertation (Chapter 4 and 5) add to the increasing evidence (Balvanera *et al.*, 2002; Duivenvoorden *et al.*, 2002; Cottenie, 2005; Holyoak & Loreau, 2006) that gradients in environmental variables and distance-dispersal related processes act, sometimes together and sometimes decoupled, with different strength at different spatial scales influencing species richness and community composition. Thus, any study of the mechanisms influencing them should

necessarily consider both neutral and non-neutral processes.

6.3 Limitations of the Study and Suggestions for Further Research

As stated above, complete vascular plant inventories like that done in Los Volcanes are notoriously difficult. Worldwide, there are very few other comparable studies and most were performed in neotropical rain forests (Whitmore *et al.*, 1985; Gentry & Dodson, 1987; Duivenvoorden, 1994; Balslev *et al.*, 1998; Galeano *et al.*, 1998; Langenberger *et al.*, 2006). The data presented in Chapter 2 suggest some very important patterns, but it would be interesting to explore how different life-forms contribute to overall species richness and total abundances in other (neo-)tropical vegetation types.

The phytogeographic study in Andean Bolivia had an important limitation, namely the use of (mostly) understory members of the studied seasonally dry forest. Since trees are the main structural element of these forests, it is unclear to what extent these results are valid for other plant groups or families, or even the whole seasonally dry forest flora. Unfortunately, few plant groups have been revised so intensively taxonomically and using geographically extensive collections as those used in Chapter 4. There is clearly a need for accurate taxonomy based on extensive distributional data for most taxa in the tropics (Campbell & Hammond, 1989; Thomas, 1999), but this information is fundamental for a better understanding of extant floristic relationships. When this information becomes available for each of the dry forest areas in Bolivia, a biogeographical analysis of a suite of representative woody genera or families (together with more and finer grained environmental data) will surely increase our understanding of the floristics and evolution of the vegetation in Andean Bolivia.

A substantial amount of the variation in species richness and community composition of the Los Volcanes plots remained unexplained. This fraction can be under the influence of unmeasured variables or it may be determined by community pro-

cesses such as competition or dispersal that need to be explored (Jones *et al.*, 2008; Legendre, 2008). A promising new avenue of research is the combination of community ecology methods such as those used in this dissertation (i.e., including several critical environmental factors and space as explanatory variables) with phylogenetic methods. The increasing resolution in many of the world's organisms phylogenies due to faster acquirement of molecular data and more powerful analyses, has the potential to bring evolutionary and phylogenetic information into a combined community assembly model (Webb *et al.*, 2002, 2006). For now, an end of the niche assembly - neutral assembly controversy is as yet not foreseeable. The final result will be most probably a synthetic theory integrating both, as well as the evolutionary history of the species in the community.

6.4 References

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Appendices

A.1 Appendix 1 to Chapter 2

Whole plant, epiphyte, liana, terrestrial herb and tree/woody plant inventories in the Neotropics. All references are cited in the main text except:

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	Reference	No.	Area	Precipitation	Altitude	Notes
		Species	(ha)	(mm/year)	(m)	
Whole plant counts						
Los Volcanes-D	This Study	297	1	1200-1500	1100	
Los Volcanes-SD	This Study	382	1	1200-1500	1000	
Los Volcanes-E	This Study	381	1	1200-1500	1000	
Nuqui (CO)	Galeano et al. 1998	488	0.4	5100	<300	Woody plant shorter than 1.3m not sampled
Coqui (CO)	Galeano et al. 1998	489	0.4	5100	<300	Woody plant shorter than 1.3m not sampled
El Amargal (CO)	Galeano et al. 1998	442	0.1	5100	<300	Saplings less than 50 cm not sampled
Caquetá (CO)	Duivenvoorden 1994	313	0.1	3060	<300	Only most diverse 0.1 plot con- sidered
La Selva (CR)	Whitmore et al. 1985	233	0.01	4000	100	Destructive sampling
Cuyabeno (EC)	Balslev et al. 1998	942	1	3555	260	Shrubs and trees 1-5 cm sam- pled in subplot of 0.49ha

Río Palenque (EC)	Gentry and Dodson 1987	365	0.1	2890	<220	
Jauneche (EC)	Gentry and Dodson 1987	169	0.1	1855	<220	
Sinamary (FG)	Bordenave et al. 1998	203	0.05	NA	40	Destructive sampling
Capeira (EC)	Gentry and Dodson 1987	173	0.1	804	<220	
Sehuencas A (BO)	Ibisch 1996	108	0.01	3540	2150	
Sehuencas B (BO)	Ibisch 1996	65	0.01	3540	2150	
Sehuencas C (BO)	Ibisch 1996	128	0.02	3540	2200	
Sehuencas D (BO)	Ibisch 1996	146	0.02	3540	2100	
Sehuencas E (BO)	Ibisch 1996	115	0.02	3540	2100	
Epiphytes						
Los Volcanes-D	This Study	67	1	1200-1500	1100	
Los Volcanes-SD	This Study	81	1	1200-1500	1000	
Los Volcanes-E	This Study	109	1	1200-1500	1000	
Caquetá (CO)	Benavides et al. 2005	213	0.75	3060	<300	Various physiographic units sampled
Chiribiquete (CO)	Arévalo and Betancur 2004	183	0.2	3100-3876	<330	Four physiognomic units
Surumoni (VE)	Nieder et al. 2000	53	1.5	2700	100	
Nuqui (CO)	Galeano et al. 1998	111	0.4	5100	<300	Erect + climbing epiphytes

Coqui (CO)	Galeano et al. 1998	174	0.4	5100	<300	Erect + climbing epiphytes
El Amargal (CO)	Galeano et al. 1998	101	0.1	5100	<300	Erect + climbing epiphytes
Caquetá (CO)	Duivenvoorden 1994	58	1	3060	<300	Various physiographic units sampled.
La Selva (CR)	Whitmore et al. 1985	61	0.01	4000	100	Destructive sampling
Cuyabeno (EC)	Balslev et al. 1998	172	1	3555	260	
Río Palenque (EC)	Gentry and Dodson 1987	127	0.1	2890	<220	Including
hemiepiphytes						
Jauneche (EC)	Gentry and Dodson 1987	13	0.1	1855	<220	Including hemiepiphytes
Sinamary (FG)	Bordenave et al. 1998	33	0.05	NA	40	Destructive sampling
Capeira (EC)	Gentry and Dodson 1987	3	0.1	804	<220	Including hemiepiphytes
Veracruz (MX)	Hietz and Hietz-Seifert 1995	39	0.0625	1850	1980	
Lianas						
Los Volcanes-D	This Study	64	1	1200-1500	1100	
Los Volcanes-SD	This Study	86	1	1200-1500	1000	
Los Volcanes-E	This Study	44	1	1200-1500	1000	

Yasuní (EC)	Burnham 2004	88	1	2400	<300	Mean of 12 subsampled 1ha plots, only lianas more than 1cm included
Yasuní (EC)	Nabe-Nielsen 2001	138	0.4	2932-3265	240	
Oquiriquia (BO)	Perez-Salicrup et al. 2001	51	1	1200-1700	200	Only lianas more than 2 cm included
La Selva (CR)	Mascaro et al. 2004	60	0.0864	4000	NA	Only lianas more than 1.3 m height and 2 cm dbh
Nuquí (CO)	Galeano et al. 1998	62	0.4	5100	<300	
Coquí (CO)	Galeano et al. 1998	25	0.4	5100	<300	
El Amargal (CO)	Galeano et al. 1998	30	0.1	5100	<300	
Caquetá (CO)	Duivenvoorden 1994	342	1	3060	<300	Various physiographic units sampled.
La Selva (CR)	Whitmore et al. 1985	20	0.01	4000	100	Destructive sampling
Cuyabeno (EC)	Balslev et al. 1998	99	1	3555	260	
Río Palenque (EC)	Gentry and Dodson 1987	48	0.1	2890	<220	
Jauneche (EC)	Gentry and Dodson 1987	101	0.1	1855	<220	
Sinamary (FG)	Bordenave et al. 1998	42	0.05	NA	40	Destructive sampling

Capeira (EC)	Gentry and Dodson 1987	77	0.1	804	<220
Terrestrial Herbs					
Los Volcanes-D	This Study	30	1	1200-1500	1100
Los Volcanes-SD	This Study	41	1	1200-1500	1000
Los Volcanes-E	This Study	57	1	1200-1500	1000
BCI (PA)	Royo and Carson 2005	47	0.1792	2600	130
Cuyabeno (EC)	Poulsen and Balslev 1991	56	1	2479-3244	260
Manaus (BR)	Costa 2004	35	0.088	2478	<300
Nuqui (CO)	Galeano et al. 1998	96	0.4	5100	<300
Coqui (CO)	Galeano et al. 1998	61	0.4	5100	<300
El Amargal (CO)	Galeano et al. 1998	63	0.1	5100	<300
Caquetá (CO)	Duivenvoorden 1994	145	1	3060	<300
					Various physiographic units sampled.
La Selva (CR)	Whitmore et al. 1985	16	0.01	4000	100
Río Palenque (EC)	Gentry and Dodson 1987	50	0.1	2890	<220
Jauneche (EC)	Gentry and Dodson 1987	18	0.1	1855	<220
Sinamary (FG)	Bordenave et al. 1998	34	0.05	NA	40
					Destructive sampling

Capeira (EC)	Gentry and Dodson 1987	50	0.1	804	<220
Trees (dbh $\geq$ 10 cm)					
Los Volcanes-D	This Study	71	1	1200-1500	1100
Los Volcanes-SD	This Study	105	1	1200-1500	1000
Los Volcanes-E	This Study	84	1	1200-1500	1000
Lowland humid forests					
Alto Ivon (BO)	Boom 1987	94	1	1550	200
R. Blanco y Negro (BO)	Vargas et al. 1994	90	1	1400	300
Río Colorado (BO)	Smith and Killeen 1998	78	1	2500	270
Los Fierros (BO)	Saldias et al. 1994	75	1	1500	300
Río Saguay (BO)	Vargas 1995	67	1	1700	360
Nuqui (CO)	Galeano et al. 1998	86	0.4	5100	<300
Coqui (CO)	Galeano et al. 1998	80	0.4	5100	<300
El Amargal (CO)	Galeano et al. 1998	34	0.1	5100	<300
Caquetá (CO)	Duivenvoorden 1994	303	1	3060	<300
					Various physiographic units.
					Trees, shrubs and woody vines
					smaller than 50 cm not sampled
La Selva (CR)	Whitmore et al. 1985	NA	0.01	4000	100
					Destructive sampling

Cuyabeno (EC)	Balslev et al. 1998	307	1	3555	260	Shrubs and trees 1-5 cm sampled in subplot of 0.49ha
Río Palenque (EC)	Gentry and Dodson 1987	32	0.1	2890	<220	
Jauneche (EC)	Gentry and Dodson 1987	30	0.1	1855	<220	
Sinamary (FG)	Bordenave et al. 1998	NA	0.05	NA	40	Destructive sampling
Lowland deciduous forests						
Las Torres (BO)	Seidel, in Smith and Killeen 1998	40	1	1500	350	
Cerro Pelao (BO)	Seidel, in Smith and Killeen 1998	62	1	1500	400	
JB Santa Cruz (BO)	Saldias 1991	34	1	1150	375	
Capeira (EC)	Gentry and Dodson 1987	29	0.1	804	<220	
Montane humid forest						
Cumbre Pilon (BO)	Smith and Killeen 1998	146	1	2500	900	
Sapecho (BO)	Seidel, in Smith and Killeen 1998	118	1	1600	700	
Montane cloud forest						

