NEOTROPICAL LOWLAND FORESTS ALONG ENVIRONMENTAL GRADIENTS

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Thesis

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Abstract

Understanding spatial patterns of tropical forests and the environmental factors determining these patterns is important for forest management and for predicting responses of forests to climate change. The main objective of this dissertation was to evaluate how environmental factors shape tropical lowland forests in Bolivia. Specifically it assessed how climatic and edaphic factors affect 1) forest structure, 2) floristic composition, 3) tree growth rates, and 4) species distribution. It also assessed how disturbance factors affect tree growth rates.

For this research, I used a network of 220 1-ha permanent sample plots distributed along environmental gradients. For each plot, all stems ≥10 cm diameter were identified, evaluated and monitored; climatic data were interpolated from weather stations and soil samples were collected. In lowland Bolivia, rainfall seasonality increased from north to south; although drier forests had more fertile soils than moister forests, some plots in moister forests were also fertile. Environmental variables were summarized, using Principal Components Analysis, into four (composite) environmental factors reflecting rainfall, temperature, soil fertility and soil texture, respectively. A stepwise selection procedure identified how these environmental factors affect tropical forest.

It is shown that rainfall and soil texture positively affected most of the 15 forest structural variables. Forest height, palm density and total basal area increased with rainfall while liana infestation decreased. While forest height and liana infestation were more affected by soil texture, palm density was negatively affected by soil fertility. Surprisingly, tree basal area was not affected by the environmental factors. For documenting the variation in floristic composition I selected a set of 100 plant species. Floristic variation was more strongly shaped by the climatic gradient than by the edaphic gradient. Detrended Correspondence Analysis ordination, based on species abundance, divided lowland Bolivia into two major groups (Southern Chiquitano and Amazonia), and a Multiple Response Permutation Procedure distinguished five floristic regions. Additionally, I described diameter growth rates at tree and stand level and evaluated the effects of environmental factors and logging on growth rates. Growth rates at both tree and stand level increased with rainfall and temperature but no clear effects of soil fertility were found. Growth rates increased in logged plots, especially those which had a high logging impact. Finally, I analyzed the species distribution and environmental response curves for each of those 100 selected species. I found a positive trend between species abundance and occurrence. While 91% of the species were affected by climate, 47% of the species were affected by soil factors.

In summary, climate was the most important factor shaping lowland forests in Bolivia. The large variation among forests and the ecological differences along the main environmental gradients have to be taken into account when developing forest-specific management plans. The results of the gradient approach suggest that with future decreases in rainfall and increases in temperature, due to climate change, drastic shifts can be expected in forest structure, composition and dynamics in these tropical lowland forests.

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Chapter 1

General introduction

Do we understand the main drivers of plant community patterns in tropical forests?

The forest heterogeneity in tropical regions is a fascinating phenomenon. Deciphering the underlying determinants of this phenomenon is a major challenge as it is a complex issue that requires insights from various fields like biogeography and ecology. Historical processes (i.e. movement of tectonic plates, changes in climate and sea level, past human impacts) determine what species make up the regional species pool, while environmental filters like climate, soils, natural disturbances, and human land use determine which species are recruited from the regional species pool and make up the local plant community (Ricklefs 1987, ter Steege & Zagt 2002). These environmental filters determine, therefore, how species abundance and distribution vary over large to small spatial scales.

Tropical lowland forests are extremely complex in *structure*, although they give an impression of monotony in their general appearance due to the predominance of woody plants (Richards 1996). Several factors, including seasonality and soil fertility, have been proposed to promote structural complexity of tropical forest (Quigley & Plat 2003). Higher densities and higher basal area, for example, occur more in aseasonal forests than in dry forests (Malhi *et al.* 2002, Losos *et al.* 2004). Tree density and basal area were different among four Neotropical lowland forests de Costa Rica, Panama, Peru and Brazil, with higher tree density on less fertile soils and higher basal area on more fertile soils (DeWalt & Chave 2004). Large-scale patterns in forest structure and their underlying driving factors are less known because studies quantifying the drivers included mostly only one driver, e.g. climate (Vieira *et al*. 2004, Takyu *et al*. 2005) or soil (Clark & Clark 2000, DeWalt & Chave 2004, Paoli *et al*. 2008), or studies included only one site (Bongers *et al.* 1988, Faber-Langendoen & Gentry 1991).

Large-scale patterns in *species composition* are relatively well known (Terborgh & Andresen 1998, ter Steege *et al*. 2003), but there is less understanding of the controlling mechanisms (Gentry 1992). For example, West African forests show pronounced gradients in forest composition, which are mostly determined by rainfall and to a lesser extent by soil fertility (Hall & Swaine 1976, Bongers *et al.* 2004). On the other hand, South American forests are mostly determined by soil fertility and the length of the dry period (ter Steege *et al.* 2006). The dispersal-assembly hypothesis states that ecological preferences of tree species play no role in their distribution and abundance patterns, and that differences in floristic composition between sites should be related to the distance between these sites only (Hubbell 2001). Species composition indeed varies with the geographical distance between locations, but these distances are usually also related with environmental variation (ter Steege *et al.* 2000, Pyke *et al.* 2001, Wassie *et al.* 2010).

Species distribution is largely determined by the multidimensional ecological niche space that a species occupies (MacArthur 1972). Species occurrence and abundance vary at regional and local scales in response to environmental conditions (Swaine 1996). Ecologists have found different response curve shapes, mostly for temperate species, but data for tropical forest species are surprisingly scarce (Bongers *et al.* 1999, Duque 2004). Some studies show that the occurrence of most species is strongly linked to rainfall (Swaine 1996, Holmgren & Poorter 2007) while others show that species distribution and community composition is linked to soil nutrient availability (Baillie *et al.* 1987, Potts *et al.* 2002).

Species composition and environmental conditions can influence *tree growth*. A study from the Guyana Shield found that low stand dynamics was associated with the slow growth of the dominant tree species (ter Steege & Hammond 2001). Tree growth tends to be higher in humid climates and on richer soils (Russo *et al.* 2005, Phillips *et al.* 2004). Information on the spatial patterns of tree growth and the environmental variables determining these patterns is, however, still scarce (Baker *et al.* 2003a).

Spatial scale and plant-environment relationships

Most of the geological and climatic variation in the tropics occurs at the meso-scale (> 1000 km^2), and this is also the scale at which most management and conservation planning occurs (ter Steege *et al.* 2003). Yet, only recently researchers have begun to link plant community patterns to environmental factors at this meso-scale (e.g. Condit *et al.* 2002, Duivenvoorden *et al.* 2002, ter Steege *et al.* 2006). Most insight has come from studies of species associations with habitat characteristics at small local scales (Hubbell & Foster 1990, Harms *et al.* 2001) and from descriptions at continental scales (Gentry 1988a, Parmentier *et al.* 2007).

In the Neotropics, most work on explaining species diversity, species distribution, and forest dynamics has been done using single large plots (e.g. Condit *et al.* 2000). Nowadays, networks of large plots on continental scale (i.e. CTFS – Centre for Tropical Forest Science) and many small plots on sub-continental scale (i.e. ATDN – Amazon Tree Diversity Network, RAINFOR – Amazon Forest Inventory Network) are dealing with these and another issues related mainly to understanding of the factors that allow the fascinating diversity and complex dynamics of tropical forests. The issue of scale is particularly important because it allows the understanding of how species are spatially distributed and how species composition is spatially arranged (Crawley & Harral 2001). Ricklefs (2008) argued that a better understanding in community ecology will come from considering factors that influence species distribution not only across space but also across environmental gradients.

Lowland Bolivia: a great natural laboratory

Bolivia is situated in the center of tropical South America and, as a consequence, it is a country where the Andean, Amazonian, Cerrado and Chaco biomes meet (Navarro & Maldonado 2002, Ibisch & Mérida 2003). Bolivia provides, thus, an ideal setting to study vegetation-environment relationships because it features an extraordinary display of vegetation types, geomorphological complexity and soil heterogeneity across a broad rainfall gradient (Potess 1991, Navarro & Maldonado 2002, Killeen *et al.* 2006). The large forest heterogeneity and plant species diversity might be a blessing for conservationists, but may present a challenge to forest managers, as sustainable management practices should be fine tuned to local site conditions and species characteristics.

Approximately 60% (684,000 km^2) of Bolivia is covered with lowland forests (Montes de Oca 1997), in which one of the most important activities is forest management for timber extraction (Dauber *et al.* 1999). The Forestry Law in Bolivia provides a strong stimulus for sustainable forest management. As a result Bolivia has now one of the largest areas, more than 2 millions of ha, of natural forests certified under the system of the Forest Stewardship Council in the tropics (Fredericksen *et al.* 2003, Peña-Claros *et al.* 2009). An important aspect of the Forestry Law is the establishment and monitoring of a network of permanent sample plots in forest management areas. This network was designed to provide a better understanding of logging impact on forest dynamics and timber yield.

Preliminary analyses on species specific growth rates and eco-region stand level growth rates were developed (Dauber *et al.* 2003, 2005), but logging effects on the growth rates were not considered.

In lowland Bolivia, studies on floristic composition and species abundance of the different forest types are scattered and mostly descriptive (Killeen *et al.* 1998, 2001; Jørgensen *et al.* 2006) with scarce information on the floristic variation among forest types (Navarro & Maldonado 2002, Mostacedo *et al.* 2006). In addition, factors affecting the floristic patterns in Bolivia are poorly understood because studies that link vegetation with underlying explanatory variables are surprisingly scarce (but see Killeen *et al.* 2006). Therefore, assessing plant community patterns and understanding how environmental factors affect these patterns should be regarded as an important step towards plant diversity conservation and forest management in Bolivia.

Research objectives and questions

The main objective of this research is to evaluate how environmental factors shape tropical lowland forests in Bolivia. Specifically it questions how climatic and edaphic factors affect (1) forest structure, (2) floristic composition, (3) tree growth rates, and (4) species distribution. Additionally, it questions how disturbance factors affect tree growth rates.

Thesis outline

This dissertation consists of six chapters including the general introduction (chapter 1), four research chapters (chapter 2 to 5) and the synthesis (chapter 6). To evaluate how environmental factors affect forest attributes I used a set of five climatic variables and 12 edaphic variables. These variables were summarized into four environmental axes using a Principal Component Analysis (PCA). I used the two main climatic PCA axes (named after the most important factors they represent as rainfall axis and temperature axis) and the two soil PCA axes (named as soil fertility axis and soil texture axis) to have composite variables that represent environmental gradients and to reduce the number of correlated variables. A stepwise selection approach identified how the climatic and edaphic PCA axes affected the plant community. In all chapters, but one, I used data from 220 1-ha permanent sample plots and related those to the four environmental axes. In chapter 5, I used 165 1-ha plots and used in addition several disturbance variables that describe logging or disturbance intensity.

Chapter 2 describes how forest structure varies among forests across lowland Bolivia. I measured and evaluated each tree and palm ≥ 10 cm in diameter and considered 15 forest structural variables based on height, crown position, diameter, density and liana load. I tested the hypothesis that stem density and basal area of trees and palms will increase with water availability and liana density will increase in drier forests.

Chapter 3 evaluates patterns in floristic composition using abundance and presence-absence data of 100 plant species. I predicted that lowland Bolivia has five floristic regions and that climate is a more important factor than soil in shaping floristic composition. This chapter includes the floristic similarity among regions and the habitat preference of each species for one of these regions. I also evaluate the differences in environmental conditions among floristic regions.

Chapter 4 describes the variation in tree growth by examining growth rates at individual level (average diameter growth) and at stand level (basal area growth) across environmental gradients. Effects of anthropogenic disturbances (i.e. logging) on the growth rates were also considered. I expected that growth rates would be higher in humid than in dry sites, higher in nutrient-rich than nutrient-poor forests, and higher in logged than non-logged forests as a result of increased availability of water, nutrients and light, respectively.

Chapter 5 analyzes the distribution patterns of the 100 selected species based on combination of frequency and abundance data. Additionally, I constructed response curves for each species against each of the four environmental axes described above using logistic regression analysis on presence-absence data. I hypothesized that species frequency and abundance would be positively correlated, that the majority of the species would show unimodal response curves to the environmental gradients and that species would respond stronger to climate than to soil effects.

Finally, chapter 6 summarizes the main results of the different chapters and provides a general synthesis. The implications for forest management and climate change are discussed.

Study site

Lowland Bolivia

Lowland Bolivia is characterized by differences in geomorphology and geological history. In the west the relatively young landscapes of the Andean foothills occur, while in the east ancient rocks of the Pre-Cambrian Shield abound, extending from Brazil to the extreme north-eastern corner of Bolivia (Suárez-Soruco 2000, Alverson *et al.* 2003). Between these two regions is the Chaco–Beni Plain, a flat plain composed of Quaternary sediments. In the south, where the Amazon is separated from the watershed of the River Plate these alluvial sediments cave into older sedimentary rocks dating from the Cretaceous (Suárez-Soruco 2000). These differences lead to strong gradients in soil characteristics, which vary largely in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003). Lowland Bolivia is also characterized by two climatic gradients: a south-north gradient with *mean* annual precipitation ranging from 1100 to 1900 mm and an east-west gradient ranging from 1600 to 2200 mm. However, the precipitation in individual years can vary from 600 to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, 1970 – 2007, Servicio Nacional de Meteorología e Hidrología – SENAMHI, unpublished data). The region experiences a 4 to 7 months long dry season (with precipitation < 100 mm/month), mostly from April to September, corresponding to the austral winter. Mean annual temperature is between 24 and 26°C. Thus, lowland Bolivia has an extraordinary display of vegetation types related to geomorphological complexity and climatic variation.

The Bolivian network of permanent sample plots

For this study 220 1-ha plots were selected from the Bolivian network of permanent sample plots. The plots were established by various research projects and forestry companies, before logging activities took place. All plots have been established in forest management areas except four, which are in an ecological reserve (Reserva Ecológica El Tigre-RET). The establishment and monitoring of the network had initial support from the Proyecto de Manejo Forestal Sostenible

(BOLFOR Project, funded by USAID/PL-480). To date this network and its database is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots cover a wide range in environmental conditions and different forest types in the departments of Pando, La Paz, Beni and Santa Cruz (Fig. 1, Table 1). The plots are located between 10 – 18° S and 59 – 69° W, mostly in upland forests (terra firme; only 5% of the plots were found in areas of seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from 100 – 500 masl. Most of the plots are typically square (100 x 100 m), with 11 of them being rectangular (20 x 500 m). These plots have been established between 1995 and 2007 and re-measured in different years; thus most of them have more than one re-measurement and different census intervals (Table 1).

Table 1. Location and information for 220 1-ha permanent sample plots distributed over 21 sites across lowland forests of Bolivia. Departments (Dpt): P = Pando, B = Beni, LP = La Paz, SC= Santa Cruz. Climatic data were interpolated from meteorological stations provided by the Servicio Nacional de Meteorología e Hidrología (SENAMHI). Edaphic data were analyzed by the Centro de Investigación Agrícola Tropical (CIAT-Bolivia). Years of establishment and the year of last measurement on the plots of each site are provided. Forest types: PA = Pre-Andean Amazonian, A = Amazonian AC = Amazonian-Chiquitano, C = Chiquitano dry.

Sites	Dpt	# plots (ha)	Altitude (masl)	Annual rainfall (mm)	Annual temperature (T°)	pH	CEC (cmol Kg^{-1})	Years*	Forest type**
AGROFOR	LP	1	230	2200	26.0	4.4	4.5	03-06	PA
Ixiamas	LP	5	274	2190	25.8	4.0	5.3	03-05	PA
San Pedro	LP	2	223	2130	25.7	5.3	12.3	03-05	PA
Fátima	B	6	239	2025	25.2	5.3	9.8	95-02	PA
Bolivia Mahogany	B	5	208	1980	25.3	4.9	8.4	95-02	PA
IMAPA	P	8	256	1980	25.5	4.1	2.6	00-07	A
SAGUSA	P	16	191	1950	25.7	4.4	3.0	03-06	A
MABET	P	15	150	1940	26.2	3.5	4.2	99-07	A
CIMAGRO	P	3	217	1935	25.9	3.9	3.1	07	A
Verdum	B	3	176	1840	26.4	4.2	3.6	01-06	A
RET	B	4	150	1835	26.4	3.8	5.3	95-06	A
Lago Rey	SC	19	217	1735	26.3	5.0	3.4	05-07	AC
CIBAPA	SC	16	229	1675	26.0	4.5	2.5	04-07	AC
San Martín	SC	8	242	1655	25.9	4.4	2.7	05-07	AC
CIMAL Guarayos	SC	3	317	1515	25.1	6.5	6.1	07	AC
La Chonta	SC	48	340	1470	24.7	6.9	9.4	00-07	AC
INPA	SC	32	449	1185	24.2	5.3	5.5	02-07	C
CIMAL San Miguel	SC	9	230	1175	25.4	5.4	3.6	98-06	C
San José	SC	6	261	1155	25.5	5.2	4.5	06	C
CIMAL Velasco	SC	6	260	1150	25.2	5.7	7.5	98-06	C
Sutó	SC	5	264	1120	25.5	6.3	12.9	99-06	C

* 03-06 indicate 2003-2006.

** Source: Ibisch & Mérida 2003

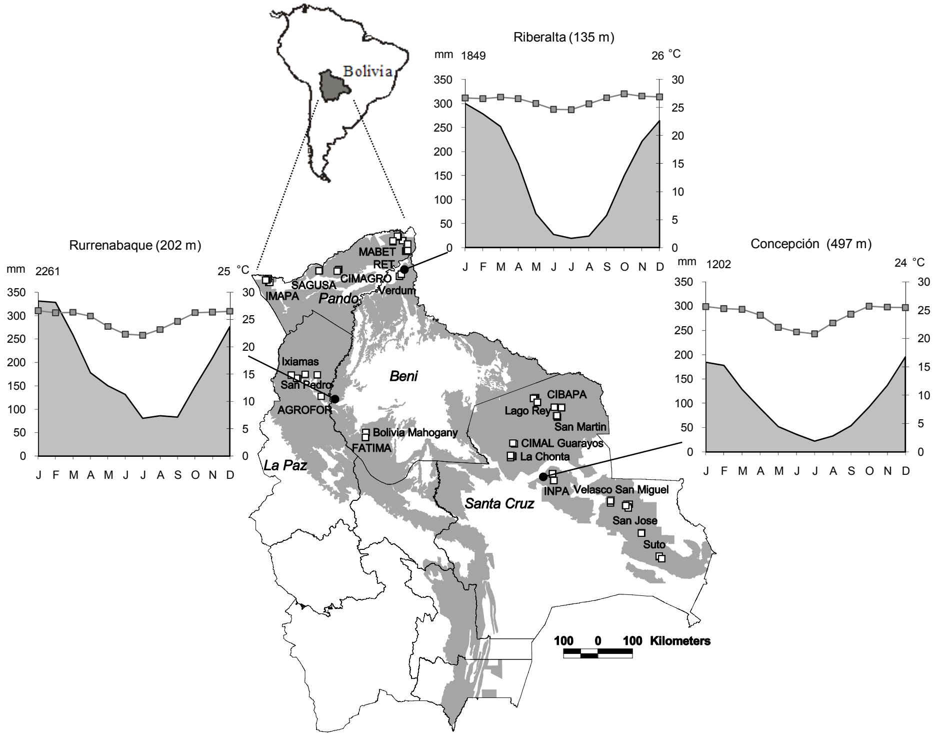

Figure 1. Location of the 220 1-ha permanent sample plots in lowland Bolivia, South America, as indicated by the dots. Grey areas are forests for timber production. Different number of plots were established in the forestry concessions located in four departments (La Paz, Pando, Beni and Santa Cruz). Climate diagrams of three localities are provided to show annual patterns in rainfall and temperature in the region. Name and altitude (m) of the station, mean annual rainfall (mm), mean annual temperature (°C) and monthly regimes of rainfall and temperature are also given. Rainfall data are averaged over a 37 years period (1970 - 2007) and temperature data are averaged over a 27 years period (1980 - 2007). Data were provided by the Servicio Nacional de Meteorología e Hidrología (SENAMHI).

Chapter 2

Climate and soil drive forest structure in Bolivian lowland forests

Marisol Toledo, Lourens Poorter, Marielos Peña-Claros, Alfredo Alarcón, Julio Balcázar, Claudio Leaño, Juan Carlos Licona and Frans Bongers

Abstract

Climate is recognized as the most important factor determining variation in forest structure, but the effect of soils on forest structure is sometimes contradictory. We describe how climate and soil affect forest structure, using a network of 220 1-ha permanent plots, in lowland Bolivia. For each plot, we obtained 5 climatic variables, interpolated from available data, and 16 edaphic properties related to fertility and texture, obtained from sampled soils. We measured each tree and palm ≥ 10 cm in stem diameter and considered 15 forest structural variables based on height, diameter, crown position, and liana infestation. Rainfall increased from north to south and drier forest soils were more fertile while moister forests had generally poor soils. Some plots in moister forests were more fertile due to young parent material or past anthropogenic activities. Overall, moister forests showed larger variation in soil texture and drier forests showed larger variation in soil fertility. Forest structural variables that responded most to environmental variation were maximum height, total basal area, palm density and liana infestation. Height, palm density and basal area increased with rainfall while lianas decreased with rainfall. While forest height and lianas were more affected by soil texture, palm density was negatively affected by soil fertility. We found that rainfall, temperature and soil texture were more important drivers than soil fertility. Thus climatic and edaphic factors have strong effects on variation in forest structure at the landscape-scale.

Key words: climate, environmental gradient, forest structure, liana, lowland Bolivia, palm, permanent plot network, soil, tree.

Introduction

Tropical lowland forests are extremely complex in structure, although they give an impression of monotony in their general appearance due to the predominance of woody plants (Richards 1996). Describing forest structure is as complex as defining it, because forest structure encompasses many components that can be described in numerous ways. In general, the term "forest structure" is used to describe the architecture, organization, composition or abundance of the different assemblages occurring in forests. The most common studied attributes of forest structure are maximum canopy height, strata levels, life-form density, tree size, spatial tree distribution, biomass, basal area and volume, although former studies also focused on profile diagrams and leaf-area (Davis & Richards 1933, Webb 1958, Proctor *et al.* 1983, Ashton & Hall 1992, Lieberman *et al.* 1996, Killeen *et al.* 1998, Clark & Clark 2000, DeWalt & Chave 2004, Poorter *et al.* 2008). The display of these structural attributes can be vertical or horizontal, and their variation can be spatial or temporal (Spies 1998, Bongers 2001). In this paper we analyze the spatial variation of forest structure in terms of vertical and horizontal structure focusing on three woody life forms (trees, palms and lianas). These life-forms are key components of tropical forests because they largely determine the structure, biomass and diversity of these forests (Gentry 1991, Schnitzer & Bongers 2002).

Several factors have been proposed to be strong drivers of forest structure in tropical regions, climate and soil being the most important ones (Murphy & Lugo 1986, Clark & Clark 2000, Malhi *et al.* 2002). It is widely recognized that forest structure components vary along gradients of these major factors (Richards 1996, Losos *et al.* 2004). For example, canopy height tends to be higher in wetter and less seasonal forests, but tends to be independent of soil nutrient level. Consequently, dry forests usually have a short stature, because their soils are subject to frequent water deficits as well as high soil nutrient content (Swaine *et al.* 1990, Ashton & Hall 1992). Evidence from tropical ecosystems suggests that stem density and basal area tend to vary with the intensity of dry season; higher densities and higher basal area occur in more aseasonal forests (Malhi *et al.* 2002, Losos *et al.* 2004). A comparison of four Neotropical lowland forests showed that stem density and basal area tended to be higher on less fertile soils and richer soils were characterized by a low tree but high palm density (DeWalt & Chave 2004). Significant positive relationships between palm densities and soil fertility have been also found in other forests (Clark *et al.* 1995, Sesnie *et al.* 2009). In contrast, Vormisto (2002) found the lowest palm density on the richest soils. Several studies have shown that tropical forests vary considerably in liana density (DeWalt *et al.* 2000, Phillips *et al.* 2005), with seasonal forests showing the highest densities (Pérez-Salicrup *et al.* 2001, Schnitzer 2005, DeWalt *et al.* 2009). Relationships between soil fertility and density of lianas are equivocal, as a positive relationship was found in Amazonian and Malaysian forests (Putz & Chai 1987, Laurence *et al.* 2001, DeWalt *et al.* 2006) but not in other tropical forests (Ibarra-Manríquez & Martínez-Ramos 2002, DeWalt & Chave 2004).

Effects of environmental gradients on forest structure thus remain unclear because studies have found contradictory results. In addition, large-scale patterns in forest structure and their underlying driving factors are less known (but see Proctor *et al.* 1983, DeWalt & Chave 2004, Lewis *et al.* 2004), because studies describing forest structure included only one site (Bongers *et al.* 1988, Newbery *et al.* 1992, Milliken 1998, Poulsen *et al.* 2006) or studies quantifying the drivers included mostly one driver only, e.g. climate (Vieira *et al.* 2004, Takyu *et al.* 2005) or soil (Faber-Langendoen & Gentry 1991, Clark & Clark 2000, Nebel *et al.* 2001a, White & Hood 2004, Paoli *et al.* 2008). Understanding the patterns and causes of spatial variation in forest structure is not only important to understand the history and function of forest ecosystems but also to provide a sound basis for evidence-based forest management.

In this context, the Bolivian network of permanent plots provides an appropriate system to study vegetation-environment relationships because it covers an extraordinary display of vegetation types and soil heterogeneity across a rainfall gradient. We used 220 1-ha permanent sample plots from this network established in lowland Bolivia, to describe the spatial variation in environment and forest structure and to analyze the effects of climate and soil on forest structure.

The following questions were addressed: (1) how do climate, soil, and forest structure vary across the plots in lowland Bolivia? (2) how are components of climate-, soil-, and forest structure associated among themselves? and (3) how do climate and soil affect forest structure? We hypothesized that components of climate, soil, and forest structure will have a high variation due to the high heterogeneity of environmental conditions in Bolivia (Navarro & Maldonado 2002, Ibisch & Mérida 2003). Secondly, we expected a negative relationship between rainfall and soil nutrients status due to that higher rainfall leads to low nutrient levels in soils as a result of leaching (Baillie 1996). Finally, forest structural components will be positively related to climate properties and will be negatively related to soil properties. Specifically, we predict that stem density and basal area of trees and palms will increase with water availability (Malhi *et al*. 2002, Losos *et al.* 2004), due to higher resource availability permits more stems to coexist; and liana density will increase in drier forests due to its dry season advantage (Schnitzer 2005, Swaine & Grace 2007).

Material and Methods

Study area

For this study a total of 220 1-ha plots were selected from the National Network of Permanent Plots (NNPP) in lowland Bolivia (Fig. 1). These plots were established in old growth forests (10–18°S, 59–69°W) between 1995 and 2007 by various projects and forestry concessionaries (see Acknowledgements for more details). Currently, the NNPP is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). Nearly all plots are in upland forests (*terra firme;* only 5% of the plots were found in areas with seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range of 100–500 masl.

The selected plots are distributed along the two main climatic gradients in lowland Bolivia: a south-north gradient with *mean* annual precipitation ranging from 1100 to 1900 mm and an east-west gradient from 1600 to 2200 mm. However, the precipitation in individual years can vary from 600 to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, 1970 – 2007, Servicio Nacional de Meteorología e Hidrología − SENAMHI, unpublished data). In general, this area experiences a 4 – 7 months long dry period (e.g. precipitation < 100 mm/month), mostly from April to October, corresponding to the austral winter. Mean annual temperature is between 24° and 26°C. Soils in lowland Bolivia are widely variable, due to differences in geomorphology and geological history. The north contains the wide fluvial plain of the Amazon basin, while in the south the alluvial sediments from the Amazon and River Plate watersheds cave into older sedimentary rocks dating from the Cretaceous (Suárez-Soruco 2000). In the west the relatively young landscapes of the Andean foothills occur, while in the east ancient rocks of the Pre-Cambrian Shield abound, extending from Brazil to the extreme north-eastern corner of Bolivia (Suárez-Soruco 2000, Alverson *et al.* 2003). Between these two regions the Chaco – Beni Plain is located, a flat plain composed of Quaternary sediments. The soils vary largely in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003).

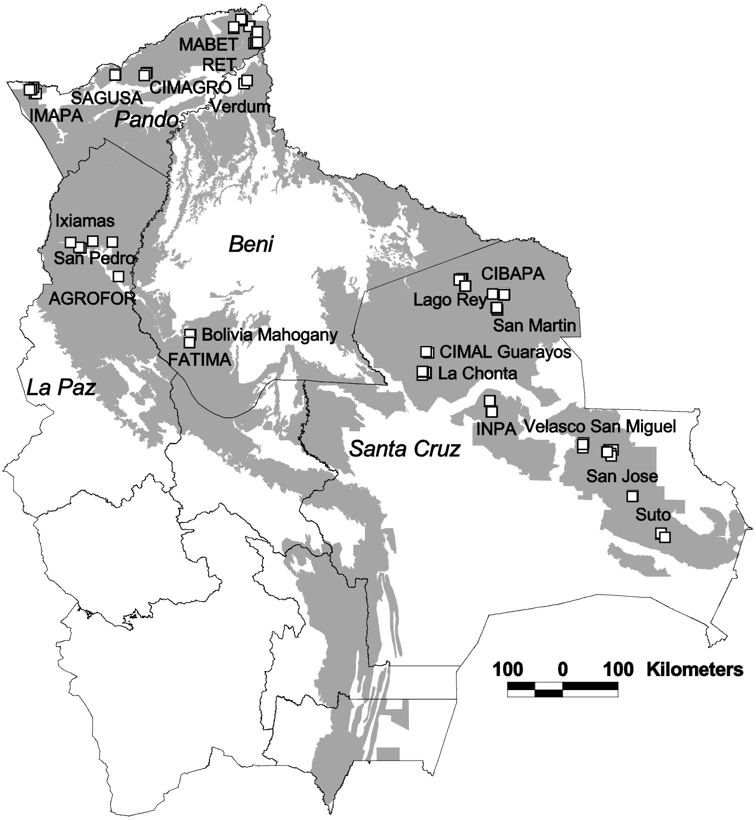

Figure 1. Location of 220 1-ha permanent sample plots in lowland Bolivia. Gray areas are forests for timber production. Different number of plots were established in the forestry concessions located in four departments: La Paz [Ixiamas (5 plots), San Pedro (2), AGROFOR (1)]; Pando [IMAPA (8), SAGUSA (16), CIMAGRO (3), MABET (15)]; Beni [RET (4), El Verdum (3), Bolivia Mahogany (5) and Fátima (6)]; and Santa Cruz [CIBAPA (16), Lago Rey (19), San Martín (8), CIMAL-Guarayos (3), La Chonta (48), INPA (32), Velasco (6), San Miguel (9), San José (6), and Sutó (5)].

Climatic data

For each of the 220 plots annual and monthly climatic data (precipitation and temperature) were obtained through interpolation of available data from 45 weather stations in the region. Precipitation (for a period of 37 years; 1970 – 2007) and temperature data (from 14 to 37 years) from 24 weather stations distributed throughout lowland Bolivia were provided by the SENAMHI. Data from additional 21 weather stations located in Brazil, Paraguay, and Peru were obtained from the Agrotecnologica Amazonica (www.agteca.com). Climatic data per plot were obtained using the kriging interpolation method, with point as kriging type and using nearest neighbor statistics. All interpolations were made using Surfer 8.0 (Golden Software). A total of five climatic variables was obtained for each plot: mean annual temperature, total annual precipitation, sum of the precipitation of the three driest months – June to August – (hereafter driest months), the length of the dry period (number of months < 100 mm) and the length of the drought period (number of months < 50 mm).

Edaphic data

In each permanent plot we collected 20 soil samples from the first 30 cm of soil depth using a bucket auger. All samples of the same plot were pooled, air-dried and stored in plastic bags. A total of 500 g per composite soil sample was analyzed at the Centro de Investigación Agrícola Tropical, CIAT in Santa Cruz, Bolivia. Soil samples were analyzed for a total of 16 characteristics; three physical and 13 chemical. The physical variables were the percentages of sand (particle size 0.05 to 2.0 mm), silt (0.002 to 0.05 mm) and clay (< 0.002 mm) obtained by using the Bouyoucos hydrometer. The pH was determined on 10 g soil sample, using 50 ml of distilled water and equilibrating for 90 min. The concentrations of four exchangeable cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+) was determined in 1 M ammonium acetate at pH 7; acidity in 1 M of potassium chloride (KCl); the exchangeable aluminium (Al^{3+}) in 1 M of hydrogen chloride (HCl). The phosphorous (P) was determined using the Olsen method; the organic matter content (OM) using the Walkley-Black method and the total nitrogen (N) using the micro Kjeldahl method (Cochrane & Barber 1993). The total exchangeable bases (TEB) is the sum of the four most important exchangeable cations (Ca, Mg, K and Na). The cation exchange capacity (CEC) is the sum of TEB plus acidity, which indicates the total concentration of positive cations held by the soil. The base saturation is the percentage of exchangeable cations or bases on the total CEC; it identifies the relative proportion of sources of acidity and alkalinity in the soils (Brady 1990). Although cations are not bases, they are referred to in this way because they decrease the acidity and increase the pH of the soils (Olaitan *et al.* 1984).

Forest data

Plots were typically square (100 x 100 m); however, 11 of them were rectangular (20 x 500 m). Each tree and palm ≥ 10 cm diameter at breast height (DBH; measured at 130 cm or higher when buttresses were present) was measured for its diameter, tagged and identified following standard protocols (Alder & Synnott 1992, Contreras *et al.* 1999). The crown position of each individual was scored into one of five categories: (1) no direct light, (2) some side light, (3) some overhead light, (4) full overhead light and (5) emergent crown (Dawkins & Field 1978). Each individual stem was scored into one of four categories of liana infestation: (0) without lianas, (1) lianas only on the trunk, (2) liana partially in trunk and crown, and (3) completely covered with lianas (Contreras *et al.* 1999). In addition to these variables, the height of the tallest individual in the plot (hereafter $\text{height}_{\text{max}}$) was measured with a clinometer for 90% of the plots.

Based on the field data we calculated 15 variables to describe forest structure. We divided these 15 variables into three components: vertical structure, horizontal structure and density of life-forms. The *vertical structure* was described using four variables: the $\text{height}_{\text{max}}$ and the percentage of individuals in three forest layers (emergent, canopy and sub-canopy). The emergent layer consists of all individuals with emergent crown, the canopy layer consists of all individuals with full and some overhead light, and the sub-canopy layer consists of all individuals with either some or no side light. The *horizontal structure* was described using six variables: the total basal area (in m^2ha^{-1}), calculated as the sum of the basal area of all stems ($0.25*pi*[DBH/100]^2$), the tree basal area, the palm basal area, the median of the stem diameter (DBH_{50}), the 99 percentile of the stem diameter (DBH_{99}) and the slope of the size-class frequency distribution at the stand level (hereafter size-class distribution – SCD). This slope was calculated by regressing the (log-transformed) number of individuals per diameter classes of 10 cm width to the average diameter of each size class. Finally, the *density of life forms* takes into account five variables: the abundance of all individuals per plot (total density), the tree density, the palm density, the density of stems with liana infestation (hereafter liana "density") and the mean liana infestation (calculated by averaging the degree of liana infestation of all trees in the plot). Although we did not measure the abundance of lianas directly, we inferred it from the latter two variables.

Data analysis

To summarize the climatic and soil data we performed two Principal Component Analyses (PCAs). The first PCA was done using the five climatic variables (annual temperature, annual precipitation, driest months, and the length of the dry and drought periods). A second PCA was done using 12 edaphic variables (CEC, Ca, K, M, Na, P, OM, N, acidity, sand, silt and clay). The first two axes resulting from the climatic PCA and from the soil PCA were used as the four main environmental axes in the analysis below. To describe the multivariate forest structure a third PCA was done using 13 forest structural variables. To avoid collinearity, highly correlated soil variables (pH, TEB, base saturation, and Al^{3+}) and forest structural variables (tree basal area and palm basal area) were excluded from the PCA (see Appendices 1 and 2 for correlations).