San Rafael, Amboró (BO)	Vargas 1995	50	1	1500	1500
Trees and Shrubs, dbh $\geq$ 2.5 cm (Gentry forest transect dataset, www.mobot.org/MOBOT/research/gentry/transect.shtml)					
Lowland humid forests					
La Selva (CR)	Gentry @ Mobot.org	102	0.1	4000	100
El Encanto (BO)	Gentry @ Mobot.org	74	0.1	1700	280
Alto Madidi (BO)	Gentry @ Mobot.org	146	0.1	3000	280
Nuevo Mundo (BO)	Gentry @ Mobot.org	116	0.1	1820	160
Río Negro (BO)	Gentry @ Mobot.org	130	0.1	1820	100
Alter do Chao (BR)	Gentry @ Mobot.org	30	0.1	2000	50
Boraceia (BR)	Gentry @ Mobot.org	102	0.1	3500	800
Ducke Reserve (BR)	Gentry @ Mobot.org	203	0.1	2200	80
Manaus (BR)	Gentry @ Mobot.org	84	0.1	2000	85
Belem-Mocambo (BR)	Gentry @ Mobot.org	101	0.1	2760	20
Anchicaya (CO)	Gentry @ Mobot.org	111	0.1	3100	300
Araracuara (CO)	Gentry @ Mobot.org	217	0.1	3250	200
Bajo Calima (CO)	Gentry @ Mobot.org	212	0.1	7470	50
Tutunendo (CO)	Gentry @ Mobot.org	226	0.1	9000	90
Fila de Bilsa (EC)	Gentry @ Mobot.org	86	0.1	2500	280

Jatun Sacha (EC)	Gentry @ Mobot.org	182	0.1	4100	450
Río Palenque (EC)	Gentry @ Mobot.org	98	0.1	2650	150
Saul (GF)	Gentry @ Mobot.org	120	0.1	2358	300
Berbice River (GU)	Gentry @ Mobot.org	90	0.1	2200	160
Allpahuayo (PE)	Gentry @ Mobot.org	208	0.1	3000	130
Bosque von Humboldt (PE)	Gentry @ Mobot.org	118	0.1	2500	270
Cabeza de Mono (PE)	Gentry @ Mobot.org	123	0.1	4000	320
Lowland deciduous forests					
Curuyuqui (BO)	Gentry @ Mobot.org	29	0.1	450	350
Perseverancia (BO)	Gentry @ Mobot.org	70	0.1	1350	100
Quiapaca (BO)	Gentry @ Mobot.org	53	0.1	900	300
Santa Cruz (BO)	Gentry @ Mobot.org	37	0.1	1200	375
Yanaigua (BO)	Gentry @ Mobot.org	27	0.1	400	250
Coloso 1 (CO)	Gentry @ Mobot.org	74	0.1	1000	300
Galerazamba (CO)	Gentry @ Mobot.org	34	0.1	500	10
Loma de los Colorados (CO)	Gentry @ Mobot.org	84	0.1	1000	200
Lomas de Santo Tomas (CO)	Gentry @ Mobot.org	57	0.1	1500	320
Tayrona National Park (CO)	Gentry @ Mobot.org	49	0.1	1500	50

Capeira (EC)	Gentry @ Mobot.org	40	0.1	800	50
Perro Muerto (EC)	Gentry @ Mobot.org	50	0.1	1550	450
Tarapoto (PE)	Gentry @ Mobot.org	73	0.1	1400	350
Blohm Ranch (VE)	Gentry @ Mobot.org	46	0.1	1400	100
Boca de Uchire (VE)	Gentry @ Mobot.org	51	0.1	1200	150
Montane humid forest					
Calabatea (BO)	Gentry @ Mobot.org	89	0.05	2000	1500
Chaquimayo (BO)	Gentry @ Mobot.org	52	0.1	1600	1000
Incahuara (BO)	Gentry @ Mobot.org	141	0.1	3500	1520
Sacramanto (BO)	Gentry @ Mobot.org	78	0.1	2450	2380
Alto de Cuevas (CO)	Gentry @ Mobot.org	90	0.1	4000	1670
Alto de Saa (CO)	Gentry @ Mobot.org	50	0.1	4500	2660
Alto de Mirador (CO)	Gentry @ Mobot.org	65	0.1	2500	1180
Antado (CO)	Gentry @ Mobot.org	113	0.1	4500	1560
Carpanta Siete Cuerales (CO)	Gentry @ Mobot.org	61	0.1	3000	2350
Carpanta (CO)	Gentry @ Mobot.org	34	0.1	3000	2900
Cuangos (EC)	Gentry @ Mobot.org	119	0.1	2500	1500
El Corazon (EC)	Gentry @ Mobot.org	40	0.1	3700	3150

Maquipuna (EC)	Gentry @ Mobot.org	94	0.1	3000	1630
Cerro Aypate (PE)	Gentry @ Mobot.org	41	0.1	1800	2770
La Genoa (PE)	Gentry @ Mobot.org	81	0.1	2000	1140

A.2 Appendix 2 to Chapter 2

Presence/Absence species list collected in the Los Volcanes deciduous (DF), semi-deciduous (SDF) and evergreen (EF) forest plots in Santa Cruz, Bolivia. Life-forms: h=terrestrial herb, e=epiphyte, he=hemiepiphyte, l=liana, s=shrub, ss=subshrub, t=tree, tl=treelet, p=parasite

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Acanthaceae	Cylindrosolenium	sp.			s	1	0	0
Acanthaceae	Justicia	lilloi			s	1	1	0
Acanthaceae	Justicia	ramulosa			s	1	0	0
Acanthaceae	Justicia	tenuistachys			s	0	1	1
Acanthaceae	Lophostachys	alvarezia		Nees	s	1	1	1
Acanthaceae	Mendocia	bivalvis		(Linn.)Merr.	s	0	0	1
Acanthaceae	Mendoncia	glabra		Nees	l	1	0	0
Acanthaceae	Ruellia	brevifolia			s	1	1	0
Acanthaceae	Ruellia	sanguinea			e	0	0	1
Acanthaceae	Ruellia	sp.			s	1	0	0
Acanthaceae	Ruellia	sp.1			s	1	0	0
Acanthaceae	Ruellia	sp.2			s	1	0	0
Acanthaceae	Schaueri	azaleifolia			s	1	0	0
Acanthaceae		Ind.1			s	0	1	0
Acanthaceae		Ind.10			s	0	1	0
Acanthaceae		Ind.2			s	0	0	1
Acanthaceae		Ind.3			s	0	0	1
Acanthaceae		Ind.4			s	0	0	1
Acanthaceae		Ind.5			s	1	0	0
Acanthaceae		Ind.6			s	1	0	0
Actinidiaceae	Sarauria	peruviana		Buscal.	s	0	0	1
Amaranthaceae	Chamissoa	altissima		(Jacq.) Kunth	l	1	0	0
Amaranthaceae	Gomphrena	vaga		L.	s	0	1	1
Amaranthaceae	Hebanthe	occidentalis			l	0	1	1
Amaranthaceae	Irisine	diffusa	var.diffusa	Willd.	s	1	1	1

Family	Genus	Species	Variety	Author(s)	Life-form	DF	SDF	EF
Anacardiaceae	Myracrodruon	urundeuva		Allemao	t	1	0	0
Anacardiaceae	Schinopsis	hankeana		Engl.	t	1	0	0
Anacardiaceae	Tapirira	guianensis cf.		Aubl.	t	0	1	0
Annonaceae	Guatteria	alutacea	var. Steinbachii R. E. Fries	Diels	t	0	1	1
Annonaceae	Rollinia	sp.1			t,s	0	0	1
Annonaceae		Annonaceae1			t	1	0	1
Annonaceae		Annonaceae3			t	0	1	0
Annonaceae		Ind.1			t	1	0	0
Apocynaceae	Apocinaceae	sp.			t	1	0	0
Apocynaceae	Aspidosperma	cylindrocarpon		Müll. Arg.	t	1	1	1
Apocynaceae	Aspidosperma	rigidum		Rusby	t	1	1	1
Apocynaceae	Aspidosperma	sp.			t	1	1	0
Apocynaceae	Forsteronia	affinis cf.		Müll. Arg.	l	1	1	0
Apocynaceae	Forsteronia	australis cf.		Müll. Arg.	l	1	0	0
Apocynaceae	Forsteronia	pubescens cf.		A. DC.	l	1	0	0
Apocynaceae	Forsteronia	sp.a			l	1	1	0
Apocynaceae	Forsteronia	sp.b			l	1	0	0
Apocynaceae	Forsteronia	sp.c			l	1	1	0
Apocynaceae	Forsteronia	sp.d			l	0	1	0
Apocynaceae	Forsteronia	sp.e			l	0	1	0
Apocynaceae	Forsteronia	sp.f			l	0	1	1
Apocynaceae	Peltates	giganteus			l	0	1	1
Apocynaceae	Tabernaemontana	cymosa		Jacq.	t	0	1	0
Apocynaceae	Tabernaemontana	sp.			t	0	0	1
Apocynaceae		Apocynaceae			t	0	0	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Apocynaceae		Apocynaceae ind.a			l	0	0	1
Araceae	Anthurium	gracile		(Rudge)Schott	h	0	0	1
Araceae	Anthurium	paraguayense			h	1	1	1
Araceae	Monstera	obliqua		Miq.	h	1	1	1
Araceae	Philodendron	camposportoanum			e	1	1	1
Araceae	Philodendron	cataniapoense		G.S. Bunting	he	1	1	1
Araceae	Philodendron	lechlerianum			h	1	1	1
Araceae	Philodendron	sp.1			h	0	1	1
Araceae	Philodendron	sp.2			h	1	1	1
Araceae	Xanthosoma	sp.			h	0	1	1
Araliaceae	Aralia	soratensis		March.	t	1	1	1
Araliaceae	Dendropanax	arbores		(L.) Decne. & Planch.	t	0	1	1
Araliaceae	Oreopanax	steinbachianus cf.		Harms	t	0	1	1
Arecaceae	Chamaedorea	pinnatifrons cf.		(Jacq.)Oerst.	s	0	1	1
Arecaceae					s	0	0	1
Asclepiadaceae	Marsdenia	albissima		(Jacq.) Dugand	l	1	0	0
Asclepiadaceae	Matelea	macrocarpa			l	0	0	1
Asteraceae	Baccharis	dracunculifolia		DC.	h	0	1	1
Asteraceae	Dasyphyllum	brasiliense		(Sprengel)Cabrera	s	1	1	1
Asteraceae	Eupatorium	sp.			t,s	0	1	0
Asteraceae	Mikania	decora			l	0	0	1
Asteraceae	Mikania	discoreoides			l	0	1	1
Asteraceae	Mikania	sp.			l	1	0	0
Asteraceae	Oblivea	sp.a			l	0	1	1
Asteraceae	Quechualia	fulva		Griseb.	l	0	0	1