To investigate the effects of the environmental factors on forest structural variables we used a multiple backward regression, with the four main environmental axes as independent variables and each structural parameter as a dependent variable. Finally, to find out the relationships among variables we correlated (Pearson correlations) all climatic and soil variables (including the main four environmental axes) among themselves and with the forest structural variables. For each parameter the Kolmogorov-Smirnov test for normal distribution was applied. If necessary the data were logarithmic ($\log_{10}$) -, square root -, or arcsine - transformed. All statistical analyses and PCA's were performed with SPSS 15.0 for Windows (SPSS Inc.).

Results

Variation in climate and soils

In lowland Bolivia a large variation in environmental conditions was found (Table 1). The length of the drought period and the precipitation of the driest months varied almost fourfold, and annual precipitation varied twofold (from ca 1100–2200 mm), while annual temperature varied hardly. Soils varied substantially in their chemical characteristics, with TEB, cations (Mg, and Ca) and available P showing 50–70 fold variation. Soil texture varied mostly in sand content, with 51% of the plots occurring on sandy loam soils.

Table 1. Mean (± SD) and range (minimum – maximum) of 21 environmental variables from 220 1-ha permanent plots located in the lowlands of Bolivia. The ratio was calculated by dividing the maximum value by the minimum value, except for variables with zero values.

Variables	Mean	SD	Range Minimum	 Maximum	Ratio
Climate					
Annual precipitation (mm)	1592	317.6	1113	2198	2.0
Driest months (mm)	100	35.9	68	262	3.9
Dry period (# month< 100 mm)	5.6	1.0	4.0	7.0	1.8
Drought period (#month< 50 mm)	2.8	0.9	0.0	4.0	-
Annual temperature (°C)	25.3	0.7	24.2	26.4	1.1
Soil fertility					
pH	5.3	1.2	3.3	7.8	2.4
Ca (cmol kg^{-1})	3.25	3.1	0.20	13.80	69.0
Mg (cmol kg^{-1})	1.35	1.2	0.10	7.00	70.0
Na (cmol kg^{-1})	0.08	0.03	0.03	0.19	6.3
K (cmol kg^{-1})	0.27	0.13	0.05	0.79	15.8
TEB (cmol kg^{-1})	4.9	4.05	0.4	20.0	50.0
Base saturation (%)	76.3	29.9	9.0	100.0	11.1
CEC (cmol kg^{-1})	5.8	3.5	1.5	20.1	13.4
Acidity (cmol kg^{-1})	0.9	1.2	0.0	6.1	-
Al (cmol kg^{-1})	0.5	1.04	0.0	4.8	-
P (cmol kg^{-1})	5.5	6.6	1.0	51.0	51.0
OM (%)	2.7	0.98	0.9	5.2	5.8
N (%)	0.2	0.1	0.05	0.4	7.8
Soil texture					
Sand (%)	56.3	16.6	2.0	83.0	41.5
Silt (%)	22.5	11.6	3.0	68.0	22.7
Clay (%)	21.2	10.2	6.0	50.0	8.3

The first two axes of the climatic PCA explained 94% of the variation (Fig. 2a). The first axis (hereafter rainfall axis) explained 65% and correlated positively with the annual precipitation and negatively with the dry period. The second axis (hereafter temperature axis) explained 29% and correlated positively with the mean annual temperature and negatively with the precipitation in the driest months.

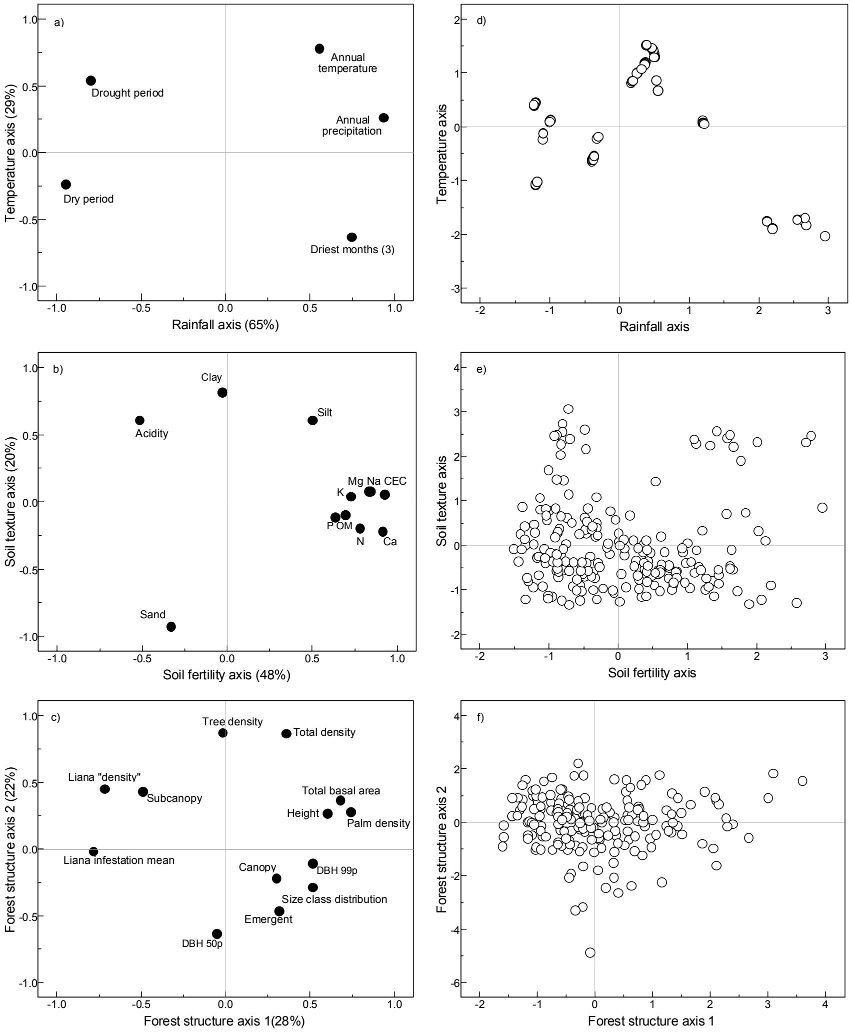

Figure 2. Results of the Principal Component Analysis (PCA) for (a, d) climate, (b, e) soil, and (c, f) forest structural variables. Panels a – c show the position of the variables and the percentage of the variation explained for the first two axes. Panels d – f show the loading scores of the 220 plots.

In PCA space, plots from less seasonal areas (e.g. higher annual precipitation and shorter dry period) were on the right, while plots from more seasonal areas were on the left (Fig. 2d). The first two axes of the PCA of edaphic properties explained 68% of the variation (Fig. 2b). The first axis (hereafter soil fertility axis) explained 48% and correlated positively with soil fertility variables (CEC, Ca, Mg, Na, K, P, OM and N), and negatively with acidity. The second axis (hereafter soil texture axis) explained 20% and correlated positively with clay and silt, and negatively with sand content. In PCA space, plots with higher sand content were found across whole fertility gradient, while plots with high silt content and high nutrient level were on the right, and plots with high clay content, high acidity and lower nutrient levels were on the left (Fig. 2e).

The rainfall axis was weakly and negatively related to the soil fertility axis, but strongly and positively to the soil texture axis (Figs. 3a and 3b). Specifically, the rainfall axis was positively correlated to silt and clay content, and acidity, and negatively to sand content, pH, Ca, K, OM and N (Appendix 1). Although drier forests tended to have higher soil fertility than moister forests, some plots in moist areas had also soils with high fertility (Figs. 3a and 3b). These latter plots were all situated in the foothills of the Andes.

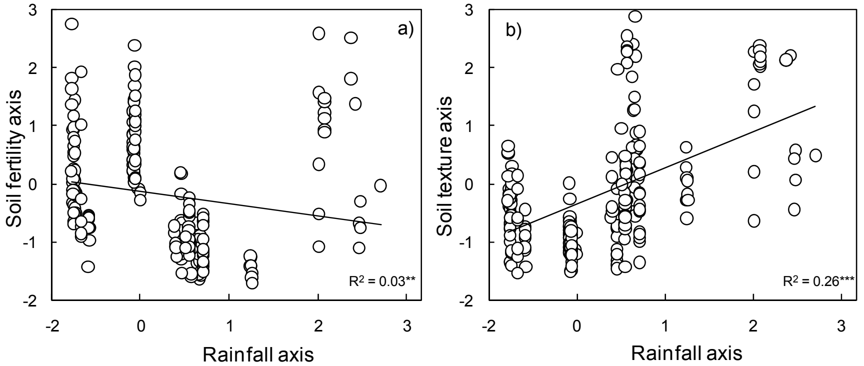

Figure 3. Relationships between the PCA rainfall axis with (a) the PCA soil fertility axis and (b) the PCA soil texture axis of 220 1-ha permanent plots located in the lowland forests of Bolivia. Regression lines, corresponding coefficient of determination (R^2), and significance levels are shown ** $P < 0.01$, *** $P < 0.001$.

Variation in forest structure

Forest structure varied considerably across the plots, with the largest variation in the sub-canopy and emergent layers and in palm density (Table 2). In terms of vertical structure, the height_{max} was on average 30 m (range 20 – 54); on average 50% of the stems were in the canopy layer and only 12% in the emergent layer (range 0 – 62). In terms of horizontal structure, the total basal area averaged 21 m^2/ha (range 10 – 33), the DBH_{50} was 17 cm, and the DBH_{99} was 78 cm (range 47 – 147). Average total density was 405 stems ha^{-1} (range 124 – 765). Palms presented the largest variation in density among life forms followed by lianas.

Table 2. Mean (± SD) and range (minimum – maximum) of 15 structural variables from 220 1-ha permanent plots located in the lowlands of Bolivia. The ratio was calculated by dividing the maximum value by the minimum value, except for variables with zero values.

Variables	Mean	SD	Range Minimum	 Maximum	Ratio
Vertical Structure					
Height_{max} (m)	30.3	7.4	20.0	54.0	2.7
Emergent layer (%)	12.2	9.2	0.1	62.2	622
Canopy layer (%)	50.3	13.9	20.4	97.9	4.8
Sub-canopy layer (%)	36.8	15.8	0.13	70.4	541.5
Horizontal Structure					
Total basal area (m^2ha^{-1})	20.7	4.6	9.6	32.9	3.4
Tree basal area (m^2ha^{-1})	19.9	4.2	9.5	30.5	3.2
Palm basal area (m^2ha^{-1})	0.79	1.2	0	8.5	-
Size class distribution (slope)	-0.03	0.0	-0.04	-0.02	0.4
DBH_{50} (cm)	17.4	2.2	14.2	30.2	2.1
DBH_{99} (cm)	78.1	16.6	46.9	146.6	3.1
Density of life-forms					
Total density (#/ha)	405.8	83.3	124	763	6.2
Tree density (#/ha)	377.9	70.4	124	536	4.3
Palm density (#/ha)	27.9	43.5	0	353	-
Liana “density” (#/ha)	198.7	77.7	36	371	10.3
Liana infestation (mean)	0.96	0.4	0.12	2.1	17.2

The PCA of the forest structure explained 50% of the variation in the 12 structural variables (Fig. 2c). The first PCA axis (28%) correlated positively with palm density, total basal area and height_{max}, and negatively with liana infestation and liana “density”. The second axis (22%) correlated positively with total density and tree density, and negatively with DBH_{50}. The plots differed gradually and continuously in their multivariate forest structure (Fig. 2f).

Forest-environment relationships

The rainfall axis was significantly related to 13 of the 15 forest structural variables studied, the soil texture axis to 12 of the variables and the temperature axis to 9 variables. Surprisingly, the soil fertility axis was related to only eight forest structural variables (Table 3). The variation explained by the backward regression models ranged from 6 – 82%. Palm density, palm basal area, height$_{max}$ and mean liana infestation were the forest structural variables best explained by the models. Most of the forest structural variables were affected by a combination of both climatic and soil factors, tree basal area and DBH$_{50}$ were the only variables affected by a single factor. Overall, climatic and edaphic factors had more positive effects than negative effects on the forest structural variables (Table 3).

Table 3. Backward multiple regression of 15 structural variables on four environmental factors of 220 1-ha permanent plots located in lowland Bolivia. The standardized regression coefficient, F-value, and coefficient of determination (R^2) are provided. Significance levels are shown * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Structural components & variables	Environmental factors (PCA Axes)					
	Rainfall	Temperature	Fertility	Texture	F	R^2
Vertical structure						
Height$_{max}$ (m)	0.64***	0.19***		0.11*	86.38	0.57
Emergent layer (%)	-0.24**	-0.21*	-0.25 **	0.30***	5.14	0.09
Canopy layer (%)	0.32***	0.16*	-	-	16.20	0.13
Sub-canopy layer (%)	-0.21**	-0.13*	-	-0.17*	10.34	0.13
Horizontal structure						
Total basal area (m^{2}ha^{-1})	0.16*	-	-	0.28***	19.16	0.15
Tree basal area (m^{2}ha^{-1})	-	-	-	0.26***	16.37	0.07
Palm basal area (m^{2}ha^{-1})	0.70***	-	-0.14***	0.16***	157.81	0.69
Size class distribution (slope)	0.58***	0.39***	0.38***	-0.16*	22.20	0.29
DBH$_{50}$ (cm)	-0.39***	-	-	-	18.73	0.15
DBH$_{99}$ (cm)	0.42***	0.35***	0.32***	-	19.71	0.21
Density of life-forms						
Total density (#/ha)	0.16*	-0.36***	-0.33***	0.27***	16.71	0.24
Tree density (#/ha)	-0.21*	-0.24**	-0.24**	0.21**	3.49	0.06
Palm density (#/ha)	0.80***	-	-0.13***	0.14***	330.81	0.82
Liana “density” (#/ha)	-0.19*	-	-	-0.26***	19.97	0.15
Mean liana infestation	-	0.21**	0.31***	-0.52***	32.84	0.31

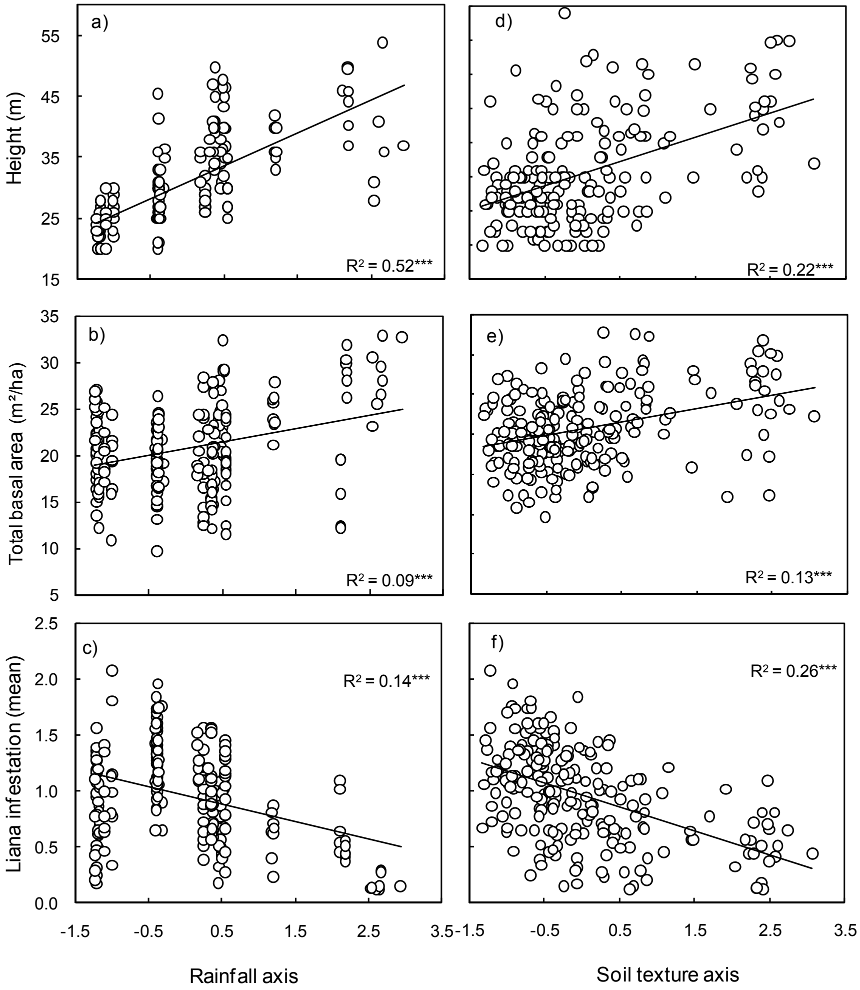

Figure 4. Relationships of the PCA rainfall axis and the PCA soil texture axis with (a, d) height$_{max}$, (b, e) total basal area, and (c, f) mean liana infestation of 220 1-ha plots located in lowland Bolivia. Regression lines, corresponding coefficient of determination (R^2), and significance levels are shown *** *P* < 0.001.

In Figures 4 and 5 we present the bivariate relationships of selected forest structural variables with the rainfall and soil axes. Height$_{max}$ increased with rainfall and the silt content of the soils (Figs. 4a and 4d). In general, the total basal area was highly variable along the gradients considered, the highest basal area being found in moister forests and in plots with silty soils (Figs. 4b and 4e). Liana infestation tended to decrease along the rainfall gradient and in plots with clay-silty soils (Figs. 4c and 4f). Palm density increased significantly with rainfall, but tree density was highly variable along the rainfall gradient: both drier and moister sites varied largely in tree density (Figs. 5a and 5c). While total density and tree density were variable along the soil fertility gradient, the palm density was highest in the intermediate level of fertility (Figs. 5d and 5f).

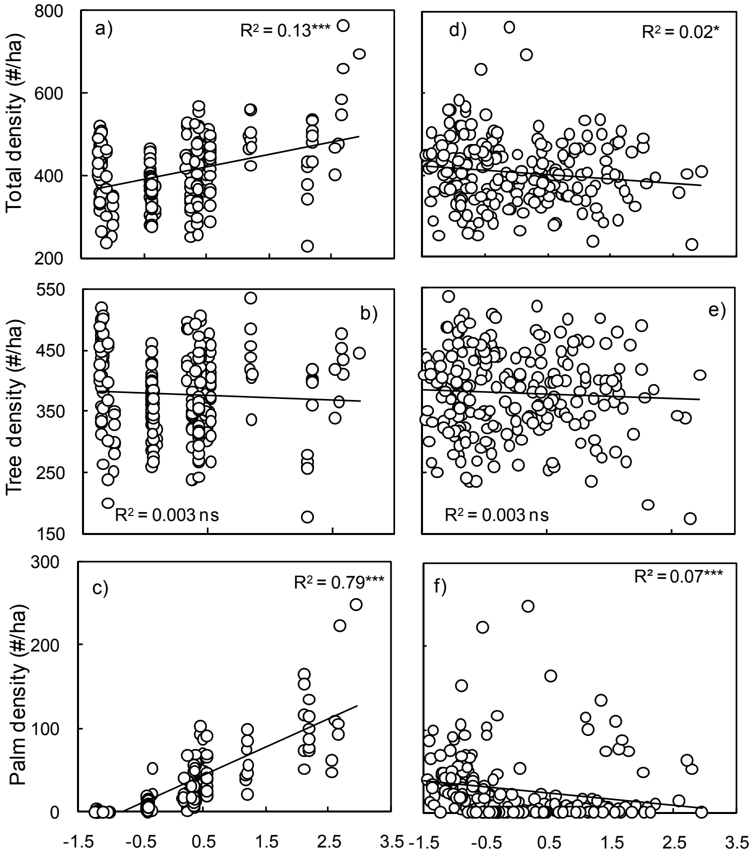

Figure 5. Relationships of the PCA rainfall axis and the PCA soil fertility axis with (a, d) total density (b, e) tree density and (c, f) palm density of 220 1-ha plots located in lowland Bolivia. Regression lines, corresponding coefficient of determination (R^2), and significance levels are shown * *P* <0.05, *** *P* < 0.001, ns = no significant.

Discussion

In this study we described how climate, soil, and forest structure differed among Bolivian forests and we analyzed how climatic and edaphic factors affected the forest structure of these tropical lowland forests.

Patterns in environment

Almost all tropical forests are to some extent seasonal with respect to rainfall (Walsh 1996). In lowland Bolivia, rainfall seasonality increases from north to south, with the southern driest forest having seven dry months per year. This seasonality influences not only the forest structure, but also the soil conditions (Leigh 2004). As hypothesized, drier forest soils were fertile and had higher OM content, Olsen P and exchangeable cations, while moister forests had poor soils and higher levels of acidity (Fig. 3a). Tropical forests for a long time were considered poorer and more homogeneous than they in fact are (Sánchez 1976, Baillie 1996). Tropical soils simply cannot be uniform because of the wide variety in climate, vegetation, parent material, geomorphology, age, and human activities (Sánchez 1976, Sollins 1998). In lowland Bolivia, soils shape a mosaic with high local variability caused by a combination of these factors. Poor soils were located in the northern Amazon and in the ancient Pre-Cambrian Shield in Eastern Bolivia. Most Amazonian soils are nutrient poor due to the lack of recent geologic activity and a longer period of weathering and leaching (Baillie 1996). Some plots located in the moistest forests in the foothills of the Andean mountains were more fertile, with high amounts of Ca, Mg and Olsen P, and low acidity (Figs. 2e and 3a). The rich soils closer to the Andes have been less weathered and have obtained available nutrients from geological recent deposits during the Quaternary (Jordan & Herrera 1981, Baillie 1996). Similar results were found in the middle Caquetá basin in Colombia (Lips & Duivenvoorden 1996). In cases where lowland rain forests had rich soils, such as in Mexico (Bongers *et al*. 1988) and in Costa Rica (Lieberman *et al*. 1996), they were derived from bedrock of volcanic origin. In other lowland forests in the Amazon, Pre-Columbian agriculture left patches of black and fertile soil known as *terra preta do indio* (Mann 2002). Some of our plots in Eastern Bolivia occurred on such patches of *terra preta,* displaying high levels of extractable Ca, OM content and P (Paz-Rivera & Putz 2009).

Patterns in forest structure

The most important structural variables that responded most to environmental variation were $\text{height}_{\text{max}}$, total basal area, palm density and liana infestation (Fig. 2c, Table 3). In general, moister forests had taller stems, higher total basal area and palm density and lower liana abundance than drier forests. The maximum tree height in Bolivian lowland forests was 54 m; average height in rain forests usually ranges between 45 and 55 m, although in some tropical rain forests individuals can reach over 60 m (Ashton & Hall 1992, Richards 1996). Dry forests are smaller in stature and tend to have an even canopy (Murphy & Lugo 1986, Swaine *et al.* 1990, Richards 1996).

In our study the total basal area for stems ≥ 10 cm DBH averaged 20 $m^2 ha^{-1}$ and ranged from 10 to 33 $m^2 ha^{-1}$ which is at the lower end of the range (20–70 $m^2 ha^{-1}$) found for tropical forests worldwide (De Gouvenain & Silander 2003, Losos *et al.* 2004). The variation of total basal area in tropical forests can be due to variation in stem density combined with variation in tree thickness. A high basal area can be the result of many slender stems or few thick stems (Bongers *et al.* 1988). In contrast, a low basal area could be also the result from disturbance by logging, wind and fire, directly affecting forest structure or indirectly through changing the floristic composition and consequently the forest structure (Spies 1998). In lowland Bolivia, we found several plots with lower tree density and basal area due to the massive abundance of some herbs or shrubs (e.g. *Phenacospermum guianense, Erythrochiton fallax, Metrodorea flavida,* and *Pausandra trianae*).

Palms are a striking feature of tropical forests, being very abundant and often even dominant, forming “oligarchic” forests (Vormisto *et al.* 2004, Primack & Corlett 2005). Some forests in the lowland Bolivia had a relatively high palm density (48–353 palms/ha) compared to other tropical forests: 103 palms/ha in Cocha Cashu, Peru (Gentry & Terborgh 1990); 90–129 palms/ha in Bajo Calima, Colombia (Faber-Langendoen & Gentry 1991) and 11–115 palms/ha in La Selva, Costa Rica (Lieberman *et al.* 1996). Higher palm density in Bolivia could be due to local dominance of palm rich habitats such as flooded forests; we found the highest palm densities in such habitats.

Around 50% of all trees measured in our plots had some degree of liana infestation. Although we did not measure liana abundance directly, our results are in line with those studies that show that lianas are more abundant in drier than in moister forests (Putz 1984, Pérez-Salicrup *et al.* 2001, Schnitzer 2005, DeWalt *et al.* 2009, Madeira *et al.* 2009). Drier forests in Bolivia, as reported for other studies (Carse *et al.* 2000, Pérez-Salicrup *et al.* 2001, Uslar *et al.* 2004), had between 50 and 80% of their trees infested by lianas while moister forest had less than 50% (Licona-Vasquez *et al.* 2007, Toledo *et al.* 2008). Mascaro *et al.* (2004) hypothesized that high palm abundance could negatively affect the regeneration, and consequently, the abundance of liana in wet forests. Although we have found that in lowland Bolivia moister forests have lower liana “density” and higher palm density (Appendix 2), lianas and palms respond independently to rainfall, as discussed in the next section. Other components of forest structure, such as the amount of small-diameter stems and branches are important for liana support and success (Putz 1984, Schnitzer & Bongers 2002). Liana “density” tended to increase with the percentage of trees in the sub-canopy layer and to decrease with increasing canopy height (Appendix 2). Similar results were found in South Africa (Balfour & Bond 1993) and Panama (DeWalt *et al.* 2000), where more lianas were found in short trees and low canopies. This result suggests that connected crowns of trees in lower canopies are suitable support to lianas.

Environmental effects on forest structure

In the tropics, water availability is one of the most important environmental drivers of forest structure and function (Murphy & Lugo 1986, Malhi *et al.* 2002, Primack & Corlett 2005). Water availability is determined by the amount and seasonal distribution of rainfall, and the water retention capacity of soils. The importance of rainfall and water retention capacity is underscored by the fact that they were the most important environmental determinants of forest structure in our study. The rainfall axis was significant in 87% of the cases, and the soil texture axis in 80%. Both environmental factors worked often in a similar direction, as indicated by the sign of the regression coefficient (Table 3). For example, forest height increased with rainfall and the water holding capacity of the soils (e.g. silt content). This confirms the hypothesis of Ashton & Hall (1992) that canopy height is mostly related to soil water supply.

Temperature and soil fertility factors had also the same direction for some structural variables. Both factors had positive effects in the size-class distribution, DBH_{99}, and liana infestation; and negative effects in the emergent layer, total density, and tree density (Table 3). Temperature axis considers the annual temperature as well as the three driest month precipitation (Fig. 2a). Whereas the annual temperature showed a higher relationship with the canopy and sub-canopy strata, the driest month precipitation showed a higher relationship with the total basal area and the total density (Appendix 3). Plots located in northern and southern sites with higher annual temperature tended to have a higher percentage of trees in the canopy layer and a lower tree percentage in the sub-canopy layer. Annual temperature (from 24 to 26°C) and altitude (100 – 480 masl) were negatively correlated (Pearson $r = -0.91$, $P < 0.001$) and the variation of these variables among plots was small. From the data available, we can state that higher temperature (and hence decreasing altitude) may increase tree stature. Plots located in western sites with lesser seasonality tended to have a higher total basal area and total stem density, clearly influenced by the palm abundance.

Table 4. Average of tree density and basal area (stems ≥ 10 cm DBH) of selected lowland tropical forests. Studies are ordered by decreasing precipitation, from moist to dry forests.

Site	No plots (ha)	Annual Precipitation (mm/y)	Tree density (#/ha)	Basal area ($m^2\ ha^{-1}$)	References
Bajo Calima, Colombia	1	7000	535	23	Faber-Langendoen & Gentry 1991
Korup, Cameroon	50	5272	492	26	Losos *et al*. 2004
Los Tuxtlas, Mexico	1	4600	346	35	Bongers *et al*. 1988
Kalimantan, Indonesia	4.8	4125	521	40	Paoli *et al*. 2008
La Selva, Costa Rica	4	4000	504	26	Lieberman *et al*. 1996
Tampolo, Madagascar	2	3600	507	23	de Gouvenain & Silander 2003
Luquillo, Puerto Rico	50	3548	874	34	Losos *et al*. 2004
Yasuní, Ecuador	15	3200	654	30	Pitman *et al*. 2002
BCI, Panama	50	2551	429	28	Losos *et al*. 2004
Manú, Peru	9	2300	598	29	Pitman *et al*. 2002
Manaus, Brazil	4	2300	677	37	Ferreira & Prance 1998
Maré, Brazil	1	2000	645	31	Milliken 1998
La Paz, Bolivia	2	2000	592	26	DeWalt *et al*. 1999
Maracá, Brazil	1.5	1696	419	24	Thompson *et al*. 1992
Lowland Bolivia	220	1590	378	20	This study*
Beni, Bolivia	1	1566	649	21	Boom 1986
Santa Cruz, Bolivia	1	1120	549	26	Uslar *et al*. 2004

* Tree density range: 124 – 536 stem/ha, basal area range: 10 – 30 $m^2\ ha^{-1}$.

We hypothesized that stem density, and consequently the total basal area, would increase with water availability, because higher resource availability could permit more stems to coexist. Our results did not support this hypothesis for trees; however, as the tree density and the tree basal area were highly variable among both moist and dry forests (Figs. 4e and 5b, Table 4). Consequently, other factors than climate and soil appear to affect tree density and tree basal area. For example, extreme disturbance events such as the occurrence of cyclones can temporarily increase tree density, as shown in Africa and Madagascar (De Gouvenain & Silander 2003).

The results for palm density supported our hypothesis that moister forests had more palms than drier forests; the highest palm density occurring in seasonally flooded forests. Although palms are widely distributed in the tropics and grow in a wide range of habitats, from upland and cleared forests to the slopes of mountains, some species tend to be denser in seasonally flooded forests (Kahn & Henderson 1999, Vormisto 2002, Velarde & Moraes 2008). In lowland Bolivia, palm density peaked at an intermediate level of soil fertility (Fig. 5f). Similar results were found by Vormisto (2002) in the Peruvian Amazonia, where the lowest palm density was found on the richest soils and the highest palm density at an intermediate level of fertility. In contrast to these results, other studies reported higher palm density on richer soils (Gentry & Terborgh 1990, Nebel *et al.* 2001a, Sesnie *et al.* 2009). In conclusion, palm density was found to be strongly determined by rainfall but still no clear pattern was found in relation to edaphic factors. This lack of a clear pattern implies either that palms have a better relationship with soil properties at species level (Clark *et al.* 1995) or that other factors, e.g. dispersion (Velarde & Moraes 2008), are responsible for their density.

We hypothesized that lianas would have higher densities at low water availability due to their capacity for taking water from deep soils layers (Schnitzer 2005). Liana "density" was indeed higher at low rainfall and on coarse soils with a low water holding capacity (Table 3, Figs. 4c and 4f). Other studies also found that liana density increases with a decrease in rainfall (Parthasarathy *et al.* 2004, Schnitzer 2005, Swaine & Grace 2007, DeWalt *et al.* 2009). These results support the hypothesis that lianas have a growth advantage over trees in areas with a long dry season because of their deep and efficient root and vascular systems (Schnitzer 2005). A weak positive relationship between liana abundance and soil fertility was found in lowland Bolivia (Appendix 3), the highly fertile *terra preta* plots in

Eastern Bolivia having one of the highest levels of liana infestations on trees (60-80%). Other studies also found that liana abundance increases slightly with soil fertility (Proctor *et al.* 1983, Putz & Chai 1987, Balfour & Bond 1993, Poulsen *et al.* 2006). Recently, higher phosphorus concentrations were found in liana litter (Cai 2007); in this way lianas have the potential to enhance the availability of nutrients in areas where they already are abundant. Although climate and soil factors affect liana density, studies and our data suggest that forest structural components can also affect liana density (Balfour & Bond 1993, DeWalt *et al.* 2000, Addo-Fordjour *et al.* 2009, Madeira *et al.* 2009).

Finally, what is the role of climate and soil on forest structure? Our study supports earlier results indicating that forest structure is strongly influenced by climate (Murphy & Lugo 1986, Gentry 1988a, Clinebell *et al.* 1995, ter Steege *et al.* 2003). Climatic conditions may increase or decrease chemical and biological processes, including photosynthesis, respiration, soil nutrient availability and ontogenetic development (Saxe *et al.* 2001). Currently, the main concern is the effect of climate change on forest components. Although our data show the spatial variation of forest structure in tropical lowland forests, they consider an environmental gradient in terms of precipitation and temperature. Small changes in these variables, especially in the temperature (IPCC 2007), could alter the structure as well as the function of tropical forests, due to the fact that the climate is one of the main factors driving them.

Climatic factors and the edaphic heterogeneity have been demonstrated to have strong effects on the variation and complexity of forest structure at landscape-scale. The composite rainfall and soil texture factors, both determining variability in water availability, clearly were more important drivers of forest structure than soil fertility. Although the climatic gradient (especially the seasonal distribution of rainfall) is an important driver, few studies have quantified its effects (Vieira *et al.* 2004, Takyu *et al.* 2005). Compared to soil fertility (Clark & Clark 2000, Nebel *et al.* 2001a, White & Hood 2004, DeWalt & Chave 2004, Paoli *et al.* 2008) modest attention has been given to soil texture as a driving factor (but see Jha & Singh 1990), a property that helps to determine not only the nutrient-supplying ability but also the supply of water and air necessary for plant root activities (Brady 1990).

Concluding remarks

In lowland Bolivia, rainfall seasonality increases and precipitation decreases, from north to south which influences not only the forest structure but also the soil conditions. In general, moister forests had poor soils and drier forest soils were more fertile. Some plots in moister forests, however, were also fertile due to younger parent material or past anthropogenic activities. Of the 15 structural variables analyzed, maximum height, palm density and liana infestation were the most affected by environmental factors. Forest height and palm density increased with rainfall while liana abundance decreased with rainfall. While forest height and liana abundance were more affected by soil texture palm density was negatively affected by soil fertility. The composite climate and soil texture axes determine together plant water availability, and these were more important drivers of forest structure than soil fertility.

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Appendix 1. Pearson correlations between climate parameters, soil properties and environmental PCA axes. n = 220 * p ≤ 0.05, ** p ≤ 0.01. Driest = precipitation of the driest months, Temp = temperature, CEC = Cation Exchange Capacity, OM = organic matter. See table 1 for parameter details

	Driest	Temp	pH	Ca	Mg	Na	K	CEC	Acidity	P	OM	N	Sand	Silt	Clay	Rainfall axis	Temp. axis	Fertility axis	Texture axis
Precipitation	0.52**	0.66**	-0.53**	-0.38**	-0.29**	-0.17*	-0.40**	-0.24**	0.56**	0.05	-0.51**	-0.52**	-0.34**	0.28**	0.24**	0.93**	0.26**	-0.35**	0.49**
Driest		-0.05	0.04	0.19**	0.27**	0.49**	0.29**	0.28**	-0.03	0.39**	-0.09	-0.06	-0.41**	0.58**	0.01	0.74**	-0.63**	0.33**	0.31**
Temp.			-0.63**	-0.56**	-0.36**	-0.34**	-0.48**	-0.44**	0.57**	-0.28**	-0.64**	-0.62**	-0.11	-0.10	0.30**	0.55**	0.78**	-0.57**	0.36**
pH				0.85**	0.48**	0.54**	0.49**	0.69**	-0.71**	0.53**	0.48**	0.67**	0.19**	0.13*	-0.47**	-0.43**	-0.48**	0.73**	-0.50**
Ca					0.60**	0.69**	0.64**	0.94**	-0.55**	0.69**	0.58**	0.72**	-0.10	0.35**	-0.24**	-0.26**	-0.52**	0.91**	-0.22**
Mg						0.60**	0.67**	0.65**	-0.48**	0.31**	0.31**	0.38**	-0.27**	0.37**	0.01	-0.10	-0.49**	0.73**	0.04
Na							0.76**	0.73**	-0.40**	0.48**	0.42**	0.53**	-0.32**	0.46**	0.00	0.05	-0.58**	0.83**	0.08
K								0.69**	-0.48**	0.32**	0.63**	0.63**	-0.33**	0.34**	0.15*	-0.18**	-0.59**	0.84**	0.08
CEC									-0.31**	0.65**	0.58**	0.68**	-0.33**	0.49**	-0.02	-0.11	-0.50**	0.92**	0.06
Acidity										-0.28**	-0.28**	-0.41**	-0.31**	0.04	0.47**	0.41**	0.46**	-0.52**	0.61**
P											0.28**	0.39**	-0.12	0.38**	-0.24**	0.13	-0.39**	0.63**	-0.11
OM												0.89**	-0.12	0.10	0.08	-0.46**	-0.43**	0.69**	-0.09
N													-0.07	0.13	-0.04	-0.45**	-0.41**	0.78**	-0.20**
Sand														-0.80**	-0.72**	-0.42**	0.19**	-0.33**	-0.93**
Silt															0.15*	0.39**	-0.41**	0.50**	0.61**
Clay																0.24**	0.17*	-0.03	0.82**
Rainfall axis																		-0.18**	0.51**
Temp. axis																		0.64**	-0.06

Appendix 2. Pearson correlations between forest structural variables. n=220 * p≤ 0.05, ** p ≤ 0.01. BA = basal area, SCD = size class distribution. See table 2 for parameter details.