Family	Genus	Species	Variety	Author(s)	Life-form	DF	SDF	EF
Asteraceae	Vernonanthura	patens		Kunth	h, ss, s, tl	0	0	1
Asteraceae	Vernonia	sp.			t,s	0	0	1
Asteraceae		Ind.2			s	0	1	0
Asteraceae		Ind.3			s	1	0	0
Asteraceae		Ind.5			s	1	1	0
Asteraceae		Ind.6			s	0	1	0
Balanophoraceae	Lophophytum	mirabile	subsp. bolivianum		p	1	0	0
Begoniaceae	Begonia	glabra			l	0	0	1
Begoniaceae	Begonia	juntasensis		Kuntze	h	0	1	1
Begoniaceae	Begonia	leathermarmaniae		O'Reilly & Kar.	h	0	0	1
Begoniaceae	Begonia	sp.2			h	1	1	0
Begoniaceae	Begonia	sp.3			h	0	0	1
Begoniaceae	Begonia	sp.4			h	0	0	1
Begoniaceae	Begonia	sp.5			h	0	0	1
Begoniaceae	Begonia	spec.			e	0	0	1
Bignoniaceae	Melloa	quadrivalvis cf.		(Jacq.) A.H. Gentry	l	1	0	0
Bignoniaceae	Mussatia	hyacinthina		(Standl.) Sandwith	l	1	1	0
Bignoniaceae	Mussatia	sp.a			l	0	1	0
Bignoniaceae	Mussatia	sp.b			l	1	0	0
Bignoniaceae	Mussatia?				l	0	1	0
Bignoniaceae	Paragonia	pyramidata			l	0	1	1
Bignoniaceae	Pleonotoma	meloides		(S. Moore) A. H. Gentry	l	1	0	0
Bignoniaceae	Tabebuia	heptaphylla		(Vell.) Toledo	t	1	1	0
Bignoniaceae	Tabebuia	lapacho		(Schumann)Sandw.	t	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Bignoniaceae	Tabebuia	serratifolia		(Vahl)Nicholson	t	0	1	1
Bignoniaceae	Tanaecium	nocturnum		(Barb. Rodr.) Bureau & K. Schum.	l	1	1	1
Bignoniaceae	Zeyheria	tuberculosa		(Vell.) Bureau	t	0	1	0
Bignoniaceae		Bign1436			l	0	1	1
Bignoniaceae		Bign1468			l	0	1	1
Bignoniaceae		Bign1469			l	0	1	0
Bignoniaceae		Bign1471			l	0	1	0
Bignoniaceae		Bign1472			l	1	0	0
Bignoniaceae		Bign1474			l	0	1	0
Bignoniaceae		Bign1477			l	1	1	0
Bignoniaceae		Bign1478			l	1	1	0
Bignoniaceae		Bign1481			l	1	0	0
Bignoniaceae		Bign1483			l	1	0	0
Bignoniaceae		Bign1487			l	0	1	0
Bignoniaceae		Bign1489			l	0	1	0
Bignoniaceae		Bign1494			l	1	0	0
Bignoniaceae		Bign1495			l	0	1	0
Bignoniaceae		Bign1496			l	1	0	0
Bignoniaceae		Bign1499			l	1	0	0
Bignoniaceae		Bign1504			l	1	0	0
Bignoniaceae		Bign1506			l	1	1	0
Bignoniaceae		Bign1507			l	1	1	0
Bignoniaceae		Bign1553			l	1	0	0
Bignoniaceae		Bign1555			l	0	1	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Bignoniaceae		Bign1556			l	0	0	1
Bignoniaceae		Bign1557			l	1	1	1
Bombacaceae	Ceiba	boliviana		Britton & Baker f.	t	1	1	0
Bombacaceae		Ind.1			t	1	1	0
Boraginaceae	Cordia	alliodora		(Ruiz & Pav.) Cham	t	1	1	0
Boraginaceae	Cordia	bifurcata		Roem. & Schult.	s	1	0	0
Boraginaceae	Cordia	sp.			t,s	1	0	0
Bromeliaceae	Bromelia	serra		Griseb.	h	1	0	0
Bromeliaceae	Catopsis	sessiliflora			e	0	1	1
Bromeliaceae	Deuterocohnia	longipetala		(Baker) Mez	h	1	0	0
Bromeliaceae	Fosterella	albicans			e	0	0	1
Bromeliaceae	Fosterella	floridensis			h	1	0	0
Bromeliaceae	Fosterella	latifolia			h	1	0	0
Bromeliaceae	Pitcairnia	cardenasii		L.M.Sm	h	1	0	1
Bromeliaceae	Racinaea	parviflora			e	1	1	1
Bromeliaceae	Racinaea	spiculosa			e	1	1	1
Bromeliaceae	Tillandsia	bandensis		Baker	e	0	0	1
Bromeliaceae	Tillandsia	bryoides (aggr.)			e	1	0	0
Bromeliaceae	Tillandsia	fendleri			e	0	0	1
Bromeliaceae	Tillandsia	junceae			e	1	1	0
Bromeliaceae	Tillandsia	rusbyi			e	1	1	1
Bromeliaceae	Tillandsia	sp.1			e	0	1	1
Bromeliaceae	Tillandsia	sp.2			e	0	1	1
Bromeliaceae	Tillandsia	sp.3			e	0	1	1
Bromeliaceae	Tillandsia	sp.4			e	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Bromeliaceae	Tillandsia	sp.5			e	0	0	1
Bromeliaceae	Tillandsia	spiralipetala			e	1	1	1
Bromeliaceae	Tillandsia	streptocarpa			e	1	1	1
Bromeliaceae	Tillandsia	temuifolia			e	1	1	1
Bromeliaceae	Tillandsia	usneoides			e	0	1	1
Bromeliaceae	Tillandsia	vernica			e	1	1	1
Bromeliaceae	Vriesea	heliconioides			e	1	0	1
Bromeliaceae	Vriesea	maxoniana			e	1	1	1
Cactaceae	Cereus	haenkeus			t	1	0	0
Cactaceae	Cleistocactus	baumanii			t,s	1	0	0
Cactaceae	Cleistocactus	samaipatanus			s	1	0	0
Cactaceae	Epiphyllum	phyllanthus			e	1	0	0
Cactaceae	Hylocereus	setaceus			e	1	1	1
Cactaceae	Hylocereus	sp.			l	0	1	0
Cactaceae	Opuntia	brasiliensis		(Willd.) Haw.	t	1	1	0
Cactaceae	Pereskia	aculeata		Mill.	l	1	0	0
Cactaceae	Rhipsalis	baccifera			e	1	1	1
Cactaceae		cact ind a			l	0	0	1
Cactaceae		cact ind b			l	1	0	0
Capparidaceae	Capparis	flexuosa		(L.) L.	t	1	1	0
Capparidaceae	Capparis	prisca		Macbr.	t	1	0	0
Caricaceae	Carica	glandulosus		A.DC.	t	0	1	1
Caricaceae	Carica	microcarpa		Jaquin	s	0	1	1
Caricaceae	Carica	papaya			t	0	1	1
Cecropiaceae	Cecropia	sp.			t	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Celastraceae	Maytenus	ilicifolia		(Burch. Planch.	t,s	1	0	0
Celastraceae	Maytenus	sp.			t,s	0	0	1
Celastraceae	Maytenus	sp.1			t,s	0	1	0
Celastraceae	Schaefferia	argentinensis		Speg.	t,s	1	0	1
Chloranthaceae	Hedyosum	racemosum		(Ruiz. & Pav.) G.Don	t	1	0	0
Chloranthaceae	Hedyosum	sp.			t	0	1	0
Chrysobalanaceae	Couepia	sp.			t	0	1	1
Combretaceae	Combretum	lanceolatum			l	0	1	0
Commelinaceae	Commelina	erecta			h	1	1	1
Commelinaceae	Commelina	robusta			h	0	1	1
Commelinaceae	Commelina	sp.1			h	0	1	1
Commelinaceae	Commelina	sp.2			h	0	0	1
Commelinaceae	Commelina	spec.			e	1	0	0
Costaceae	Costus	scandens		Ruiz & Pav.	h	0	1	1
Costaceae	Costus	sp.			h	0	0	1
Cucurbitaceae	Fevillea	pergamentacea			l	0	1	1
Cucurbitaceae	Gurania	acuminata cf.			l	0	1	0
Cucurbitaceae	Siolmatra	brasiliensis		Baill.	l	1	1	1
Cyperaceae	Eleocharis	sp.			h	1	0	0
Ebenaceae	Diospyrus	sp.1			t	0	1	0
Ebenaceae	Diospyrus	sp.2			t	0	1	0
Ebenaceae	Diospyrus	sp.3			t	0	1	0
Erythroxylaceae	Erythroxylum	ulei		O.E. Schulz	t	1	1	1
Euphorbiaceae	Acalypha	brasiliensis		Muell.Arg.	s	1	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Euphorbiaceae	Acalypha	macrostachya		Jacq.	s	0	1	1
Euphorbiaceae	Acalypha	plicata		Muell.Arg.	s	1	0	0
Euphorbiaceae	Acalypha	sp.1			s	1	1	1
Euphorbiaceae	Acalypha	sp.2			s	1	1	0
Euphorbiaceae	Acalypha	sp.3			s	1	0	1
Euphorbiaceae	Acalypha	sp.4			s	0	0	1
Euphorbiaceae	Acalypha	sp.5			s	0	0	1
Euphorbiaceae	Acalypha	stricta		Poepp.Britton	s	0	1	1
Euphorbiaceae	Acalypha	villosa		Jacq.	s	1	0	0
Euphorbiaceae	Alchornea	castaneifolia		(Willd.)Adr.Juss.	s	1	1	0
Euphorbiaceae	Alchornea	glandulosa		Poeppig	s	1	1	1
Euphorbiaceae	Croton	piluliferus		Rusby	t	1	0	0
Euphorbiaceae	Croton	sp.			t,s	0	0	1
Euphorbiaceae	Drypetes	amazonica		Steyerh.	t	1	1	1
Euphorbiaceae	Euphorbia	cotinifolia			s	1	1	0
Euphorbiaceae	Pachystroma	longifolium		(Nees) I.M. Johnst.	t	1	1	1
Euphorbiaceae	Phyllanthus	acuminatus		Vahl	t	0	1	0
Euphorbiaceae	Sebastiania	brasiliensis		Spreng.	t,s	1	0	0
Euphorbiaceae		Ind.1			s	0	1	0
Euphorbiaceae		Ind.2			s	0	0	1
Flacourtiaceae	Casearia	gossypiosperma		Briq.	t	1	1	1
Flacourtiaceae	Casearia	sp.			t	0	1	0
Flacourtiaceae	Casearia	sp.1			t,s	0	1	1
Flacourtiaceae	Casearia	sp.2			t,s	0	1	0
Flacourtiaceae	Hasseltia	floribunda		Kunth	t	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Flacourtiaceae	Prockia	crucis		L.	s	1	1	1
Flacourtiaceae	Prockia	sp.			s	0	0	1
Flacourtiaceae		Ind.1			s	1	0	0
Flacourtiaceae					t,s	0	0	1
Gesneriaceae	Gloxinia	purpurascens		(Rusby) Wiehler	h	0	1	1
Heliconiaceae	Heliconia	rostrata		Ruiz & Pav.	h	0	0	1
Heliconiaceae	Heliconia	subulata		Ruiz & Pav.	h	0	1	1
Hippocrataceae	Peritassa	huanucana		(Loes.) A.C. Sm.	l	1	1	1
Hippocrataceae	Pristimera	andina			l	1	1	1
Lacistemaceae	Lacistema	aggregatum cf.		(P.J. Bergius) Rusby	t,s	0	0	1
Lauraceae	Aniba	sp.			t	0	1	1
Lauraceae	Licaria	triandra cf.		(Sw.) Kosterm.	t	1	1	1
Lauraceae	Nectandra	cuspidata cf.		Nees & Mart.	t	0	1	1
Lauraceae	Nectandra	sp.1			t	0	1	1
Lauraceae	Nectandra	sp.2			t	0	1	1
Lauraceae	Nectandra	sp.3			t	0	0	1
Lauraceae	Ocotea	sp.			t	0	0	1
Lauraceae		Ind.3			t	1	0	0
Lauraceae		Ind.5			t	0	1	0
Lauraceae		Lauraceae1			t,s	0	1	1
Lecythidaceae	Cariniana	estrellensis		(Raddi) Kuntze	t	1	1	1
Leguminosae		Legum indet. a			l	1	0	0
Leguminosae-Caesalpinoideae	Bauhinia	microstachya			l	0	1	1
Leguminosae-Caesalpinoideae	Bauhinia	sp.1			s	0	1	0
Leguminosae-Caesalpinoideae	Bauhinia	sp.2			s	0	1	1