	Emergent (%)	Canopy (%)	Subcanopy (%)	Total BA	Tree BA	Palm BA	SCD slope	DBH_{50}	DBH_{99}	Total density	Tree density	Palm density	“Liana density”	Liana infestation
$Height_{max}$	0.03	0.06	-0.13	0.32**	0.21**	0.59**	0.36**	-0.29**	0.41**	0.31**	0.05	0.54**	-0.14*	-0.25**
Emergent		-0.18**	-0.43**	0.13*	0.10	0.09	-0.07	0.43**	-0.08	-0.02	-0.11	0.13	-0.42**	-0.31**
Canopy			-0.78**	-0.15*	-0.22**	0.20**	0.09	-0.08	-0.05	-0.03	-0.15*	0.19**	-0.25**	-0.23**
Subcanopy				-0.01	0.07	-0.28**	-0.07	-0.20**	0.05	-0.01	0.18**	-0.31**	0.52**	0.43**
Total BA					0.97**	0.44**	0.33**	0.05	0.48**	0.56**	0.41**	0.42**	-0.29**	-0.49**
Tree BA						0.21**	0.29**	0.10	0.45**	0.48**	0.45**	0.18**	-0.22**	-0.41**
Palm BA							0.33**	-0.25**	0.36**	0.44**	-0.05	0.94**	-0.36**	-0.44**
SCD-slope								-0.03	0.78**	-0.27**	-0.45**	0.21**	-0.32**	-0.13
DBH_{50}									-0.07	-0.41**	-0.34**	-0.24**	-0.25**	-0.01
DBH_{99}										-0.13*	-0.29**	0.20**	-0.21**	-0.13
Total density											0.85**	0.53**	0.05	-0.35**
Tree density												0.01	0.29**	-0.14*
Palm density													-0.37**	-0.46**
liana “density”														0.81**

Appendix 3. Pearson correlation coefficients of environmental variables and environmental axes with forest structural variables. n=220 * p≤ 0.05, ** p ≤ 0.01.

DBH= diameter at breast height, SCD= Size-class distribution, BA = basal area, Temp. = temperature, CEC = Cation Exchange Capacity, OM = organic matter.

	$\text{Height}_{\text{max}}$	Emergent %	Canopy %	Subcanopy %	Total BA	SCD slope	DBH_{50}	DBH_{99}	Total density	Tree density	Palm density	Liana “density”	Liana infestation
Precipitation	0.74**	-0.08	0.26**	-0.21**	0.25**	0.42**	-0.44**	0.41**	0.31**	-0.05	0.86**	-0.19**	-0.28**
Driest month	0.36**	0.01	0.16*	-0.16*	0.32**	0.27**	-0.30**	0.20**	0.36**	0.00	0.62**	-0.34**	-0.28**
Temperature	0.56**	0.05	0.38**	-0.40**	0.14*	0.37**	-0.06	0.30**	0.08	-0.13	0.53**	-0.27**	-0.31**
Dry	-0.74**	0.15*	-0.33**	0.23**	-0.22**	-0.45**	0.44**	-0.40**	-0.30**	0.06	-0.85**	0.19**	0.28**
Drought	-0.47**	-0.05	-0.22**	0.24**	-0.29**	-0.24**	0.24**	-0.18**	-0.34**	0.04	-0.68**	0.34**	0.35**
pH	-0.36**	-0.15*	-0.28**	0.36**	-0.22**	-0.03	0.14*	-0.05	-0.32**	-0.12	-0.52**	0.26**	0.49**
Ca	-0.36**	-0.09	-0.24**	0.29**	-0.07	0.07	0.16*	-0.03	-0.24**	-0.09	-0.43**	0.13	0.33**
Mg	-0.37**	-0.04	-0.07	0.13	-0.07	0.04	0.18*	-0.06	-0.22**	-0.12	-0.33**	0.04	0.26**
Na	-0.19**	0.04	0.05	-0.07	0.03	0.09	0.06	0.05	-0.07	-0.12	0.07	-0.19**	0.01
K	-0.35**	0.01	0.05	-0.03	-0.01	-0.12	0.15*	-0.14*	-0.09	-0.02	-0.29**	-0.12	0.01
CEC	-0.16**	-0.01	-0.21**	0.17**	0.12	0.07	0.14*	0.11	-0.05	-0.05	-0.17*	-0.02	0.13*
Acidity	0.51**	0.16*	0.15*	-0.30**	0.32**	0.12	-0.12	0.20**	0.36**	0.12	0.61**	-0.26**	-0.45**
P	0.03	-0.20**	-0.13*	0.22**	0.10	0.29**	0.17*	0.24**	-0.02	-0.09	0.10	-0.01	0.15
OM	-0.41**	-0.16*	-0.12	0.21**	-0.03	-0.27**	0.06	-0.16*	-0.05	0.13*	-0.42**	0.24**	0.23**
N	-0.38**	-0.19**	-0.15*	0.26**	-0.08	-0.13*	0.06	-0.07	-0.15*	0.06	-0.47**	0.26**	0.34**
Sand	-0.35**	-0.13	-0.05	0.14*	-0.36**	-0.18**	0.14*	-0.22**	-0.27**	-0.07	-0.41**	0.31**	0.39**
Silt	0.21**	0.14*	-0.14*	0.01	0.37**	0.18**	-0.11	0.20**	0.20**	0.08	0.29**	-0.26**	-0.26**
Clay	0.29**	0.06	0.18**	-0.21**	0.14*	0.00	-0.06	0.06	0.15*	0.05	0.28**	-0.17**	-0.31**
Rainfall axis	0.72**	-0.04	0.32**	-0.29**	0.31**	0.43**	-0.39**	0.37**	0.36**	-0.06	0.89**	-0.32**	-0.37**
Temp. axis	0.27**	-0.04	0.16*	-0.14*	-0.09	0.14*	0.03	0.15*	-0.13*	-0.07	-0.10	0.06	-0.02
Fertility axis	-0.28**	-0.08	-0.11	0.16*	0.04	0.03	0.09	0.02	-0.12	-0.05	-0.27**	0.01	0.17**
Texture axis	0.46**	0.17*	-0.16*	-0.28**	0.36**	0.16*	-0.14*	0.21**	0.33**	0.09	0.55**	-0.36**	-0.51**

Chapter 3

Patterns and determinants of floristic variation across lowland forests of Bolivia

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Abstract

Floristic variation is high in the Neotropics, but little is known about the factors shaping this variation at the meso-scale. We examined the floristic composition and its relationship with environmental factors, across 220 1-ha permanent plots, in lowland Bolivia. For each plot, abundance of 100 species, interpolated climatic data and soil properties were obtained. The climatic gradient shaped the floristic variation more strongly than the edaphic gradient. Floristic variation was strongly associated to differences in water availability and temperature. Detrended Correspondence Analysis ordination divided lowland Bolivia primarily into two major groups (Southern Chiquitano region versus the Amazonian region) and a Multiple Response Permutation Procedure distinguished five floristic regions: Western Pre-Andean, Northern Amazonian, Eastern Amazonian-Bajo Paraguá, Eastern Amazonian-Guarayos, and the Southern Chiquitano region. Of the 100 species, 10 occurred in only one floristic region and 90 occurred in two or more floristic regions. We distinguished 92 strong indicator species, which had significant environmental preferences for one floristic region, so these species can be used as indicators of environmental conditions or to determine to what floristic region a certain forest belongs. All the environmental variables tested were significantly different among the floristic regions. Given the predicted decreases in rainfall and increases in temperature for lowland forests, our gradient approach suggests that species composition may drastically shift with climate change.

Key words: climate, floristic composition, lowland Bolivia, indicator species, soil, species distribution.

Introduction

To understand the coexistence of species locally, it is necessary to gain knowledge on the factors determining the spatial variation in floristic composition and species distribution (Chave 2008). The distribution of a given species within a region depends on several factors, ranging from ecological requirements to historical events and interactions with other species (Hutchinson 1959, ter Steege & Zagt 2002). Several studies have demonstrated that climate (ter Steege *et al*. 2000, Pyke *et al*. 2001, Killeen *et al.* 2006, Parmentier *et al*. 2007) and soils (ter Steege *et al*. 1993, Clark *et al*. 1999a, Vormisto 2002, Phillips *et al*. 2003, but see Newbery & Proctor 1984, Pitman *et al*. 1999) affect floristic composition. A better understanding in community ecology will come from considering factors that influence species distribution, not only across space, but also across environmental gradients (Ricklefs 2008). Few studies, however, have evaluated the relative contributions of climate and soil on plant community composition across gradients (Swaine 1996, Bongers *et al*. 2004, ter Steege *et al*. 2006). West African forests, for example, showed pronounced gradients in forest composition, which were mostly correlated to rainfall and to a lesser extent to soil fertility (Swaine 1996, Bongers *et al*. 2004). In contrast, in South American forests species composition was explained mostly by a gradient in soil fertility and to a lesser extent by dry season length (ter Steege *et al*. 2006).

Vegetation patterns have long been recognized to be associated with environmental heterogeneity (Gentry 1988a, Barberis *et al*. 2002). Studies reporting that floristic composition responds to edaphic differences rarely allow general conclusions about the degree of habitat association of plant species across tropical lowland forests (Phillips *et al*. 2003). Plants are more likely to be consistent indicators than other taxa because of their sessile growth form and because many species have widespread distribution (Bakker 2008). Species are considered as bio-indicators of their environment when their frequency or abundance within sites of a particular habitat is high compared to other habitats.

Lowland in the Neotropics feature an extraordinary display of vegetation types, most probably related to both geomorphological complexity and climatic variation (Hueck 1978, Daly & Prance 1988). This is especially the case for Bolivia where three biogeographical regions of South America, Amazonian, Brazilian-Paranaense and Chaco converge in the lowlands (Navarro & Maldonado 2002). The most recent classification for lowland Bolivia (Ibisch & Mérida 2003) recognizes five different Amazonian forest types (inundated forests, pre-Andean forests, and evergreen forests in Pando, Beni, and Santa Cruz) and two dry forest types in the southern part (the Chiquitano forest, and the Gran Chaco dry forest). However, factors affecting the floristic variation in Bolivia are poorly understood because studies that link vegetation and explanatory environmental variables are surprisingly scarce. Recently, Killeen *et al.* (2006) produced a first analysis of large-scale patterns in community composition in relation to climatic factors and geology, but they only focused on the drier lowland forests.

In the present study we analyse plant species composition across 220 1-ha plots in Bolivian lowland forests. Our main objective is to document the floristic variation, determine what species are indicators for specific floristic regions, and examine the role of climate and soil in shaping floristic composition. We made the following three predictions: (1) Based on climatic data and geographical location there will be five floristic regions in lowland Bolivia: Western Pre-Andean, Northern Amazonian, Eastern Amazonian-Bajo Paraguá, Eastern Amazonian-Guarayos, and the Southern Chiquitano region. (2) We expected a large percentage of species to have significant habitat preferences due to the high habitat heterogeneity (Phillips *et al.* 2003). (3) Given the large geographical range we expect regional environmental factors (i.e. climate) to be more important than local factors (i.e. soil) in shaping floristic composition (cf. Swaine 1996, Pyke *et al.* 2001).

Material and Methods

Study area

For this study a total of 220 1-ha plots were selected from the Network of Permanent Sample Plots in lowland Bolivia. These plots were established in old growth forests by various research projects and forestry concessionaires, before logging activities, between 1995 and 2007 (Fig. 1, see Acknowledgements for more details). To date this network and its database is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots are located between 10 – 18° S latitude and 59 – 69° W longitude, mostly in upland areas (*terra firme;* only 5% of the plots were found in areas of seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from

100 – 500 masl. Most of the plots were typically square (100 x 100 m), with 11 of them being rectangular (20 x 500 m). The 220 plots cover a wide range in environmental conditions (Table 4).

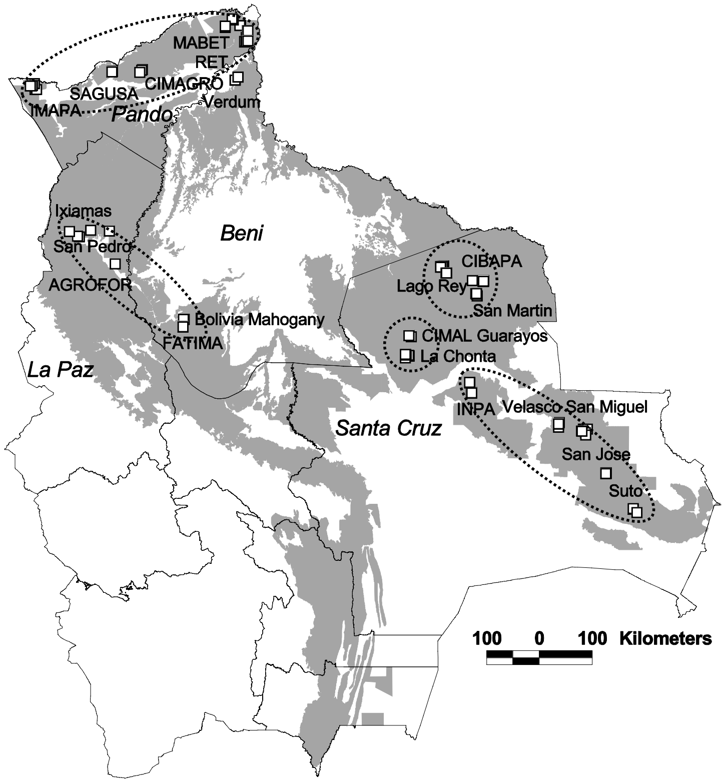

Figure 1. Location of the 220 1-ha plots in the five floristic regions of lowland Bolivia: WP = Western Pre-Andean (Ixiamas, San Pedro, Agrofor, Bolivia Mahogany, Fátima), NA = Northern Amazon (Imapa, Sagusa, Cimagro, Mabet, RET, Verdum), EA_{BP} = Eastern Amazon-Bajo Paraguá (Cibapa, Lago Rey, San Martin), EA_G = Eastern Amazon-Guarayos (Cimal-Guarayos, La Chonta), and SC = Southern Chiquitano (Inpa, San Miguel, Velasco, San Jose, Suto). The name of the departments (La Paz, Beni, Pando, Santa Cruz) are in italics. Grey areas are forests for timber production.

The Bolivian lowlands are characterized by two climatic gradients: a south-north gradient with *mean* annual precipitation ranging from 1100 to 1900 mm and an east-west gradient ranging from 1600 to 2200 mm. However, the precipitation in individual years can vary from 600 to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, Servicio Nacional de Meteorología e Hydrología – SENAMHI, unpublished data). In general, the lowlands in Bolivia experience a 4 to 7 months long dry season (with precipitation < 100 mm/month), mostly from April to September, corresponding to the austral winter. Mean annual temperature is between 24 and 26°C. Lowland Bolivia is also characterized by differences in geomorphology and geological history (Suárez-Soruco 2000) leading to strong gradients in soil characteristics. The soils vary largely in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003).

Environmental data

For each plot we obtained five climatic variables, interpolated from available data from weather stations, and 12 edaphic variables obtained from sampled soils. To summarize these environmental data we performed two independent Principal Component Analyses, (PCA's). The climatic PCA considered annual temperature, annual precipitation, total precipitation of the three driest months, length of the dry period (# months < 100 mm), and length of the drought period (# months < 50 mm). The first two axes of the climatic PCA explained 94% of the variation. The first axis (65%) correlated positively with annual precipitation and negatively with dry period length (hereafter referred to as the rainfall axis). The second axis (29%) correlated positively with mean annual temperature and negatively with the precipitation of the driest months (hereafter temperature axis). The edaphic PCA considered Cation Exchange Capacity (CEC), cations (Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}), Phosphorous (P), Organic Matter (OM), Nitrogen (N), acidity and percentage of particles content (sand, silt and clay). The first two axes of the edaphic PCA explained 68% of the variation. The first axis (48%) correlated positively with variables related with soil fertility (CEC, Ca, Mg, Na, K, P, OM, and N), and negatively with acidity (hereafter soil fertility axis). The second axis (20%) represented variation in soil texture and correlated positively with clay and silt and negatively with sand (hereafter soil texture axis) (see details on Chapter 2).

Recording of species

In each plot all stems ≥ 10 cm diameter at breast height (DBH, measured at 130 cm height or higher height when buttresses were present) were evaluated and identified with a common name by local experts. When necessary, botanical collections were made to verify the species identity. Specimen vouchers are available at LPB and

USZ herbaria in Bolivia in the number series of M. Toledo. We selected 100 plant species, including trees and palms, that were reliably identified and that occurred in at least 11 of the 220 plots (5% of all plots). The use of abundant species, instead of rare or infrequent species, is a commonly used approach because the main pattern of floristic variation is usually established by the common species. Two variables per species were considered: the occurrence (presence-absence in the plot) and the abundance (number of stems per plot).

Data analysis

Correspondence Analysis (CA) and Detrended Correspondence Analysis (DCA) were used to summarize the floristic variation into two main floristic axes. Only DCA ordinations are presented here as they provided a better resolution of the data along the second ordination axis (Hill & Gauch 1980). DCA analysis was carried out with the matrix of 220 plots and 100 species using log-transformed abundance data of each species and using detrending by 26 segments without downweighting of rare species. DCA is well suited to estimate gradient lenghts since its axes are scaled in units of the mean standard deviation (SD) of species turnover (Jongman *et al*. 1995).