Family	Genus	Species	Variety	Author(s)	Life-form	DF	SDF	EF
Leguminosae-Caesalpinoideae	Bauhinia	sp.3			s	1	0	0
Leguminosae-Caesalpinoideae	Bauhinia	sp.4			s	0	0	1
Leguminosae-Caesalpinoideae	Nissolia	sp.			s	0	1	0
Leguminosae-Caesalpinoideae	Senna	sp.			t	1	0	0
Leguminosae-Mimosoideae	Acacia	glomerosa cf.		Benth.	t	1	0	0
Leguminosae-Mimosoideae	Acacia	polyphylla		DC.	t	1	1	0
Leguminosae-Mimosoideae	Acacia	sp.1			t,s	1	1	0
Leguminosae-Mimosoideae	Acacia	sp.2			t,s	1	0	0
Leguminosae-Mimosoideae	Acacia	sp.3			t,s	1	0	0
Leguminosae-Mimosoideae	Anadenanthera	macrocarpa		(Benth.) Brenan	t	1	0	0
Leguminosae-Mimosoideae	Cojoba	arborea	var. angustifolia		t	0	1	1
Leguminosae-Mimosoideae	Coursetia	brachyrhachis		Harms	t	1	0	0
Leguminosae-Mimosoideae	Inga	marginata		Willd.	t	0	1	1
Leguminosae-Mimosoideae	Inga	punctata cf.		Willd.	t	0	1	1
Leguminosae-Mimosoideae	Inga	sp.			t	0	1	1
Leguminosae-Mimosoideae	Inga	sp.1			t	0	1	1
Leguminosae-Mimosoideae	Inga	sp.2			t	0	0	1
Leguminosae-Mimosoideae	Parapiptadenia	excelsa		(Griseb.) Burkart	t	1	1	1
Leguminosae-Mimosoideae	Piptadenia	buchtienii		Barneby	t	1	0	1
Leguminosae-Papilionoideae	Dahlbergia	sp.			s	0	1	0
Leguminosae-Papilionoideae	Erythrina	falcata		Benth.	t	0	1	1
Leguminosae-Papilionoideae	Lonchocarpus	hedyosmus		Miq.	t	1	1	0
Leguminosae-Papilionoideae	Machaerium	acutifolium			l	1	1	1
Leguminosae-Papilionoideae	Machaerium	inundatum		(Mart. ex Benth.) Ducke	t	1	1	1
Leguminosae-Papilionoideae	Machaerium	pilosum		Benth.	t	1	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Leguminosae-Papilionoideae	Machaerium	punctatum cf.			l	0	1	1
Leguminosae-Papilionoideae	Machaerium	scleroxylon cf.		Tul.	t,l	1	0	1
Leguminosae-Papilionoideae	Machaerium	sp.1			l	0	1	0
Leguminosae-Papilionoideae	Myroxylon	balsamun		(L.) Harms.	t	1	0	0
Leguminosae-Papilionoideae	Ormosia	bolivarensis		C.H. Stirt.	t	0	1	1
Leguminosae-Papilionoideae	Platymiscium	stipulare cf.		Benth.	t	0	1	0
Leguminosae-Papilionoideae	Pterocarpus	amazonicus		Huber	t	0	1	0
Leguminosae-Papilionoideae	Swartzia	jorori		Harms	t,s	1	1	1
Leguminosae-Papilionoideae	Swartzia	sp.			t	0	1	1
Leguminosae-Papilionoideae	Tipuana	tipu		(Benth.) Kuntze	t	1	0	0
Leguminosae-Papilionoideae		Ind.1			t	0	1	0
Liliaceae	Herreria	montevidensis		Klotzsch ex Griseb.	l	1	1	0
Liliaceae		Ind.			h	1	0	0
Loganiaceae	Strychnos	tarapotensis			l	0	1	1
Malpighiaceae	Bunchosia	paraguariensis cf.		Nied.	s	1	0	1
Malpighiaceae	Heteropterys	sylvatica		A. Juss.	l	1	0	0
Malpighiaceae	Hiraea?				l	0	0	1
Malpighiaceae	Mascagnia	chlorocarpa cf.		(A. Juss.) Griseb.	l	1	1	0
Malpighiaceae	Mascagnia	sp.			l	0	1	0
Malpighiaceae					l	0	1	0
Maranthaceae	Ischnosiphon	puberulus cf.		Loes	h	0	0	1
Marcgraviaceae	Souroubea	guianensis			l	0	0	1
Melastomataceae	Miconia	minutiflora cf.		(Bonpl.) DC.	t,s	0	0	1
Melastomataceae	Miconia	multiflora		Cogn.	t	0	0	1
Melastomataceae	Miconia	sp.			t,s	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Melastomataceae		Ind.1			t	0	1	1
Melastomataceae		Ind.2			t	0	1	1
Melastomataceae		Ind.3			t	0	1	1
Melastomataceae		Ind.4			t	0	1	1
Melastomataceae		Ind.5			s	0	0	1
Meliaceae	Cedrela	lilloi		C. DC.	t	1	1	0
Meliaceae	Guarea	macrophylla	subsp. Pendulispica	(C. DC.) T.D. Penn.	t	0	0	1
Meliaceae	Trichilia	clausenii		C.DC.	t	1	1	1
Meliaceae	Trichilia	elegans		A. Juss.	t	1	1	1
Meliaceae	Trichilia	plecana		(A. Juss.) C. DC.	t	0	1	1
Meliaceae	Trichilia	stellatomentosa		Kunze	s	0	0	1
Morimiaceae	Siparuna	subinodora		(Ruiz & Pav.) A. DC.	s	0	0	1
Moraceae	Clarisia	biflora		Ruiz & Pav.	t	0	1	1
Moraceae	Ficus	eximia		Schott in Spreng.	he	0	0	1
Moraceae	Ficus	macbridei		Standl.	t	0	0	1
Moraceae	Ficus	maxima		Mill.	he	0	0	1
Moraceae	Ficus	obtusifolia		Kunth	he	0	1	1
Moraceae	Ficus	pertusa		L. F.	he	0	0	1
Moraceae	Ficus	sp.			he	0	1	0
Moraceae	Ficus	trigona		L. f.	he	0	1	1
Moraceae	Maclura	tinctoria		(L.) D. Don ex Steud.	t	0	1	1
Moraceae	Sorocea	guilleminiana		Gaudich	t	1	1	1
Myrcinaceae	Myrsine	umbellata		Mart.	t	1	1	1
Myrtaceae	Eugenia	moraviana cf.		O. Berg	t	0	1	1
Myrtaceae	Eugenia	muricata		DC.	t	0	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Myrtaceae	Eugenia	sp.			t,s	1	1	1
Myrtaceae	Eugenia	sp.1			t	1	0	1
Myrtaceae	Eugenia	sp.2			t	1	1	1
Myrtaceae	Eugenia	sp.3			t	1	1	0
Myrtaceae	Eugenia	uniflora		L.	t	1	0	1
Myrtaceae	Myrcianthes	pseudomato		(Legrand) Mc. Vough.	t	1	1	1
Myrtaceae	Myrcianthes	sp.			t	1	1	0
Myrtaceae	Myrcianthes	sp.1			t	1	0	0
Myrtaceae	Myrciaria	cauliflora		Berg	t	1	1	0
Myrtaceae	Myrciaria	floribunda		(Willd.)Berg	t	0	1	0
NA	NA	NA			l	1	0	0
NA	NA	NA			l	0	1	0
NA	NA	NA			e	0	0	1
NA	NA	Ind.1			l	1	0	0
NA	NA	Ind.10			l	1	0	0
NA	NA	Ind.11			l	0	1	0
NA	NA	Ind.12			l	0	0	1
NA	NA	Ind.13			l	0	1	0
NA	NA	Ind.14			l	0	1	0
NA	NA	Ind.15			l	0	1	0
NA	NA	Ind.1501			l	0	1	0
NA	NA	Ind.1506			l	1	0	0
NA	NA	Ind.1509			l	0	1	0
NA	NA	Ind.1558			l	0	0	1
NA	NA	Ind.1559			l	0	0	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
NA		Ind.1560			1	1	0	0
NA		Ind.16			1	0	1	0
NA		Ind.17			1	0	1	0
NA		Ind.18			1	1	0	0
NA		Ind.19			1	1	0	0
NA		Ind.2			1	0	1	0
NA		Ind.20			1	0	1	0
NA		Ind.21			1	0	1	0
NA		Ind.22			1	0	1	0
NA		Ind.23			1	1	0	0
NA		Ind.25			1	1	0	0
NA		Ind.26			1	0	1	0
NA		Ind.27			1	1	0	0
NA		Ind.28			1	0	1	0
NA		Ind.29			1	0	1	0
NA		Ind.3			1	0	0	1
NA		Ind.30			1	0	0	1
NA		Ind.31			1	1	1	0
NA		Ind.32			1	0	0	1
NA		Ind.33			1	0	1	0
NA		Ind.34			1	0	1	0
NA		Ind.35			1	1	0	0
NA		Ind.36			1	0	1	0
NA		Ind.37			1	0	0	1
NA		Ind.38			1	0	1	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
NA		Ind.39			1	0	1	0
NA		Ind.4			1	0	0	1
NA		Ind.40			1	0	1	0
NA		Ind.41			1	0	0	1
NA		Ind.42			1	0	0	1
NA		Ind.43			1	1	0	0
NA		Ind.44			1	0	1	0
NA		Ind.45			1	1	0	0
NA		Ind.46			1	1	0	0
NA		Ind.47			1	1	0	0
NA		Ind.48			1	0	1	0
NA		Ind.49			1	0	0	1
NA		Ind.5			1	0	1	0
NA		Ind.50			1	1	0	0
NA		Ind.51			1	1	0	0
NA		Ind.52			1	1	0	0
NA		Ind.6			1	0	1	0
NA		Ind.7			1	0	0	1
NA		Ind.8			1	0	1	0
NA		Ind.9			1	0	1	0
NA					e	1	0	0
NA					1	0	0	1
Nyctaginaceae	Bougainvillea	stipitata		Griseb.	t,s	1	0	0
Nyctaginaceae	Guapira	olfersiana aff.		(Link et al) Standl.	t	1	1	1
Nyctaginaceae	Neea	sp.			t	1	0	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Nyctaginaceae	Pisonia	aculeata cf.			l	0	0	1
Nyctaginaceae					t	1	0	0
Ochnaceae	Ouratea	angulata cf.		Tiegh.	t	0	1	1
Olacaceae	Ximenia	americana		L.	t,s	1	0	0
Orchidaceae	Bulbophyllum	sp.			e	1	0	0
Orchidaceae	Bulbophyllum	weberbauerianum			e	1	0	0
Orchidaceae	Campylocentrum	spec.			e	0	1	0
Orchidaceae	Capanemia	micromera			e	0	1	1
Orchidaceae	Cyclopogon	elegans			e	1	0	1
Orchidaceae	Cyclopogon	millei			e	1	1	1
Orchidaceae	Cyclopogon	truncatus			h	0	1	0
Orchidaceae	Encyclia	pflanzii			e	1	1	1
Orchidaceae	Epidendrum	albiflorum			e	0	0	1
Orchidaceae	Epidendrum	amplum			e	0	1	1
Orchidaceae	Epidendrum	avicula			e	1	0	0
Orchidaceae	Epidendrum	compressum			e	0	0	1
Orchidaceae	Epidendrum	peperomia			e	1	1	1
Orchidaceae	Epidendrum	purum			e	1	1	1
Orchidaceae	Epidendrum	rigidum			e	1	1	1
Orchidaceae	Epidendrum	samaipatense			e	0	0	1
Orchidaceae	Epidendrum	siphonocephalum			e	0	0	1
Orchidaceae	Gongora	rufescens			e	0	0	1
Orchidaceae	Isochilus	linearis			e	1	1	1
Orchidaceae	Kefersteinia	spec.			e	0	0	1
Orchidaceae	Lockhartia	lunifera			e	1	1	1

Family	Genus	Species	Variety	Author(s)	Life-form	DF	SDF	EF
Orchidaceae	Lycaste	ciliata			e	0	0	1
Orchidaceae	Lycaste	dyeriana			e	0	0	1
Orchidaceae	Masdevallia	bicolor			e	0	1	0
Orchidaceae	Maxillaria	mapiriensis			e	0	0	1
Orchidaceae	Maxillaria	polybulbon			e	1	1	1
Orchidaceae	Maxillaria	rufescens			e	0	0	1
Orchidaceae	Maxillaria	spec.			e	0	1	0
Orchidaceae	Notylia	spec.			e	1	1	1
Orchidaceae	Oncidium	bifolium			e	1	1	1
Orchidaceae	Oncidium	spec.			e	1	0	0
Orchidaceae	Oncidium	trilobium			e	0	0	1
Orchidaceae	Orleanesia	maculata			e	1	1	1
Orchidaceae	Pleurothallis	aphthosa			e	1	0	0
Orchidaceae	Pleurothallis	aurantio-lateritia			e	1	1	1
Orchidaceae	Pleurothallis	auriculata			e	1	1	1
Orchidaceae	Pleurothallis	citrina			e	1	0	1
Orchidaceae	Pleurothallis	crinita			e	0	1	0
Orchidaceae	Pleurothallis	erinacea			e	0	0	1
Orchidaceae	Pleurothallis	humboldtiana			e	0	0	1
Orchidaceae	Pleurothallis	loranthophylla			e	1	1	0
Orchidaceae	Pleurothallis	micklowii			e	0	1	1
Orchidaceae	Pleurothallis	obovata			e	1	1	1
Orchidaceae	Pleurothallis	pubescens			e	1	1	1
Orchidaceae	Pleurothallis	rhabdosepala			e	1	0	0
Orchidaceae	Pleurothallis	sp.			e	0	0	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Orchidaceae	Pleurothallis	tripterantha			e	0	1	1
Orchidaceae	Ponera	striata			e	1	1	1
Orchidaceae	Prosthechea	grammatoglossa			e	0	0	1
Orchidaceae	Prosthechea	pygmaea			e	0	0	1
Orchidaceae	Psychmorchis	spec.			e	0	0	1
Orchidaceae	Scaphyglottis	morph spec.1			e	0	1	1
Orchidaceae	Scaphyglottis	prolifera			e	1	1	1
Orchidaceae	Scaphyglottis	violacea			e	0	0	1
Orchidaceae	Schelochilus	coimbrae			e	1	1	1
Orchidaceae	Schomburgkia	undulata			e	1	1	0
Orchidaceae	Stanhopea	xytriophora			e	0	1	1
Orchidaceae	Stelis	sp.1			e	0	1	0
Orchidaceae	Stelis	sp.2			e	0	1	0
Orchidaceae	Stelis	sp.3			e	0	1	0
Orchidaceae	Stelis	spec.			e	0	1	1
Orchidaceae	Trichocentrum	neudeckerii			e	0	1	1
Orchidaceae	Trichopilia	laxa			e	1	0	1
Orchidaceae	Trichosalpinx	berlineri			e	0	1	1
Orchidaceae	Xylobium	spec.			e	1	1	1
Orchidaceae	Xylobium	variegatum			e	0	0	1
Orchidaceae	Zygostates	apiculata			e	1	1	1
Orchidaceae		Ind.(758)			h	0	0	1
Orchidaceae		Ind.(773)			e	0	0	1
Orchidaceae		Ind.(777)			e	0	0	1
Orchidaceae		Ind.(799)			e	0	0	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Orchidaceae		Ind.(816)			e	0	0	1
Orchidaceae		Ind.(821)			e	0	0	1
Orchidaceae		Ind.(843)			e	0	0	1
Orchidaceae		Ind.(871)			e	0	0	1
Orchidaceae		Ind.(872)			e	0	0	1
Orchidaceae		Ind.1			e	1	0	0
Orchidaceae		Ind.2			e	1	0	0
Orchidaceae		Ind.3			e	1	0	0
Orchidaceae		Ind.4			h	0	1	0
Orchidaceae		Ind.5			e	0	1	0
Orchidaceae		Ind.6			e	0	1	0
Orchidaceae		Ind.7			e	0	1	0
Orchidaceae		Ind.8			e	0	1	0
Orchidaceae		Ind.9			e	0	1	0
Phytolaccaceae	Gallesia	integrifolia		(Sprengel) Harms	t	1	1	1
Phytolaccaceae	Hillieria	latifolia cf			l	0	1	0
Phytolaccaceae	Hillieria cf.				l	1	0	0
Phytolaccaceae	Petiveria	alliacea		L.	s	1	0	0
Phytolaccaceae	Rivina	humilis		L.	s	1	0	0
Piperaceae	Peperomia	aceroana			e	1	1	1
Piperaceae	Peperomia	alata			e	1	1	1
Piperaceae	Peperomia	blanda			h	1	0	0
Piperaceae	Peperomia	comarapana		C.DC.	h	1	1	1
Piperaceae	Peperomia	dahlstedtii			h	1	1	1
Piperaceae	Peperomia	fibrigii			h	1	1	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Piperaceae	Peperomia	rhombea			e	1	1	1
Piperaceae	Peperomia	sp.			h	0	0	1
Piperaceae	Peperomia	sp.2			e	0	0	1
Piperaceae	Peperomia	tetragona			e	1	1	1
Piperaceae	Peperomia	tetraphylla			e	1	1	1
Piperaceae	Piper	amalago		L.	t	1	1	1
Piperaceae	Piper	bangii		C.DC.	s	0	1	1
Piperaceae	Piper	callosum		Ruiz & Pav.	s	1	1	1
Piperaceae	Piper	crassinervium			s	0	0	1
Piperaceae	Piper	sp.			s	0	0	1
Piperaceae	Piper	sp.1			s	0	0	1
Piperaceae	Piper	sp.2			s	1	0	1
Poaceae	Chusquea	picta cf.			h	1	1	0
Poaceae	Olyra	fasciculata		Trin.	h	1	1	1
Poaceae	Paspalum	ekmanianum			h	0	1	1
Poaceae	Paspalum	humboldtianum		Flüggé	h	0	1	1
Poaceae	Paspalum	plicatulum		Michx.	h	0	1	0
Poaceae	Paspalum	plicatum			h	0	0	1
Poaceae	Rhipidocladum	neumanii			h	1	1	0
Poaceae	Zeugitis	americana			h	0	1	0
Poaceae		Ind.1			h	0	0	1
Poaceae		Ind.2			h	1	0	0
Poaceae		Ind.3			h	1	0	0
Poaceae		Ind.4			h	1	0	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Polygonaceae	Coccoloba	meissneriana		(Britton Schum.	t,s	1	0	0
Polygonaceae	Coccoloba	spinescens		Lindau	t,s	0	1	1
Polygonaceae	Coccoloba	tiliacea		Lindau	t	1	1	0
Polygonaceae	Ruprechtia	apetala		Wedd.	t,s	1	0	0
Polygonaceae	Triplaris	americana		Loefl	t	1	1	1
Polygonaceae	Triplaris	gardneriana		Wedd.	t	0	1	0
Polygonaceae	Triplaris	poepigiana		Wedd.	t	0	1	0
Proteaceae	Roupala	meisneri		Sleumer	t	0	0	1
Proteaceae	Roupala	montana		Aubl.	t	0	1	1
Pteridophyta-Anemiaceae	Anemia	herzogii		Rosenst.	h	1	1	0
Pteridophyta-Anemiaceae	Anemia	phyllitidis			h	1	1	0
Pteridophyta-Aspleniaceae	Asplenium	auritum		L.Sw.	e	1	1	1
Pteridophyta-Aspleniaceae	Asplenium	bangii		Sw.	h	0	1	1
Pteridophyta-Aspleniaceae	Asplenium	discrepans		Rosent.	h	0	0	1
Pteridophyta-Aspleniaceae	Asplenium	drepanophyllum			h	1	0	1
Pteridophyta-Aspleniaceae	Asplenium	inaequilaterale		Lam.	h	0	1	1
Pteridophyta-Blechnaceae	Blechnum	occidentale		L.	h	0	1	1
Pteridophyta-Cyatheaaceae	Alsophila	incana			t	0	0	1
Pteridophyta-Dennstaedtiaceae	Dennstaedtia	bipinnata		(Cav.) Maxon	h	0	0	1
Pteridophyta-Dennstaedtiaceae	Paesia	glandulosa		(Sw.) Kuhn	h	0	0	1
Pteridophyta-Dryopteridaceae	Bolbitis	serratifolia			e	0	0	1
Pteridophyta-Dryopteridaceae	Dryopteris	pedata		(L.) Fée	h	1	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Pteridophyta-Dryopteridaceae	Lastreopsis	effusa		(Sw.) dale (Willd.)Tindale	Tin- h ssp.divergens	0	0	1
Pteridophyta-Dryopteridaceae	Polybotrya	crassirhizoma cf.		Lellinger	he	0	0	1
Pteridophyta-Dryopteridaceae	Polystichum	platyphyllum		Willd.	h	0	1	1
Pteridophyta-Dryopteridaceae	Stigmatopteris	spec.			e	0	0	1
Pteridophyta-Hymenophyllaceae	Trichomanes	hymenoides			e	0	1	0
Pteridophyta-Lomariopsidaceae	Lomagramma	guianensis		(Aublet) Ching	he	0	0	1
Pteridophyta-Polypodiaceae	Campyloneurum	coarctatum		(Kunze) Fée	e	0	0	1
Pteridophyta-Polypodiaceae	Campyloneurum	nitidissimum			e	1	1	1
Pteridophyta-Polypodiaceae	Campyloneurum	sp. (group)			e	1	1	1
Pteridophyta-Polypodiaceae	Campyloneurum	sp.1			e	0	1	0
Pteridophyta-Polypodiaceae	Campyloneurum	sp.2			e	0	0	1
Pteridophyta-Polypodiaceae	Campyloneurum	sp.3			e	0	0	1
Pteridophyta-Polypodiaceae	Microgramma	percussa		(Cav.) de la Sota	e	0	1	1
Pteridophyta-Polypodiaceae	Microgramma	squamulosa		(Kaufl.) Alston	e	1	1	1
Pteridophyta-Polypodiaceae	Niphidium	crassifolium			e	0	0	1
Pteridophyta-Polypodiaceae	Pechuma	filicula			e	1	1	1
Pteridophyta-Polypodiaceae	Phlebodium	decumanum			e	1	0	0
Pteridophyta-Polypodiaceae	Phlebodium	pseudoaureum			e	0	0	1
Pteridophyta-Polypodiaceae	Pleopeltis	macrocarpa			e	1	1	1
Pteridophyta-Polypodiaceae	Polypodium	fraseri			e	1	1	1
Pteridophyta-Polypodiaceae	Polypodium	fraxinifolium			e	0	0	1
Pteridophyta-Polypodiaceae	Polypodium	furfuraceum			e	0	1	0
Pteridophyta-Polypodiaceae	Polypodium	remotum		Desv.	e	1	0	1