We contrasted the species composition of plots using a Multiple Response Permutation Procedure (MRPP), which is a non-parametric procedure for testing the hypothesis of no difference between *a priori* groups (Biondini *et al*. 1988). The *a priori* groups, (hereafter floristic regions), were defined by plots that had similar climatic conditions and were located closely together in space (Fig. 1). Differences among the five floristic regions were evaluated with MRPP, using Sørensen distance as a distance measure. The Jaccard index (based on the presence-absence of each species), was thereafter used to do a pair-wise comparison of regions and describe the similarity in species composition among all five floristic regions (Magurran 2004).

We identified species association with floristic regions using the Indicator Species Analysis (hereafter ISA). This analysis allows for the detection of non-random distribution of species. ISA accounts for both the abundance and the frequency of each species per group and can be applied to *a priori* classifications (Dufrêne & Legendre 1997). ISA calculates the relative abundance (% of average abundance of a given species in a given group over the average abundance of that species in all plots), the relative frequency (% of plots in a given group where a given species is present) and the Indicator Value (IV, % based by multiplying both relative abundance and relative frequency). Species with an IV > 25% are considered to be strong indicators of a certain group (Dufrêne & Legendre 1997, Bakker 2008). We used Monte Carlo permutation test with 4999 randomizations to test whether species have a significant preference ($P < 0.01$) for one region and occur there more often than expected by chance alone.

To evaluate the relative importance of environmental factors in determining the floristic composition we applied a forward multiple linear regression of abundance-based ordination axes scores on four environmental axes. To account for non-linear relationships, the four environmental axes (rainfall, temperature, soil fertility and soil texture) and their quadratic terms were included as predictor variables in the model. To account for interactions between factors the products of them were also included. We present results for models excluding the interaction terms as the interactions did not improve the total variation explained by the models. The partial variation explained from the regression analysis by each of the environmental axes was calculated as the increase in variation when that variable was included in the model. In case that both a simple and squared variable were included in the model (e.g., rainfall axis and its quadratic term), then their individual explained variances were summed to calculate the total amount of explained variance by that environmental factor. Additionally we applied a Detrended Canonical Correspondence Analysis (DCCA), to test whether floristic composition can be explained by environmental variables (Jongman *et al.* 1995). Because DCCA results are similar to those of the forward multiple regressions we present the latter one only.

To test whether environmental variables among the five *a priori* regions were statistically different ($P \leq 0.05$), we applied one-way ANOVA using the Tamhane's T2 *post hoc* test that takes into account the different sample size of each region. Plot scores from the two DCA axes were also correlated to the four environmental axes (PCA axes) and to each of the individual climatic and edaphic variables. Variables were transformed, when necessary, to meet the assumptions of normality. All statistical analyses were done using SPSS for Windows 15.0; MRPP and ISA were carried out using PC-Ord 5.12 (McCune & Mefford 1999) and the CA, DCA and DCCA ordinations were carried out using Canoco for Windows 4.5.

Results

The 220 plots contained ca. 89,200 stems ≥ 10 cm DBH and the 100 selected species represented together, on average 56% (range 25-93%) of the stems. For these 100 species, the species number per plot ranged from 12 to 39. The 100 species represent 36 families and 86 genera (Table 1). Fabaceae (19 species, 29% of all stems) and Arecaceae (7 species, 10%) had the highest number of species and the highest number of stems, along with Moraceae in case of stem abundance (18%).

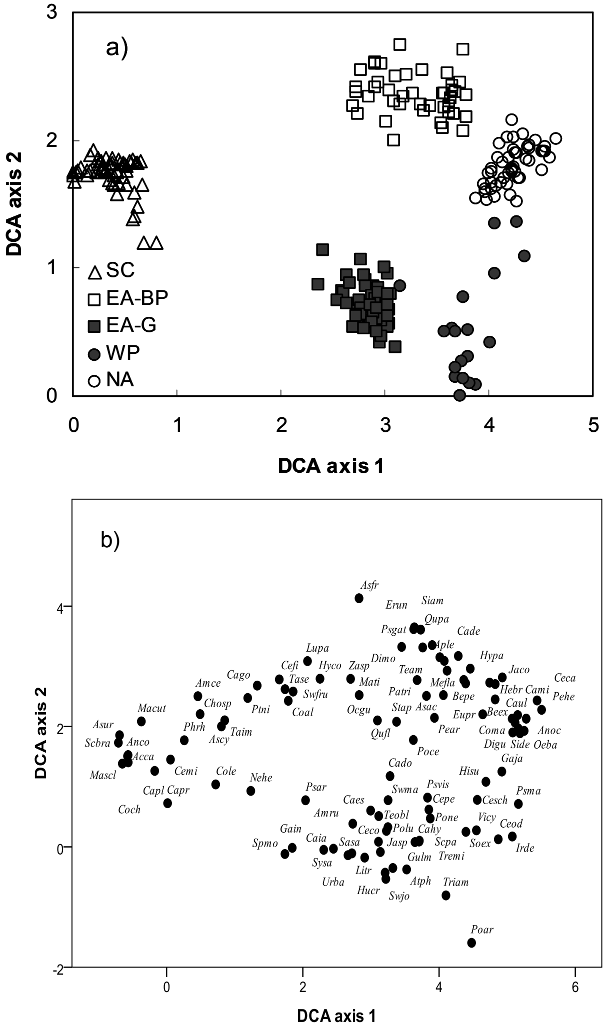

Figure 2. Scatterplots of the first two axes of a species-site DCA ordination. The ordination is based on log-transformed abundance data (number of stems ≥ 10 cm DBH per hectare) of 100 species across 220 1-ha plots in lowland Bolivia.

a) Sites scores. The symbols refer to the *a priori* identified regions: WP = Western Pre-Andean, NA = Northern Amazon, EA_{BP} = Eastern Amazon-Bajo Paraguá, EA_{G} = Eastern Amazon-Guarayos, SC = Southern Chiquitano.

b) Species scores. Species names are represented by the first two letters of their genera and species names (see Table 1 for complete names).

Table 1. Floristic DCA axes scores, floristic region (number of region where the species is indicator), indicator value (IV), significance level (*P*) and occurence (x) of the 100 plant species in five floristic regions: (1) WP = Western Pre-Andean, (2) NA = Northern Amazon, (3) EA$_{BP}$ = Eastern Amazon-Bajo Paraguá, (4) EA$_{G}$ = Eastern Amazon-Guarayos, (5) SC = Southern Chiquitano. * indicates species that occur in one floristic region. ** indicates species that occur in all five floristic regions. Bold *P* value show non-significant indicator species. The species list is alphabetically ordered by family and scientific name.

Family	***Scientific name***	**DCA Axis 1**	**DCA Axis 2**	**Floristic Region**	**IV (%)**	***P***	**WP 1**	**NA 2**	**EABP 3**	**EAG 4**	**SC 5**
Anacardiaceae	*Astronium lecontei*	4.82	2.71	2	30	0.00	x	x	x		
	Anacardium occidentale	5.28	2.13	2	24	0.00	x	x			
	Astronium urundeuva	-0.69	1.85	5	53	0.00			x		x
	Astronium fraxinifolium	2.83	4.13	3	39	0.00			x		x
	**Schinopsis brasiliensis*	-0.71	1.73	5	48	0.00					x
	***Spondias mombin*	1.74	-0.12	1	51	0.00	x	x	x	x	x
Apocynaceae	*Aspidosperma cylindrocarpon*	0.80	2.00	5	72	0.00			x	x	x
	Himatanthus sucuuba	4.69	1.08	2	28	0.00	x	x	x		
	***Peschiera arcuata*	3.93	2.14	2	21	0.00	x	x	x	x	x
Araliaceae	*Didymopanax morototoni*	3.45	3.32	3	73	0.00	x	x	x	x	
	Dendropanax arboreus	3.14	-0.08	4	59	0.00	x		x	x	
Arecaceae	*Astrocarium aculeatum*	4.06	2.52	1	30	0.00	x	x	x	x	
	Attalea phalerata	3.52	-0.38	1	46	0.00	x	x		x	x
	Euterpe precatoria	4.64	2.20	2	43	0.00	x	x	x		
	Iriartea deltoidea	5.08	0.17	1	44	0.00	x	x			
	Oenocarpus bataua	5.19	1.89	2	45	0.00	x	x			
	Socratea exorrhiza	4.39	0.25	1	67	0.00	x	x	x	x	
	Syagrus sancona	2.31	-0.05	4	52	0.00	x		x	x	x
Bignoniaceae	*Jacaranda copaia*	4.46	2.96	2	37	0.00		x	x		
	Tabebuia serratifolia	1.74	2.62	5	25	**0.01**		x	x	x	x
	Tabebuia impetiginosa	0.85	2.10	5	26	0.00	x	x	x		x
Bombacaceae	*Cavanillesia hylogeiton*	3.71	0.09	4	19	0.00	x	x		x	
	Ceiba pentandra	3.85	0.62	1	31	0.00	x	x	x	x	
	***Chorisia speciosa*	0.49	2.21	5	81	0.00	x	x	x	x	x
Boraginaceae	***Cordia alliodora*	1.79	2.43	3	18	**0.14**	x	x	x	x	x
Capparidaceae	*Capparis prisca*	0.01	0.73	5	28	0.00	x		x		x
Caricaceae	*Jacaratia spinosa*	3.23	0.27	4	39	0.00	x	x	x	x	
Cecropiaceae	*Cecropia membranacea*	4.01	3.15	3	60	0.00	x	x	x		
	Cecropia concolor	3.11	0.08	4	32	0.00	x		x	x	
	Pourouma cecropiifolia	3.62	1.78	3	38	0.00	x	x	x	x	
Combretaceae	*Combretum leprosum*	0.72	1.04	5	25	0.00			x	x	x
	Terminalia oblonga	3.11	0.51	4	86	0.00		x	x	x	
	Terminalia amazonica	4.12	2.93	3	40	0.00	x	x	x	x	
Euphorbiaceae	*Hevea brasiliensis*	4.82	2.45	2	59	0.00		x	x		
	Hura crepitans	3.22	-0.53	4	43	0.00	x			x	
	Pausandra trianae	3.68	2.77	3	33	0.00		x	x	x	
Fabaceae	**Acosmium cardenassi*	-0.57	1.51	5	100	0.00					x
	Amburana cearensis	0.46	2.50	5	33	0.00		x	x		x
	Anadenanthera colubrina	-0.57	1.53	5	100	0.00				x	x
	Apuleia leiocarpa	4.08	3.09	3	53	0.00	x	x	x		
	Caesalpinia pluviosa	-0.17	1.26	5	86	0.00				x	x
	Cedrelinga catenaeformis	4.93	2.82	2	23	0.00	x	x	x		
	Centrolobium microchaete	0.06	1.45	5	50	0.00				x	x
	**Copaifera chodatiana*	-0.56	1.40	5	79	0.00					x
	**Dialium guianense*	5.08	1.90	2	71	0.00		x			
	Hymenaea courbaril	2.25	2.79	3	16	**0.02**		x	x	x	x
	Hymenaea parvifolia	4.74	2.73	2	22	0.00		x	x		
	Machaerium acutifolium	-0.37	2.09	5	93	0.00			x		x
	**Machaerium scleroxylon*	-0.65	1.38	5	81	0.00					x
	**Peltogyne heterophylla*	5.51	2.28	2	22	0.00		x			

Table 1. Continued

Family	***Scientific name***	**DCA Axis 1**	**DCA Axis 2**	**Floristic Region**	**IV (%)**	***P***	**WP 1**	**NA 2**	**EABP 3**	**EAG 4**	**SC 5**
Fabaceae	*Pterogyne nitens*	1.19	2.47	5	6	**0.16**			x	x	x
	Schizolobium parahyba	3.71	0.10	1	25	0.00	x	x	x	x	
	Swartzia jorori	3.21	-0.43	1	50	0.00	x		x	x	x
	***Sweetia fruticosa*	1.86	2.58	3	45	0.00	x	x	x	x	x
	**Tachigali paniculata*	5.16	1.97	2	86	0.00		x			
Flacourtiaceae	***Casearia gossypiosperma*	1.33	2.68	5	49	0.00	x	x	x	x	x
Lauraceae	*Ocotea guianensis*	3.10	2.10	4	44	0.00			x	x	
	Licaria triandra	2.91	-0.18	4	96	0.00			x	x	
Lecythidaceae	**Bertholletia excelsa*	5.12	2.06	2	78	0.00		x			
	Cariniana domestica	3.28	1.18	4	15	**0.01**		x	x	x	
	Cariniana estrellensis	3.00	0.60	4	44	0.00	x	x	x	x	
	Cariniana ianeirensis	2.45	-0.03	4	67	0.00	x		x	x	x
	**Cariniana micrantha*	5.44	2.43	2	53	0.00		x			
	**Couratari macrosperma*	5.07	2.13	2	33	0.00		x			
Melastomataceae	*Bellucia grossularioides*	4.39	2.72	2	13	**0.03**		x	x	x	
Meliaceae	*Cedrela odorata*	4.87	0.13	1	27	0.00	x	x			
	Cedrela fissilis	1.65	2.78	3	14	**0.07**		x	x	x	x
	Swietenia macrophylla	3.25	0.78	4	15	**0.01**	x		x	x	
	Trichilia pallida	3.90	3.35	3	58	0.00			x	x	
Monimiaceae	*Siparuna decipiens*	5.25	1.93	2	70	0.00	x	x			
Moraceae	*Castilla ulei*	5.15	2.19	2	32	0.00	x	x			
	Maclura tinctoria	2.83	2.52	4	18	0.00			x	x	
	Poulsenia armata	4.48	-1.59	1	79	0.00	x	x			
	Pseudolmedia macrophylla	5.17	0.71	2	26	0.00	x	x			
	Pseudolmedia laevis	3.83	0.82	4	52	0.00	x	x	x	x	
	Pseudolmedia laevigata	3.63	3.62	3	91	0.00		x	x		
Myrtaceae	***Psidium sartorianum*	2.04	0.77	4	42	0.00	x	x	x	x	x
Nyctaginaceae	*Neea hermaphrodita*	1.24	0.93	5	45	0.00			x	x	x
Phytolaccaceae	*Gallesia integrifolia*	1.84	-0.02	4	26	0.00	x	x		x	x
Polygonaceae	*Triplaris americana*	4.10	-0.81	1	65	0.00	x	x		x	
Quiinaceae	*Quiina florida*	3.38	2.08	3	27	**0.01**	x	x	x	x	
Rubiaceae	*Capirona decorticans*	4.28	3.17	3	58	0.00	x	x	x		
Rutaceae	*Galipea jazminiflora*	4.92	1.25	2	33	0.00	x	x			
	Metrodorea flavida	4.36	2.77	2	31	0.00	x	x	x		x
	Zanthoxylum sprucei	2.70	2.79	3	43	0.00		x	x	x	x
Sapindaceae	*Sapindus saponaria*	2.72	-0.11	4	88	0.00				x	x
Sapotaceae	*Pouteria nemorosa*	3.87	0.47	2	49	0.00		x	x	x	
	Pouteria lucuma	3.25	0.33	4	62	0.00	x	x	x	x	
Simaroubaceae	*Simarouba amara*	3.76	3.31	3	75	0.00	x	x	x	x	
Sterculiaceae	*Guazuma ulmifolia*	3.32	-0.35	1	31	0.00	x	x	x	x	
	***Sterculia apetala*	3.82	2.51	2	49	0.00	x	x	x	x	x
Tiliaceae	*Luehea paniculata*	2.07	3.09	3	39	0.00	x		x	x	x
Ulmaceae	*Ampelocera ruizii*	2.73	0.39	4	90	0.00	x		x	x	x
	Celtis schipii	4.56	0.78	1	39	0.00	x	x	x		
	Phyllostylon rhamnoides	0.26	1.77	5	52	0.00			x	x	x
	Trema micrantha	3.65	0.08	4	27	0.00	x	x		x	
Urticaceae	***Urera baccifera*	2.66	-0.14	4	83	0.00	x	x	x	x	x
Verbenaceae	*Vitex cymosa*	4.55	0.28	1	9	**0.03**	x	x		x	
Vochysiaceae	*Erisma uncinatum*	3.64	3.65	3	84	0.00		x	x		
	Qualea paraensis	3.73	3.61	3	88	0.00	x	x	x		

Main floristic patterns

The MRPP test detected significant differences in woody species composition among all five *a priori* regions (Delta = 0.33; $P = < 0.001$). The first two axes of the abundance-based DCA ordination explained 27% of the floristic variation.

On the DCA axis 1 (19% of explained variation), plots from the Southern Chiquitano were clearly separated from the other regions (Fig. 2a). On the DCA axis 2 (8% of explained variation), plots located in Eastern Amazon-Bajo Paraguá were more related to the Northern Amazon and plots located in Eastern Amazon-Guarayos were more related to the Western Pre-Andean. The Jaccard index, comparing species occurrence among all five floristic regions, showed that Northern Amazon and Western Pre-Andean are floristically the most similar regions (28% of similarity) while the Northern Amazon and Southern Chiquitano are floristically the most distinct regions (13% of similarity) (Table 2).

Table 2. Relative similarity (Jaccard's index) of floristic composition among all five *a-priori* recognized floristic regions. Pair-wise comparison is based on species occurrence.

	Floristic regions				
	WP	NA	EA$_{BP}$	E$_{G}$	SC
WP	1	0.28	0.25	0.24	0.16
NA		1	0.26	0.23	0.13
EA$_{BP}$			1	0.27	0.21
EA$_{G}$				1	0.23
SC					1

The DCA axes showed also a clear separation between species from humid forests on the right side and species from drier forests on the left side of axis 1 and a separation between species from poor soils at the top and species from rich soils at the bottom of axis 2 (Fig. 2b). Thus the scores of plots on DCA axis 1 correlated positively with the densities of *Peltogyne heterophylla,* and *Cariniana micrantha* and negatively with the densities of *Schinopsis brasiliensis* and *Astronium urundeuva.* DCA axis 2 correlated positively with the densities of *Astronium fraxinifolium* and *Erisma uncinatum,* and negatively with the densities of *Poulsenia armata* and *Triplaris americana* (Table 1, Fig. 2b).