Family	Genus	Species	Variety	Author(s)	Life-form	DF	SDF	EF
Pteridophyta-Polypodiaceae	Polypodium	squalidum			e	1	1	1
Pteridophyta-Pteridaceae	Adiantopsis	radiata		L.(Fée)	h	1	1	0
Pteridophyta-Pteridaceae	Adiantum	raddianum		C.Presl.	h	1	0	1
Pteridophyta-Pteridaceae	Adiantum	tetraphyllum		Willd.	h	0	1	1
Pteridophyta-Pteridaceae	Antrophyum	lineatum			e	0	1	1
Pteridophyta-Pteridaceae	Hemionitis	tomentosa		(Lam.) Raddi	h	1	1	0
Pteridophyta-Pteridaceae	Pteris	denticulata		Sw.	e	1	1	0
Pteridophyta-Pteridaceae	Pteris	quadriaurita		Retz.	h	0	0	1
Pteridophyta-Thelypteridaceae	Thelypteris	chrysodioides		(Fée) Morton	h	0	1	1
Pteridophyta-Thelypteridaceae	Thelypteris	dentata		(Forsk.) E.John	h	0	1	1
Pteridophyta-Thelypteridaceae	Thelypteris	jamesonii		(Decne.) Reed	h	0	1	1
Pteridophyta-Thelypteridaceae	Thelypteris	lancea		A.R.Smith	h	0	1	1
Pteridophyta-Thelypteridaceae	Thelypteris	patens		(Sw.) Sm.	h	0	1	1
Pteridophyta-Thelypteridaceae	Thelypteris	serrata		(Cav.) Alston	h	0	0	1
Pteridophyta-Woodsiaceae	Diplazium	cristatum		(Desv.) Alston	h	0	0	1
Pteridophyta-Woodsiaceae	Diplazium	expansum		Willd.	h	0	0	1
Pteridophyta-Woodsiaceae	Diplazium	sp.			h	0	0	1
Rhamnaceae	Rhamnidium	elaeocarpum		Reisek	t	1	1	1
Rosaceae	Prunus	guanaensis		Rusby	t	0	1	1
Rubiaceae	Chomelia	sessilis cf.		Mull. Arg.	s	1	1	1
Rubiaceae	Coffea	arabica		L.	s	0	1	1
Rubiaceae	Hamelia	sp.			s	1	1	0
Rubiaceae	Hoffmannia	latifolia		(Bartl. ex DC.) Kuntze	s	0	0	1
Rubiaceae	Macrocneum	roseum		(Ruiz & Pav.) Wedd.	t	0	0	1
Rubiaceae	Palicourea	guianensis cf.		Aubl.	t,s	0	0	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Rubiaceae	Pogonopus	sp.			t,s	0	1	0
Rubiaceae	Pogonopus	tubulosus		(A. Rich.) K. Schum.	t,s	1	1	1
Rubiaceae	Psychotria	sp.			s	0	1	1
Rubiaceae	Psychotria	sp.1			s	0	1	1
Rubiaceae	Psychotria	sp.2			s	0	0	1
Rubiaceae	Psychotria	sp.3			s	0	0	1
Rubiaceae	Psychotria	sp.4			t	0	1	0
Rubiaceae	Psychotria	trivialis cf.		Rusby	s	0	1	0
Rubiaceae	Randia	sp.			t,s	0	1	0
Rubiaceae	Randia	sp.1			t,s	0	1	1
Rubiaceae	Randia	sp.2(372)			s	0	1	0
Rubiaceae	Randia	sp.3			s	0	1	1
Rubiaceae	Randia	spinosa		(Jacq.) H. Karst.	s	1	1	1
Rubiaceae		Ind.10			t	0	0	1
Rubiaceae		Ind.3			t	0	1	0
Rubiaceae		Ind.4			t	1	0	0
Rubiaceae		Ind.8			t	0	1	0
Rutaceae	Citrus	aurantium		L.	t	0	1	0
Rutaceae	Citrus	sp.			t	0	1	0
Rutaceae	Zanthoxylum	petiolare		St.-Hil. & Tul.	t	1	0	0
Sabiaceae	Meliosma	hebertii		Rolfe	t	0	0	1
Sapindaceae	Allophylus	edulis		(A. St.-Hil., Cambess. & A. Juss.) Radlk.	t	1	1	1
Sapindaceae	Allophylus	sp.2			t	0	1	0
Sapindaceae	Diatenopteryx	sorbifolia		Radlk.	t	1	1	1

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Sapindaceae	Paullinia	alata cf.			l	0	1	0
Sapindaceae	Paullinia	dasytachya cf.			l	0	0	1
Sapindaceae	Paullinia	elegans cf.	subsp. neglecta	(Radlk.) D.R. Simpson	l	1	0	0
Sapindaceae	Paullinia	sp.			l	0	1	0
Sapindaceae	Paullinia	sp.a			l	0	1	0
Sapindaceae	Sapindus	saponaria		L.	l	1	0	0
Sapindaceae	Serjania	lethalis cf.		A. St. -Hil.	l	1	1	0
Sapindaceae	Serjania	leucocephala cf.			l	0	1	0
Sapindaceae	Serjania	minytilora		Radlk.	l	1	1	0
Sapindaceae	Serjania	perulacea cf.		Radlk.	l	1	1	0
Sapindaceae	Tahsia	sp.			l	0	1	0
Sapindaceae		Ind.1			l	0	1	0
Sapindaceae		sapindaceae1			t,s	0	0	1
Sapindaceae					t,s	0	1	0
Sapotaceae	Chrysophyllum	gonocarpum		(Mart. & Gickl.) Engl.	t	1	1	1
Sapotaceae	Chrysophyllum	marginatum		(Hook. & Arn.) Radlk.	t	1	0	0
Sapotaceae	Chrysophyllum	venezuelanense		(Pierre) T.D. Penn.	t	0	1	1
Sapotaceae	Pouteria	nemorosa		Baehni	t	0	1	1
Sapotaceae	Sarcaulus	sp.			t	1	1	1
Simaroubaceae	Picramnia	excelsa			t	0	1	0
Simaroubaceae	Picramnia	monninaefolia		Rusby	s	0	1	1
Simaroubaceae	Picramnia	sellowii		Planch.	t	0	1	0
Smilacaceae	Smilax	sp.a			l	1	1	1
Solanaceae	Brunfelsia	grandiflora		D.Don	s	1	1	1
Solanaceae	Capsicum	baccatum		L.	s	1	1	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Solanaceae	Cestrum	marguitense		HBK	s	0	1	0
Solanaceae	Cestrum	strigilatum		Ruiz & Pav.	s	0	1	0
Solanaceae	Lycianthes	inaequilatera		(Rusby) Bitter	s	0	1	1
Solanaceae	Solanum	riparium		Pers.	t	0	1	0
Solanaceae	Solanum	sessile		Ruiz & Pav.	t,s	0	0	1
Solanaceae	Solanum	sp.			t	0	1	0
Solanaceae		Ind.2			s	0	0	1
Solanaceae		Ind.1			s	1	0	0
Staphyleaceae	Huetea	sp.			t	0	0	1
Sterculiaceae	Helicteres	Ihotzkyana		(Schott & Endl.) Schum. in Mart.	K. t,s	1	0	0
Theophrastaceae	Clavija	nutans			s	1	1	1
Tiliaceae	Heliocarpus	americanus		L.	t,s	0	1	1
Ulmaceae	Celtis	brasiliensis		(Gardner) Planch.	s	1	0	1
Ulmaceae	Celtis	iguanea			l	0	1	1
Ulmaceae	Phyllostylon	rhannoides		(J. Poiss.) Taub.	t	1	0	0
Urticaceae	Boehmeria	pavonii		Wedd.	s	0	0	1
Urticaceae	Myriocarpa	stipitata		Benth.	s	0	1	1
Urticaceae	Phenax	angustifolius		(Kunth) Wedd.	s	1	1	1
Urticaceae	Phenax	hirtus		(Sw.) Wedd.	s	0	0	1
Urticaceae	Pouzolzia	sp.			t	1	1	1
Urticaceae	Urera	baccifera		(L.) Gaudich	t	1	1	1
Urticaceae		Ind.2			s	0	0	1
Verbenaceae	Aegiphila	steinbachii		Moldenke	t	1	0	1
Verbenaceae	Aloysia	sp.			s	1	0	0

Family	Genus	Species	Variety	Author(s)	Life- form	DF	SDF	EF
Verbenaceae	Lantana	camara		L.	s	0	0	1
Verbenaceae		Ind.			t	1	0	0
Verbenaceae		Verbenaceae1			t,s	1	0	0
Violaceae	Rinorea	ovalifolia			s	1	0	0
Zingiberaceae	Renalmia	alpinia		(Rottb.)Maas	h	0	0	1
Zingiberaceae	Renalmia	racemosa		Poepp. & Endl.	h	0	0	1

A.3 Appendix to Chapter 3

Table 3: Presence-absence data of the tree species with diameter at breast height 10 cm recorded in each plot at the Refugio Los Volcanes, Santa Cruz, Bolivia. DF: deciduous forest plot, SDF: semi-deciduous forest plot, EF: evergreen forest plot.

Family	Species	DF	SDF	EF
ACT	Saurauria peruviana Buscal.			x
ANA	Myracrodruon urundeuva Allemao	x		
ANA	Schinopsis hankeana Engl.	x		
ANA	Tapirira cf. guianensis Aubl.		x	
ANN	Guatteria alutacea Diels var. Steinbachii R. E. Fries		x	x
ANN	Rollinia sp.1			x
APO	Aspidosperma cylindrocarpon Mull. Arg.	x	x	x
APO	Aspidosperma rigidum Rusby	x	x	x
APO	Tabernaemontana cymosa Jacq.		x	
ARA	Aralia soratensis March.		x	
ARA	Dendropanax arboreus (L.) Decne. & Planch.		x	x
ARA	Oreopanax cf. steinbachianus Harms			x
BIG	Tabebuia heptaphylla (Vell.) Toledo	x	x	
BOM	Ceiba boliviana Britton & Baker f.	x	x	
BOR	Cordia alliodora (Ruiz & Pav.) Cham.	x	x	
CAP	Capparis flexuosa (L.) L.	x		
CAP	Capparis prisca Macbr.	x		
CEC	Cecropia sp.		x	x
CEL	Schaefferia argentinensis Speg.			x
CHR	Couepia sp.		x	
EUP	Alchornea glandulosa Poepp.			x
EUP	Croton piluliferus Rusby	x		
EUP	Drypetes amazonica Steyerl.	x	x	x
EUP	Pachystroma longifolium (Nees) I.M. Johnst.	x	x	x
EUP	Sebastiania brasiliensis Spreng.	x		
FLA	Casearia gossypiosperma Briq.	x		x
FLA	Casearia sp.1		x	
FLA	Casearia sp.2		x	

Family	Species	DF	SDF	EF
FLA	Hasseltia floribunda Kunth		x	x
JUG	Juglans australis Griseb.			x
LAC	Lacistema cf. aggregatum (P.J. Bergius) Rusby			x
LAU	Aniba sp.		x	x
LAU	Lauraceae 1		x	
LAU	Lauraceae 2		x	
LAU	Licaria cf. triandra (Sw.) Kosterm.		x	x
LAU	Nectandra cf. cuspidata Nees & Mart.		x	
LAU	Nectandra sp. 1		x	x
LAU	Nectandra sp. 2		x	x
LAU	Nectandra sp. 3			x
LAU	Ocotea sp.			x
LEC	Cariniana estrellensis (Raddi) Kuntze	x	x	x
LEG	Acacia cf. glomerosa Benth.	x		
LEG	Acacia sp. 3	x		
LEG	Anadenanthera colubrina (Vell.) Brenan	x		
LEG	Erythrina falcata Benth.		x	x
LEG	Inga marginata Willd.		x	x
LEG	Inga sp. 1		x	x
LEG	Lonchocarpus hedyosmus Miq.	x	x	
LEG	Machaerium cf. punctatum (Poir.) Pers.		x	
LEG	Machaerium cf. scleroxylon Tul.	x		
LEG	Machaerium pilosum Benth.	x		
LEG	Myroxylon balsamun (L.) Harms.	x		
LEG	Ormosia bolivarensis C.H. Stirt.		x	
LEG	Parapiptadenia excelsa (Griseb.) Burkart	x	x	
LEG	Piptadenia buchtienii Barneby	x		
LEG	Platymiscium cf. stipulare Benth.		x	
LEG	Senna sp.	x		
LEG	Swartzia jorori Harms	x	x	x
LEG	Tipuana tipu (Benth.) Kuntze	x		
MAL	Bunchosia cf. paraguariensis Nied.	x		x
MEL	Cedrela lilloi C. DC.	x	x	
MEL	Trichilia claussenii C. DC.	x	x	x

Family	Species	DF	SDF	EF
MEL	<i>Trichilia elegans</i> A. Juss.		x	x
MEL	<i>Trichilia pleeana</i> (A. Juss.) C. DC.		x	x
MELA	<i>Miconia</i> cf. <i>minutiflora</i> (Bonpl.) DC.			x
MOR	<i>Clarisia biflora</i> Ruiz & Pav.		x	x
MOR	<i>Ficus</i> cf. <i>eximia</i> Schott in Spreng.			x
MOR	<i>Ficus macbridei</i> Standl.			x
MOR	<i>Ficus maxima</i> Mill.			x
MOR	<i>Ficus obtusifolia</i> Kunth in Humb., Bonpl. & Kunth		x	x
MOR	<i>Ficus pertusa</i> L. f.			x
MOR	<i>Ficus</i> sp.		x	
MOR	<i>Ficus trigona</i> L. f.		x	x
MOR	<i>Maclura tinctoria</i> (L.) D. Don ex Steud.		x	
MOR	<i>Sorocea guilleminiana</i> Gaudich.		x	x
MYRS	<i>Myrsine umbellata</i> Mart.		x	x
MYRT	<i>Eugenia</i> cf. <i>moraviana</i> O. Berg		x	
MYRT	<i>Eugenia muricata</i> DC.			x
MYRT	<i>Eugenia</i> sp.	x	x	x
MYRT	<i>Myrciantes</i> cf. <i>pseudomato</i> (Legrand) Mc. Vough.	x	x	
MYRT	<i>Myrciantes</i> sp. 1	x		
NYC	<i>Bougainvillea stipitata</i> Griseb.	x		
NYC	<i>Guapira</i> aff. <i>olfersiana</i> (Link et al) Standl.		x	x
NYC	<i>Neea</i> sp.	x		
NYC	Nyctaginaceae Indet	x		
OCH	<i>Ouratea</i> cf. <i>angulata</i> Tiegh.			x
OLA	<i>Ximenia americana</i> L.	x		
PHY	<i>Gallesia integrifolia</i> (Sprengel) Harms	x	x	x
PIP	<i>Piper amalago</i> L.		x	
POL	<i>Ruprechtia apetala</i> Wedd.	x		
POL	<i>Triplaris americana</i> L.		x	x
RHA	<i>Rhamnidium elaeocarpum</i> Reissek		x	
ROS	<i>Prunus guanaiensis</i> Rusby		x	
RUB	<i>Chomelia</i> cf. <i>sessilis</i> Mull. Arg.		x	x
RUB	<i>Macrocnemum roseum</i> (Ruiz & Pav.) Wedd.			x
RUB	<i>Palicourea</i> cf. <i>guianensis</i> Aubl.			x

Family	Species	DF	SDF	EF
RUB	Pogonopus sp.		x	
RUB	Pogonopus tubulosus (A. Rich.) K. Schum.		x	
SAB	Meliosma herbertii Rolfe			x
SAPI	Allophylus cf. edulis (A. St.-Hil., Cambess. & A. Juss.) Radlk.		x	x
SAPI	Diatenopteryx sorbifolia Radlk.	x	x	x
SAPO	Chrysophyllum gonocarpum (Mart. & Gichl.) Engl.	x	x	x
SAPO	Chrysophyllum marginatum (Hook. & Arn.) Radlk.	x		x
SAPO	Chrysophyllum venezuelanense (Pierre) T.D. Penn.		x	x
SAPO	Pouteria nemorosa Baehni		x	x
SAPO	Sarcaulus sp.		x	x
SIM	Picrasma excelsa		x	
SOL	Solanum riparium Pers.		x	
SOL	Solanum sessile Ruiz & Pav.			x
TIL	Heliocarpus americanus L.		x	x
ULM	Celtis iguanaea (Jacq.) Sarg.		x	
URT	Myriocarpa stipitata Benth.		x	x
URT	Pouzolzia sp.	x	x	
URT	Urera baccifera (L.) Gaudich.		x	x
VER	Aegiphila steinbachii Moldenke	x		x

A.4 Appendix to Chapter 4

Table S1. Pair-wise Sørensen (Bray-Curtis) similarity coefficients between seasonal forest areas. in Bolivia. RT: Río Tuichi, CA: Camata, CS: Consata, CO: Coroico, RL: Río La Paz, CT: Río Cotacajes, RC: Río Caine, CQ: Chiquitanía, CH: Chaco, GR: Río Grande, PA: Río Parapetí, PI: Río Pilcomayo.

All Plant Groups

	RT	CA	CS	CO	RL	CT	RC	CQ	CH	GR	PA
CA	0.53										
CS	0.47	0.66									
CO	0.65	0.58	0.55								
RL	0.58	0.60	0.54	0.69							
CT	0.41	0.56	0.54	0.48	0.67						
RC	0.26	0.42	0.46	0.28	0.39	0.50					
CQ	0.37	0.40	0.39	0.40	0.48	0.38	0.30				
CH	0.23	0.15	0.18	0.20	0.24	0.20	0.20	0.45			
GR	0.37	0.41	0.41	0.44	0.52	0.43	0.45	0.53	0.40		
PA	0.37	0.37	0.38	0.44	0.47	0.39	0.39	0.47	0.43	0.69	
PI	0.26	0.39	0.34	0.32	0.42	0.42	0.49	0.47	0.37	0.65	0.57

Acanthaceae

	RT	CA	CS	CO	RL	CT	RC	CQ	CH	GR	PA
CA	0.22										
CS	0.26	0.62									
CO	0.67	0.26	0.36								
RL	0.53	0.25	0.34	0.77							
CT	0.55	0.26	0.43	0.68	0.87						
RC	0.10	0.18	0.50	0.08	0.07	0.15					
CQ	0.19	0.06	0.11	0.21	0.24	0.21	0.11				
CH	0.21	0.07	0.12	0.19	0.18	0.19	0.13	0.45			
GR	0.29	0.10	0.18	0.33	0.33	0.30	0.24	0.44	0.71		
PA	0.28	0.12	0.16	0.29	0.29	0.25	0.17	0.41	0.75	0.88	
PI	0.21	0.11	0.19	0.23	0.22	0.23	0.29	0.51	0.69	0.78	0.79

Bromeliaceae

	RT	CA	CS	CO	RL	CT	RC	CQ	CH	GR	PA
CA	0.63										
CS	0.57	0.82									
CO	0.65	0.66	0.63								
RL	0.65	0.63	0.63	0.74							
CT	0.48	0.63	0.66	0.54	0.65						
RC	0.40	0.49	0.54	0.45	0.52	0.55					
CQ	0.37	0.25	0.29	0.27	0.30	0.29	0.24				
CH	0.29	0.22	0.26	0.24	0.31	0.30	0.32	0.81			
GR	0.38	0.40	0.42	0.43	0.47	0.42	0.59	0.35	0.36		
PA	0.39	0.41	0.48	0.46	0.46	0.43	0.53	0.39	0.41	0.80	
PI	0.27	0.38	0.41	0.38	0.38	0.39	0.56	0.21	0.22	0.66	0.59