When species occurrence was related to each floristic region, only 10 species occurred in one floristic region and 90 occurred in two or more floristic regions. Only nine species had a wide distribution being found in all five floristic regions (Table 1). The ISA test, combining the relative abundance and the relative frequency of each species (Appendix 1), allowed identification of species that were significant indicators of a particular region (Table 1). Most of the 100 selected species (82 species had IV > 25%) can be considered significant indicator species. The indicator species for the Chiquitano region were *Acosmium cardenasii* (IV = 100%) and *Anadenanthera colubrina* (100%); for the Northern Amazon region those were *Tachigali paniculata* (86%) and *Bertholletia excelsa* (78%); for the Pre-Andean region *Poulsenia* armata (79%) and *Socratea exorrhiza* (67%); for the

Eastern Amazon-Guarayos region *Licaria triandra* (96%) and *Ampelocera ruizii* (90%); and for the Eastern Amazon-Bajo Paraguá region the indicator species were *Pseudolmedia laevigata* (91%) and *Qualea paraensis* (88%).

Environmental factors affecting plant species composition

A multiple regression analysis was carried out to evaluate how environmental gradients related to rainfall, temperature, soil fertility and soil texture could explain floristic composition. Most of the floristic variation in DCA axis 1 (94%) and in DCA axis 2 (78%) was explained by the four environmental PCA axes (Table 3), but their relative importance varied (Fig. 3). While both climatic axes had positive effects, the rainfall axis account for 93% of the variation in DCA axis 1 and the temperature axis account for 54% of the variation in DCA axis 2.

Table 3. Forward multiple regression of the floristic DCA axes and the four environmental axes of 220 1-ha permanent plots located in lowland Bolivia. For the environmental axes (rain = rainfall, temp = temperature, ferti = fertility, text = texture) single and squared values are used to account for non-linear effects. The standardized regression coefficient (B) for significant predictors included into the model, F-value, and coefficient of determination (R^2) are provided. Significance levels are shown * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Climatic axes				Soil axes				
	rain	$rain^2$	temp	$temp^2$	ferti	text	$text^2$	F	R^2
DCA 1	1.15***	-0.81***	-0.15**	0.07*	-	0.06*	-	661.5***	0.94
DCA 2	-0.57***	0.50***	0.84***	0.18**	-0.38***	-	-0.16**	121.5***	0.78

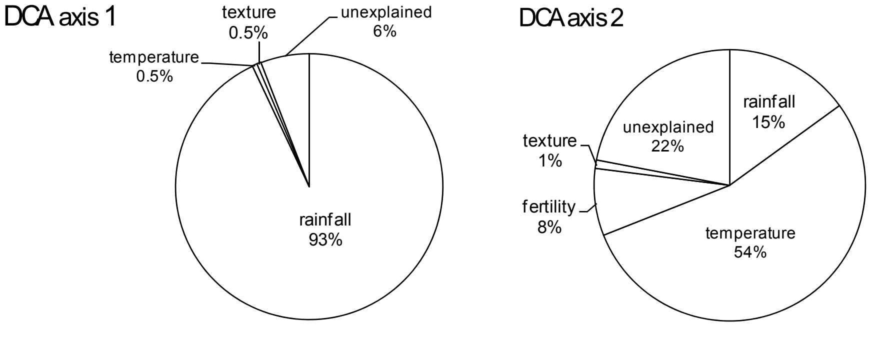

Figure 3. Percentage of the variation in the DCA floristic axes as explained by the environmental PCA axes. PCA axes are rainfall, temperature, soil fertility and soil texture.

Plot scores of the floristic DCA axes were also correlated with individual environmental variables to evaluate what components of these multivariate environmental axes were most important (Table 4). The floristic DCA axis 1 was strongly and positively related to annual precipitation (Fig. 4a) and annual temperature and negatively related to length of dry period. On the other hand, the floristic DCA axis 2 was strongly negatively related to P (Fig. 4b), CEC, Ca^{2+} and silt content.

Table 4. Range (minimum and maximum) and Pearson correlation of environmental axes and environmental variables with the first and second axis of a floristic DCA analysis on composition and abundance of 100 species across lowland Bolivia. n = 220 plots * $p \leq 0.05$, ** $p \leq 0.01$. CEC = Cation Exchange Capacity, OM = organic matter.

			Floristic DCA Axes	
	Minimum	Maximum	Axis 1	Axis 2
Environmental axes				
Rainfall axis	-1.24	2.95	0.79**	-0.16*
Temperature axis	-2.03	1.53	0.37**	0.73**
Soil fertility axis	-1.52	2.95	-0.33**	-0.67**
Soil texture axis	-1.33	3.07	0.36**	-0.02
Climate				
Annual precipitation (mm)	1113	2198	0.94**	-0.01
Driest months (mm)	68	262	0.34**	-0.61**
Dry period (# month< 100 mm)	4	7	-0.90**	-0.01
Drought period (# month< 50 mm)	0	4	-0.36**	0.44**
Annual temperature (°C)	24.2	26.4	0.61**	0.53**
Soil fertility				
pH	3.3	7.8	-0.36**	-0.60**
Ca^{2+} (cmol kg^{-1})	0.20	13.80	-0.41**	-0.70**
Mg^{2+} (cmol kg^{-1})	0.10	7.00	-0.46**	-0.54**
Na^{+} (cmol kg^{-1})	0.03	0.19	-0.21**	-0.57**
K^{+} (cmol kg^{-1})	0.05	0.79	-0.50**	-0.39**
TEB (cmol kg^{-1})	0.4	20.0	-0.31**	-0.68**
CEC (cmol kg^{-1})	1.5	20.1	-0.19**	-0.73**
Acidity (cmol kg^{-1})	0.0	6.1	0.55**	0.37**
P (cmol kg^{-1})	1.0	51.0	0.19**	-0.79**
OM (%)	0.9	5.2	-0.44**	-0.29**
N (%)	0.05	0.4	-0.38**	-0.41**
Soil texture				
Sand (%)	2.0	83.0	-0.23**	0.33**
Silt (%)	3.0	68.0	0.17*	-0.68**
Clay (%)	6.0	50.0	0.15*	0.27**

All five *a-priori* regions were also characterized with respect to their environmental conditions. All environmental variables tested were significantly different among the five regions (Table 5). Annual precipitation and the total precipitation of the three driest months (driest months) were significantly different among the five regions and the annual temperature was significantly higher in moister than drier regions. While Northern Amazon had the highest acidity, Eastern Amazon-Guarayos and Western Pre-Andean had the highest TEB, CEC and P. On the other hand, drier regions had significantly higher OM and N than moister regions. In terms of soil texture, Western Pre-Andean had significantly the highest percentage of silt, drier regions had higher percentage of sand and practically all the regions had similar percentage of clay except Eastern Amazon-Guarayos.

Table 5. Differences of environmental variables between plots belonging to the five floristic regions. WP = Western Pre-andean (n=19), NA = Northern Amazon (n=49), EA$_{BP}$ = Eastern Amazon-Bajo Paraguá (n=43), EA$_{G}$ = Eastern Amazon-Guarayos (n=51), SC = Southern Chiquitano (n=58). For each variable, the mean (± SE), the F value and significance of ANOVA results, by different letters, are shown * $P \leq 0.05$. For the floristic regions see Figure 1 and 2. For units of variables see Table 4.

	Floristic regions						
Variables	WP	NA	EA$_{BP}$	EA$_{G}$	SC	F	*P*
Climate							
Precipitation	2075.5 ± 91.1a	1935.5 ± 43.9b	1696.4 ± 37.4c	1472.3 ± 11.8d	1169.9 ± 23.2e	4039.7	*
Driest month	206.5 ± 21.0a	91.9 ± 18.5c	83.7 ± 0.7d	106.2 ± 2.0b	79.5 ± 6.6e	510.9	*
Dry period	4.0 ± 0.0d	4.8 ± 0.4c	5.0 ± 0.0c	6.0 ± 0.0b	7.0 ± 0.0a	1720.1	*
Drought period	0 ± 0d	2.8 ± 0.4c	3 ± 0b	3 ± 0b	3.2 ± 0.4a	554	*
Temperature	25.5 ± 0.3a	26.0 ± 0.3a	26.1 ± 0.1a	24.7 ± 0.1b	24.7 ± 0.6b	155.8	*
Soil fertility							
pH	4.8 ± 0.6c	3.9 ± 0.5d	4.7 ± 0.5c	6.9 ± 0.5a	5.4 ± 0.6b	210.5	*
Ca	3.8 ± 0.3b	0.6 ± 0.1c	1.1 ± 0.3c	6.9 ± 0.9a	3.6 ± 0.6b	136.8	*
K	0.4 ± 0.1a	0.1 ± 0.1c	0.2 ± 0.0b	0.3 ± 0.0a	0.7 ± 0.0a	68.1	*
Mg	2.4 ± 0.2a	0.4 ± 0.1c	0.8 ± 0.1b	1.8 ± 0.1a	1.8 ± 0.2a	57.3	*
Na	0.12 ± 0.0a	0.05 ± 0.0d	0.07 ± 0.0c	0.10 ± 0.0a	0.08 ± 0.0b	68.2	*
TEB	7.1 ± 4.5ab	1.1 ± 0.9d	2.1 ± 1.1c	9.1 ± 2.8a	5.7 ± 3.5b	126.2	*
CEC	8.2 ± 3.6a	3.6 ± 1.2c	2.9 ± 0.9d	9.2 ± 2.7a	5.9 ± 3.4b	72.3	*
Acidity	1.1 ± 1.3b	2.4 ± 1.5a	0.8 ± 0.5b	0.1 ± 0.1d	0.3 ± 0.1c	79.8	*
P	10.6 ± 5.4a	3.0 ± 1.8b	2.3 ± 1.0c	12.2 ± 9.6a	2.5 ± 1.7c	94.6	*
OM	2.3 ± 0.4b	2.0 ± 0.7b	2.2 ± 0.7b	3.2 ± 0.6a	3.2 ± 1.2a	25.6	*
N	0.16 ± 0.0c	0.12 ± 0.0c	0.17 ± 0.0c	0.27 ± 0.0a	0.22 ± 0.1b	53.5	*
Soil texture							
Sand	27.3 ± 26.0c	50.6 ± 16.5b	65.3 ± 9.9a	61.4 ± 5.0a	59.6 ± 10.5a	36.6	*
Silt	44.0 ± 16.1a	25.1 ± 8.8b	10.2 ± 4.4d	26.0 ± 4.3b	19.4 ± 6.5c	76.7	*
Clay	28.7 ± 12.3a	24.3 ± 12.7a	24.5 ± 8.1a	12.6 ± 2.2b	21.0 ± 8.1a	18.9	*

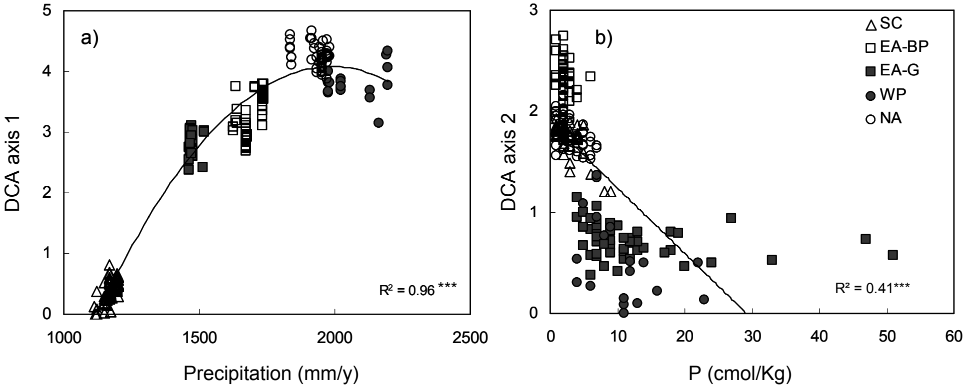

Figure 4. Relationship between DCA floristic axes and a) annual precipitation and b) phosphorous (P). Symbols indicate the five floristic regions: WP = Western Preandean, NA = Northern Amazon, EA_G = Eastern Amazon - Guarayos, EA_{BP} Eastern Amazon - Bajo Paraguá, SC = Southern Chiquitano. Regression lines, corresponding coefficient of determination (R^2), and significance levels are shown *** $P < 0.001$.

Discussion

This study is the first quantification of plant community composition and its relationship with environmental factors covering the tropical lowland forests of Bolivia. Species data were gathered over an area of ca. 160,000 km^2, covering plant distribution and abundance across large environmental gradients. The study considered a wide range of explanatory variables related to climate and soil, which control the floristic diversity of these forests.

Floristic patterns

Species composition varied largely along the latitudinal gradient going from the Southern Chiquitano dry region to the wet Amazonian region in the north. Ordination analysis divided the lowland forests of Bolivia primarily into two major groups (Southern Chiquitano region versus the rest; Fig. 2a) and the MRPP analysis distinguished five floristic regions as suggested by our hypothesis. Thus our results support the proposition that the Chiquitano dry forests merit recognition as a different eco-region in Bolivia (Olsen & Dinerstein 1998, Prado 2000, Killeen *et al*. 2006).

As expected, Fabaceae (or Leguminosae), Arecaceae (or Palmae) and Moraceae were the most dominant families, which is typical for Neotropical forests (Gentry 1988b, Terborgh & Andresen 1998, ter Steege 2010). Fabaceae, the most abundant family in terms of species and individuals in our study, was well-distributed from dry to humid forests but was most abundant in dry areas (cf. Terborgh & Andresen 1998). The seven species of Arecaceae showed a relatively wide distribution, although five were more common in humid areas of either rich or poor soils (cf. Ruokolainen & Vormisto 2000, Vormisto *et al*. 2004). Only two Arecaceae species occurred also in dry forests (Table 1). Species of Moraceae were abundant and well-distributed only in humid areas (cf. ter Steege 2010).

Our prediction that indicator species must be common in the diverse lowland Bolivia is accepted. Species were indeed more frequent and more abundant in some floristic regions than in others (Appendix 1). *Chorisia speciosa,* for example, occurs in all the five floristic regions although it is most frequent and abundant in dry forests. Although many species are widespread, the ISA underlines that most of these species have distinct environmental preferences. Our results most probably are related to the environmental differences among the regions (Table 5), as indicator species reflect relatively well the habitat conditions (Bakker 2008). Thus by knowing species-environment relationships, species can then be used as indicators of environmental conditions (Diekmann 2003). This has also important consequences for forest management and conservation because without complete floristic knowledge of a forest, a few well-chosen indicator species can be used to determine to what floristic region a certain forest belongs.

While some species were found throughout the complete region, others were restricted in their distribution to wetter or drier forests. Ten species were restricted to one of the floristic regions: six to the Northern Amazon and four to the Southern Chiquitano region (Table 1). These species had a “narrow” distribution in the country but were highly abundant and frequent in the region they occur. All these 10 species also occur in surrounding countries in similar dry (Prado & Gibbs 1993, Prado 2000) or wet forests (Ferreira & Prance 1998). Most of the selected species in lowland Bolivia had a relatively wide distribution thus covering different floristic regions (Table 1). *Cordia alliodora*, *Spondias mombin* and *Psidium sartorianum,* for example, occur from Chiquitano dry forests to the Amazonian forests, but also occur in other countries of South America and Central America (Milton *et al*. 1994). The most abundant palms in our study, *E. precatoria, I.*

deltoidea and *S. exorrhiza* are also abundant and widely distributed throughout Amazonia (Pitman *et al.* 2001, Vormisto *et al.* 2004, Kristiansen *et al.* 2009) to Central America (Pyke *et al.* 2001, Sesnie *et al.* 2009). As a result, far-away forests can be, to a certain extent, floristically similar (Honorio-Coronado *et al.* 2009).

Based on the results of this study it can be stated that the 100 woody species provided a good representation of the floristic composition in Bolivian lowland forests. In addition, this shows that a selection of species, or families, may constitute an important source of information for enhancing our knowledge on floristic variation and forest-environment relationships. This fact has been observed earlier and applied successfully to Amazonian (ter Steege *et al.* 1993, Terborgh & Andresen 1998, ter Steege *et al.* 2000) and African forests (Bongers *et al.* 2004, Réjou-Méchain *et al.* 2008).

Factors determining the floristic pattern

Our prediction that climatic factors would be the primary control of species composition at large scale is supported by the results, as climatic axis explained the most floristic variation while soil axes explained only a very minor part of the variation (Table 3, Fig. 3). Species composition was also highly related to rainfall gradient in Eastern Bolivia (Killeen *et al.* 2006). Similarly, in African (Swaine 1996, Bongers *et al.* 2004, Réjou-Méchain *et al.* 2008) and South American forests (Clinebell *et al.* 1995, ter Steege *et al.* 2006), rainfall seasonality was an important factor determining spatial patterns in species distribution and floristic variation. Temperature gradients can exert a strong control on forest structure and composition along an altitudinal gradient (Takyu *et al.* 2005, Sesnie *et al.* 2009). However, the important role of temperature in regulating floristic variation in lowland forests is surprising, especially because the gradient in mean annual temperature in Bolivian forests is rather small (24.2 - 26.4 °C). Climate change scenarios predict modest increases in annual temperature and large decreases in rainfall for lowland Bolivia (IPCC 2007). Given the fact that rainfall and temperature are the most important driver of floristic variation this suggest that climate change may lead to potentially large changes in floristic composition in Bolivia.

We used PCA axes to summarize multivariate environmental gradients. However, individual environmental variables such as annual precipitation or phosphorous showed stronger correlations with the floristic DCA axes (Pearson's r = 0.94 and 0.79, respectively) than the multivariate rainfall and temperature axes (Pearson's r = 0.79 and 0.73, respectively), suggesting that they might be the strongest underlying drivers of floristic variation (Table 4, Figs. 4a and 4b). In addition, Ca was also strongly correlated with the DCA axis 2 (Pearson's r = 0.70). Other studies have also highlighted the relation of P and Ca related to floristic composition in tropical forests (Newbery & Proctor 1984, Paoli *et al.* 2006). In addition, several studies have shown strong effects of edaphic heterogeneity on floristic composition and species distribution at smaller (ter Steege *et al.* 1993, Clark *et al.* 1998, Vormisto 2002) and larger spatial scales (Phillips *et al.* 2003).