Cactaceae

	RT	CA	CS	CO	RL	CT	RC	CQ	CH	GR	PA
CA	0.33										
CS	0.00	0.00									
CO	0.40	0.67	0.00								
RL	0.13	0.53	0.12	0.44							
CT	0.00	0.20	0.11	0.21	0.55						
RC	0.00	0.00	0.00	0.00	0.00	0.32					
CQ	0.00	0.00	0.00	0.00	0.07	0.14	0.08				
CH	0.00	0.06	0.00	0.06	0.09	0.18	0.15	0.51			
GR	0.06	0.22	0.00	0.17	0.26	0.21	0.29	0.17	0.23		
PA	0.29	0.73	0.00	0.60	0.40	0.29	0.13	0.10	0.11	0.26	
PI	0.05	0.13	0.00	0.14	0.15	0.18	0.16	0.19	0.38	0.42	0.22

Pteridophyta

	RT	CA	CS	CO	RL	CT	RC	CQ	CH	GR	PA
CA	0.51										
CS	0.44	0.59									
CO	0.67	0.59	0.57								
RL	0.61	0.67	0.59	0.67							
CT	0.36	0.65	0.58	0.41	0.66						
RC	0.18	0.44	0.44	0.23	0.44	0.59					
CQ	0.49	0.61	0.59	0.60	0.72	0.54	0.44				
CH	0.30	0.18	0.23	0.26	0.29	0.15	0.16	0.29			
GR	0.49	0.60	0.62	0.58	0.71	0.58	0.47	0.78	0.33		
PA	0.40	0.39	0.43	0.47	0.58	0.46	0.38	0.59	0.35	0.65	
PI	0.36	0.61	0.50	0.41	0.65	0.65	0.68	0.66	0.21	0.69	0.56

A.5 Appendix to Chapter 5

Pearson correlation coefficients between environmental factors in three 1-ha plots at Los Volcanes, Santa Cruz, Bolivia.

Deciduous forest

	C	N	P	K	Ca	Mg	Mn	Fe	Al	pHL	pHO	pHA	pHB	SH	TC	SC	HC	SI	St	DW	L
N	0.99***																				
P	0.02	0.01																			
K	0.35	0.35	0.29																		
Ca	0.82***	0.81***	0.17	0.48*																	
Mg	0.03	0.02	0.17	0.27	0.42*																
Mn	0.17	0.13	-0.17	-0.04	-0.23	-0.50*															
Fe	0.02	0.00	0.27	0.27	0.01	-0.18	0.38														
Al	-0.38	-0.39	-0.14	-0.43*	-0.57**	-0.61**	0.11	-0.11													
pHL	-0.25	-0.26	-0.24	-0.22	-0.45*	-0.13	0.05	0.09	0.19												
pHO	0.29	0.32	-0.05	0.22	0.23	0.18	-0.23	-0.25	-0.13	-0.03											
pHA	0.37	0.42*	-0.06	0.21	0.50*	0.31	-0.33	0.02	-0.47*	-0.37	0.50*										
pHB	0.46*	0.53**	0.27	0.32	0.54**	0.20	-0.22	0.06	-0.37	-0.37	0.39	0.54**									
SH	0.06	0.06	0.51**	0.12	0.24	0.18	-0.28	-0.41*	0.09	-0.44*	-0.13	-0.14	0.13								
TC	0.22	0.21	0.31	0.02	0.31	0.04	-0.16	-0.17	0.09	-0.22	0.00	-0.29	0.24	0.44*							
SC	-0.28	-0.28	-0.25	-0.27	-0.44*	-0.23	0.35	0.52**	0.04	0.50*	-0.17	-0.15	-0.23	-0.81***	-0.47*						
HC	0.42*	0.40*	-0.23	0.10	0.40*	-0.13	0.32	0.32	-0.13	-0.06	-0.24	0.00	0.07	-0.12	0.16	-0.05					
SI	0.14	0.16	-0.42*	-0.15	0.15	0.18	-0.25	-0.13	-0.25	0.20	0.49*	0.65***	0.19	-0.54**	-0.36	0.18	-0.01				
St	0.29	0.27	0.16	-0.08	0.22	-0.28	0.08	-0.23	0.32	-0.21	-0.23	-0.23	0.17	0.55**	0.36	-0.46*	0.38	-0.23			
DW	-0.03	-0.02	-0.12	-0.32	-0.12	-0.11	0.06	-0.25	0.37	0.21	-0.03	-0.22	-0.07	0.31	0.41*	-0.32	0.29	-0.12	0.40*		
L	0.22	0.25	-0.30	0.01	0.28	0.32	-0.27	-0.07	-0.28	0.05	0.37	0.59**	0.27	-0.21	-0.13	-0.03	0.16	0.38	-0.33	0.04	
TH	-0.03	-0.05	-0.03	0.09	-0.04	0.10	0.08	0.11	-0.05	-0.02	-0.20	-0.31	-0.17	-0.21	0.04	0.29	-0.03	-0.37	-0.34	-0.37	0.06

Semi-deciduous forest

	C	N	P	K	Ca	Mg	Mn	Fe	Al	pHL	pHO	pHA	pHB	SH	TC	SC	HC	SI	St	DW	L
N	0.96***																				
P	0.43*	0.46*																			
K	-0.07	-0.05	-0.04																		
Ca	0.71***	0.68***	0.43*	-0.06																	
Mg	0.15	0.20	0.10	0.18	0.22																
Mn	-0.32	-0.15	0.03	-0.16	-0.37	0.03															
Fe	-0.16	-0.20	-0.21	0.08	-0.17	-0.23	0.18														
Al	-0.33	-0.38	0.06	0.52**	-0.13	0.09	-0.24	-0.03													
pHL	0.49*	0.45*	0.40*	0.16	0.34	0.01	-0.37	0.17	0.08												
pHO	0.50*	0.49*	-0.01	0.39	0.15	0.05	-0.18	0.04	-0.05	0.64***											
pHA	0.49*	0.46*	0.16	0.29	0.24	-0.04	-0.51**	-0.05	0.15	0.61**	0.60**										
pHB	0.20	0.12	-0.03	-0.04	0.09	0.17	-0.29	0.09	0.28	0.39	0.19	0.58**									
SH	-0.54**	-0.49*	-0.57**	-0.26	-0.44*	-0.17	0.22	0.12	0.07	-0.41*	-0.21	-0.21	0.01								
TC	0.16	0.20	0.37	0.05	0.03	-0.11	0.23	0.07	-0.03	-0.01	-0.22	-0.09	0.02	-0.33							
SC	0.01	0.09	0.02	0.23	0.15	0.44*	-0.09	-0.37	0.05	0.11	0.17	0.24	-0.09	0.00	-0.34						
HC	-0.28	-0.25	-0.46*	0.27	-0.53**	-0.05	0.23	0.18	-0.01	-0.19	0.06	0.00	0.01	0.26	0.01	-0.11					
SI	0.37	0.30	0.54**	0.17	0.39	0.11	-0.21	-0.28	-0.08	0.13	-0.01	0.05	-0.11	-0.75***	0.36	0.05	-0.18				
St	0.10	0.15	0.15	0.16	-0.09	-0.34	-0.14	0.19	-0.16	0.36	0.12	0.44*	0.16	-0.21	0.40*	-0.20	0.06	-0.03			
DW	-0.12	-0.21	0.16	-0.05	-0.02	-0.13	0.03	0.14	0.20	0.20	-0.08	-0.06	-0.06	-0.24	-0.11	-0.09	0.06	0.10	-0.04		
L	-0.05	-0.04	-0.10	0.11	0.08	0.07	0.13	0.17	-0.17	0.20	0.23	-0.05	-0.16	-0.26	-0.06	0.43*	-0.12	0.25	-0.10	0.24	
TH	0.11	0.16	0.12	0.31	0.06	0.46*	0.19	-0.17	0.17	-0.10	0.02	0.07	0.08	-0.15	-0.03	0.40*	-0.04	0.16	-0.15	-0.05	0.22

Evergreen forest

	C	N	P	K	Ca	Mg	Mn	Fe	Al	pHL	pHO	pHA	pHB	SH	TC	SC	HC	SI	St	DW	L
N	0.99***																				
P	-0.24	-0.27																			
K	0.04	0.07	0.24																		
Ca	0.73***	0.74***	-0.12	0.11																	
Mg	0.34	0.32	0.02	-0.13	0.22																
Mn	-0.09	-0.06	-0.12	0.01	-0.03	-0.30															
Fe	-0.14	-0.14	-0.18	0.27	-0.12	0.00	0.04														
Al	-0.19	-0.20	0.11	-0.26	-0.26	0.14	-0.11	-0.15													
pHL	0.27	0.27	0.08	-0.05	0.19	0.33	-0.05	-0.03	0.16												
pHO	-0.06	-0.08	-0.09	0.03	0.00	-0.12	0.30	0.00	0.06	0.38											
pHA	-0.10	-0.09	0.12	-0.04	-0.10	0.22	-0.22	0.16	0.24	0.66***	0.32										
pHB	0.14	0.13	-0.03	0.08	0.29	0.02	0.46*	0.01	-0.03	0.19	0.45*	0.32									
SH	-0.23	-0.27	-0.22	-0.28	-0.30	0.18	-0.25	0.12	0.11	-0.27	-0.17	-0.13	-0.49*								
TC	-0.27	-0.31	-0.20	-0.24	-0.31	0.13	-0.01	0.10	0.17	0.25	0.55**	0.23	-0.08	0.61**							
SC	0.23	0.24	0.04	0.29	0.05	0.17	-0.16	-0.04	0.09	0.50*	0.06	0.30	0.10	-0.06	0.09						
HC	0.08	0.12	-0.23	0.23	0.09	0.04	0.39	0.01	-0.33	0.33	0.43*	0.29	0.38	-0.28	0.02	0.15					
SI	0.06	0.03	-0.10	-0.01	-0.04	-0.30	0.42*	-0.12	-0.22	-0.11	0.12	-0.12	0.53**	-0.23	-0.16	0.05	0.25				
St	-0.11	-0.09	-0.04	-0.23	-0.23	-0.03	-0.21	-0.20	0.49*	-0.34	-0.34	-0.25	-0.50*	0.40*	0.00	-0.10	-0.50*	-0.38			
DW	-0.32	-0.32	-0.10	-0.05	-0.27	0.02	-0.31	0.22	-0.10	-0.25	-0.51**	-0.10	-0.45*	0.23	-0.20	-0.27	-0.15	-0.16	0.21		
L	0.16	0.15	-0.41*	-0.02	0.07	0.44*	0.01	0.14	-0.15	0.33	0.20	0.34	0.28	0.20	0.22	0.50*	0.37	0.12	-0.20	0.02	
TH	-0.10	-0.06	0.14	-0.02	-0.04	0.30	-0.21	-0.01	0.27	-0.06	-0.07	0.04	-0.10	-0.20	-0.11	-0.11	-0.26	-0.60**	0.19	0.03	-0.19