The five floristic regions found in this study showed a clear and significant decrease in annual rainfall and an increase in the length of dry period, as expected (Fig. 2a, Table 5). In contrast, soil fertility did not decrease along the rainfall gradient as was observed in African forests (Swaine 1996, Bongers *et al.* 2004). The Amazonian and Western Pre-Andean region experience similar high rainfall but differ strikingly in their soil fertility. The Amazon region has geologically older, more leached and poorer soils located in the Precambrian shield, while the Western Pre-Andean region has geologically younger soils with recently deposited rich sediments (Lips & Duivenvoorden 1996, Richter & Babbar 1991, Sombroek 2000, Quesada *et al.* 2009). Plots in the Eastern Amazon – Bajo Paraguá had nutrient-poor soils similar to the Northern Amazon while plots in the Eastern Amazon-Guarayos had nutrient-rich soils similar to the Western Pre-Andean (Table 5). The Eastern Amazon forests of Bajo Paraguá and of Guarayos are usually considered to be part of one eco-region: the Amazonian-Chiquitanian transition (Dauber *et al.* 2003). Our analyses, based on floristic composition (Fig. 2a) and environmental conditions (Table 5) clearly showed that these two areas represent two different regions.

Gradients of plant composition are not only shaped by environmental factors but also by historical, geographic, and stochastic forces affecting the species distribution range (Willig *et al.* 2003, ter Steege 2010). Although our intention was not to examine the influence of historical processes, but to analyze how temporary climate and edaphic heterogeneity can affect species composition, we are aware of the possible impact of these processes on plant species composition in lowland Bolivia (Mayle *et al.* 2000). The effects of historical processes like past climate and geographic changes are, however, still controversial. It has been suggested that both ancient and recent diversification processes of species could explain current species composition (Prance 1982, Gentry 1982, Colinvaux *et al.* 2000, Pennington *et al.* 2004). As the current distribution of climatic conditions is rearranging on Earth (Malhi & Wright 2004, Loarie *et al.* 2009) the current climate, and its direct impacts, merits urgent attention.

Concluding remarks

Using 100 plant species and 220 1-ha plots distributed over lowland Bolivia, we showed that the climatic gradient was s stronger driver of the floristic variation than the edaphic gradient. Floristic variation was strongly associated to the rainfall and temperature axes, suggesting that species composition may shift with climate change. Of the individual environmental variables, annual precipitation and P seemed to be the strongest drivers of floristic variation. We distinguished five floristic regions based on floristic composition that also differed in environmental variables. Although many species were widely distributed across floristic regions, most of these species had distinct environmental preferences and can be used as indicator species for each floristic region.

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Appendix 1. Total frequency and abundance based on 220 1-ha plots and relative frequency and abundance per floristic regions based on the Indicator Species Analysis (ISA) results. Floristic regions and their sample size are given. WP = Western Pre-Andean (n=19); NA = Northern Amazon (n=49); EA_{BP} = Eastern Amazon-Bajo Paraguá (n=43); EA_{G} = Eastern Amazon-Guarayos (n=51); SC = Southern Chiquitano (n=58). The species list is alphabetically ordered by family and scientific name.

Family	Scientific name	Total		Relative frequency/abundance									
		Freq.	Abund.	WP		NA		EA_{BP}		EA_{G}		SC	
Anacardiaceae	*Anacardium occidentale*	8	0.10	11	21	31	79	0	0	0	0	0	0
	Astronium fraxinifolium	8	0.58	0	0	0	0	40	99	0	0	2	1
	Astronium lecontei	18	0.45	16	9	49	60	30	30	0	0	0	0
	Astronium urundeuva	15	0.88	0	0	0	0	2	1	0	0	53	99
	Schinopsis brasiliensis	13	0.32	0	0	0	0	0	0	0	0	48	100
	Spondias mombin	45	1.20	84	60	10	3	19	5	67	13	64	19
Apocynaceae	*Aspidosperma cylindrocarpon*	49	3.83	0	0	0	0	47	9	65	13	93	78
	Himatanthus sucuuba	10	0.19	11	16	37	76	5	7	0	0	0	0
	Peschiera arcuata	28	0.58	5	2	51	41	35	34	39	22	2	1
Araliaceae	*Dendropanax arboreus*	36	1.90	74	24	0	0	42	13	92	64	0	0
	Didymopanax morototoni	27	0.94	32	10	12	4	91	81	18	5	0	0
Arecaceae	*Astrocarium aculeatum*	24	2.02	37	81	47	8	51	11	2	0	0	0
	Attalea phalerata	28	1.38	74	63	29	21	0	0	63	16	3	1
	Euterpe precatoria	48	9.57	100	39	100	43	88	18	0	0	0	0
	Iriartea deltoidea	17	3.16	53	84	55	16	0	0	0	0	0	0
	Oenocarpus bataua	19	1.21	11	45	82	55	0	0	0	0	0	0
	Socratea exorrhiza	29	4.01	84	79	37	2	63	15	4	4	0	0
	Syagrus sancona	22	0.41	11	11	0	0	7	4	69	75	14	10
Bignoniaceae	*Jacaranda copaia*	22	0.54	0	0	63	59	40	41	0	0	0	0
	Tabebuia impetiginosa	20	1.08	11	20	24	10	16	5	0	0	40	65
	Tabebuia serratifolia	46	1.43	0	0	61	35	53	19	27	6	60	41
Bombacaceae	*Cavanillesia hylogeiton*	17	0.26	11	24	31	31	0	0	41	46	0	0
	Ceiba pentandra	25	0.45	63	49	27	14	35	20	31	16	0	0
	Chorisia speciosa	45	3.24	5	0	12	1	44	9	33	5	97	84
Boraginaceae	*Cordia alliodora*	50	1.45	26	5	29	11	56	31	65	24	57	29
Capparidaceae	*Capparis prisca*	9	0.77	5	8	0	0	2	1	0	0	31	90
Caricaceae	*Jacaratia spinosa*	30	1.04	32	23	16	4	28	24	80	49	0	0
Cecropiaceae	*Cecropia concolor*	16	0.35	11	21	0	0	12	23	57	56	0	0
	Cecropia membranacea	17	1.74	11	1	14	6	65	93	0	0	0	0
	Pourouma cecropiifolia	36	5.31	58	8	18	3	72	53	55	36	0	0
Combretaceae	*Combretum leprosum*	14	0.80	0	0	0	0	5	2	20	21	33	76
	Terminalia amazonica	24	0.90	21	23	29	11	72	56	6	10	0	0
	Terminalia oblonga	42	3.43	0	0	39	6	51	9	100	86	0	0
Euphorbiaceae	*Hevea brasiliensis*	16	0.73	0	0	63	94	12	6	0	0	0	0
	Hura crepitans	25	2.50	79	45	0	0	0	0	78	55	0	0
	Pausandra trianae	39	2.01	0	0	33	38	72	46	75	16	0	0
Fabaceae	*Acosmium cardenassi*	26	31.18	0	0	0	0	0	0	0	0	100	100
	Amburana cearensis	19	1.60	0	0	14	3	21	20	0	0	43	77
	Anadenanthera colubrina	27	5.70	0	0	0	0	0	0	2	0	100	100
	Apuleia leiocarpa	30	0.84	16	4	49	36	88	60	0	0	0	0
	Caesalpinia pluviosa	28	6.00	0	0	0	0	0	0	18	6	91	94
	Cedrelinga catenaeformis	10	0.21	5	10	31	74	12	16	0	0	0	0
	Centrolobium microchaete	18	2.54	0	0	0	0	0	0	16	7	53	93
	Copaifera chodatiana	21	1.02	0	0	0	0	0	0	0	0	79	100
	Dialium guianense	16	0.75	0	0	71	100	0	0	0	0	0	0
	Hymenaea courbaril	24	0.33	0	0	27	23	42	37	16	18	22	21
	Hymenaea parvifolia	11	0.21	0	0	39	56	14	44	0	0	0	0
Fabaceae	*Machaerium acutifolium*	27	3.77	0	0	0	0	12	2	0	0	95	98
	Machaerium scleroxylon	21	1.55	0	0	0	0	0	0	0	0	81	100
	Peltogyne heterophylla	5	0.57	0	0	22	100	0	0	0	0	0	0
	Pterogyne nitens	6	0.09	0	0	0	0	7	19	8	33	12	48
	Schizolobium parahyba	24	0.54	58	44	18	11	21	21	45	24	0	0
	Swartzia jorori	21	0.51	74	67	0	0	9	3	53	29	3	1
	Sweetia fruticosa	86	5.80	37	4	80	10	95	47	94	11	93	29
	Tachigali paniculata	19	2.15	0	0	86	100	0	0	0	0	0	0
Flacourtiaceae	*Casearia gossypiosperma*	60	5.97	5	1	33	3	74	32	63	9	90	55
Lauraceae	*Licaria triandra*	23	2.37	0	0	0	0	5	0	96	100	0	0
	Ocotea guianensis	30	1.30	0	0	0	0	63	42	76	58	0	0
Lecythidaceae	*Bertholletia excelsa*	17	0.45	0	0	78	100	0	0	0	0	0	0
	Cariniana domestica	10	0.21	0	0	10	15	14	17	22	68	0	0
	Cariniana estrellensis	21	0.36	5	3	8	5	26	17	59	75	0	0
	Cariniana ianeirensis	22	0.91	5	1	0	0	5	3	80	83	9	12

Appendix 1. Continued

Family	**Scientific name**	**Total**		**Relative frequency/abundance**									
		Freq.	**Abund.**	**WA**		**NA**		**EA$_{BP}$**		**EA$_{G}$**		**SC**	
Lecythidaceae	*Cariniana micrantha*	7	0.14	0	0	53	100	0	0	0	0	0	0
	Couratari macrosperma	12	0.28	0	0	33	100	0	0	0	0	0	0
Melastomataceae	*Bellucia grossularioides*	12	0.25	0	0	29	44	14	44	12	12	0	0
Meliaceae	*Cedrela fissilis*	25	0.48	0	0	12	7	40	35	31	22	26	37
	Cedrela odorata	15	0.29	58	46	47	54	0	0	0	0	0	0
	Swietenia macrophylla	15	0.26	16	22	0	0	28	31	33	46	0	0
	Trichilia pallida	12	1.88	0	0	0	0	58	100	2	0	0	0
Monimiaceae	*Siparuna decipiens*	21	2.62	21	18	86	82	0	0	0	0	0	0
Moraceae	*Castilla ulei*	9	0.17	11	13	37	87	0	0	0	0	0	0
	Maclura tinctoria	13	0.20	0	0	0	0	28	46	33	54	0	0
	Poulsenia armata	8	1.87	79	100	4	0	0	0	0	0	0	0
	Pseudolmedia laevigata	22	4.93	0	0	16	2	93	98	0	0	0	0
	Pseudolmedia laevis	74	34.01	100	13	100	14	100	21	100	52	0	0
	Pseudolmedia macrophylla	16	0.52	37	57	59	43	0	0	0	0	0	0
Myrtaceae	*Psidium sartorianum*	41	1.30	16	4	31	8	28	7	78	54	34	27
Nyctaginaceae	*Neea hermaphrodita*	47	4.61	0	0	0	0	35	6	94	28	69	65
Phytolaccaceae	*Gallesia integrifolia*	24	1.15	26	19	6	2	0	0	67	39	17	40
Polygonaceae	*Triplaris americana*	11	0.37	68	94	6	2	0	0	16	4	0	0
Quiinaceae	*Quiina florida*	21	0.85	5	1	2	2	42	63	53	33	0	0
Rubiaceae	*Capirona decorticans*	27	1.91	21	5	49	15	72	80	0	0	0	0
Rutaceae	*Galipea jazminiflora*	11	0.92	21	18	41	82	0	0	0	0	0	0
	Metrodorea flavida	21	2.28	11	1	59	53	35	46	0	0	2	0
	Zanthoxylum sprucei	29	0.86	0	0	12	5	63	68	43	19	16	8
Sapindaceae	*Sapindus saponaria*	21	0.92	0	0	0	0	0	0	88	99	3	1
Sapotaceae	*Pouteria lucuma*	48	2.84	74	17	33	3	60	17	98	63	0	0
	Pouteria nemorosa	44	2.25	0	0	92	53	7	1	96	46	0	0
Simaroubaceae	*Simarouba amara*	24	1.03	21	5	16	6	86	88	8	1	0	0
Sterculiaceae	*Guazuma ulmifolia*	25	0.50	63	49	4	2	12	5	69	44	0	0
	Sterculia apetala	25	0.48	11	5	71	68	21	14	10	5	7	9
Tiliaceae	*Luehea paniculata*	21	0.55	26	13	0	0	67	58	4	1	19	27
Ulmaceae	*Ampelocera ruizii*	40	4.63	21	2	0	0	56	8	100	90	16	1
	Celtis schipii	29	2.15	84	46	59	30	44	23	0	0	0	0
	Phyllostylon rhamnoides	25	4.09	0	0	0	0	30	4	20	2	55	94
	Trema micrantha	15	0.47	11	7	20	30	0	0	43	62	0	0
Urticaceae	*Urera baccifera*	30	3.05	16	4	12	2	2	0	98	85	9	9
Verbenaceae	*Vitex cymosa*	5	0.08	16	59	14	38	0	0	2	4	0	0
Vochysiaceae	*Erisma uncinatum*	20	1.65	0	0	14	2	86	98	0	0	0	0
	Qualea paraensis	21	1.70	5	1	12	2	91	98	0	0	0	0

Chapter 4

Climate is a stronger driver of tree and forest growth rates than soil and disturbance

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Abstract

Water, nutrients and light are essential resources for tree growth. Since the availability of these resources vary over space and time tree growth rates vary accordingly. We examined the effects of environmental conditions and anthropogenic disturbances on diameter growth rates at tree and at stand level using 165 1-ha permanent plots across Bolivian tropical lowland forests. We found positive basal area increases at the stand level which agree with the generally reported biomass increases in tropical forests. We predicted that growth rates would be higher in humid than in dry forests, higher in nutrient-rich than nutrient-poor forests, and higher in logged than non-logged forests because of an increase in water, nutrients and light, respectively. Multiple regression analysis demonstrated that environmental and disturbance factors significantly explained the high variation in growth rates. While rainfall and temperature had positive effects on tree growth, smaller effects of soil fertility were found. Growth rates increased in logged plots, especially those which had a high logging impact. Future decreases in rainfall and increases in temperature due to climate change can also affect growth rates. Forest managers should take into account the high variation in growth rates occurring in the lowland forests of Bolivia. Based on our results we advocate that management guidelines to be developed are specific to each forest and are in line with its characteristic and conditions.

Key words: Bolivia, basal area growth rate, climate, disturbance, environmental gradient, logging, soil, tree growth rate, tropical lowland.

Introduction

All plants depend on the availability of water, nutrients and light as essential resources for growth. In tropical rain forests, these resources vary over spatial and temporal scales and as a result, tree growth varies with resource availability. In general, tree growth increases with rainfall (Murphy & Lugo 1986, Dauber *et al.* 2003, 2005) and decreases with drought (Nepstad *et al.* 2002, Nath *et al.* 2006). Independently of rainfall, soil fertility can also affects tree growth rate (Lu *et al.* 2002, Malhi *et al.* 2004) with better growth on more nutrient-rich soils (Russo *et al.* 2005). Many tropical forests differ from temperate forests in their stocks and flows of biologically important nutrients in and from biomass resources (Richards 1996). In particular, humid tropical ecosystems are relatively rich in available N (Robertson 1982, 1984, Vitousek 1984, Sollins 1998) and growth rate is likely to be limited by P or other rock-derived nutrients (Vitousek & Denslow 1986, Tanner *et al.* 1998). While there are studies of the effects of only climate (Bullock 1997, Clark *et al.* 2003, Feeley *et al.* 2007) or soil (Vitousek & Sanford 1986, Davies 2001, Russo *et al.* 2005) on growth rate, there are very few studies considering the effects of both environmental factors on tree growth (but see Baker *et al.* 2003a).

Vieira and co-workers (2004) did not find a relationship at all between growth rates and soils, and suggested that human disturbance may have overruled more subtle environmental differences. Disturbances initiate the forest growth cycle through the creation of canopy gaps (Richards 1996). These gaps or vertical holes in the canopy open up space, increase light-, nutrient- and probably water availability, and thus create possibilities for recruitment of new plants and species (Van der Meer *et al.* 1998, Van Rheenen *et al.* 2004). Therefore, both natural disturbances (i.e. strong winds, landslides) and anthropogenic disturbances (i.e. wildfires, logging) are important drivers of forest dynamics (Hartshorn 1980). Although logging has several negative impacts on forest ecosystems and forest functions (e.g. forest degradation and associated fires; Nepstad *et al.* 1999), it also creates conditions that stimulate the growth of the remaining trees, thus, accelerating the growth of previously suppressed individuals (Carvalho *et al.* 2004). Similarly, growth rates also increase with increasing logging intensity (Finegan & Camacho 1999, Nebel *et al.* 2001b, Peña-Claros *et al.* 2008a, Villegas *et al.* 2009).

In many tropical countries, including Bolivia, forest management for timber harvesting is an important economic activity (Pacheco 1988). The current Bolivian Forestry Law provides a strong stimulus for sustainable forest management (Snook *et al.* 2007). An important aspect of this law is the establishment and monitoring of a network of permanent sample plots in the lowland forestry areas. The Bolivian network also presents an appropriate system to examine the relationship between forest components and environmental conditions as plots cover different forest types, from humid evergreen Amazon forests to dry deciduous Chiquitano forests (Navarro & Maldonado 2002). Lowland Bolivia is also characterized by differences in geomorphology and geological history: in the west the relatively young and rich-nutrient landscapes of the Pre-Andean predominate and in the east the ancient rocks and poor-nutrient soils of the Brazilian Shield (Killeen *et al.* 2006).

In this study we used 165 1-ha permanent plots of this Bolivian network to describe individual tree and stand level growth rates, and to determine how climate, soil and logging affect them. This is one of the few studies in the Neotropics doing broad-scale comparisons of tree and forest growth that considers both environmental gradients and disturbance factors. We addressed the following questions: (1) How do individual tree (diameter) and stand level (basal area) growth vary across lowland Bolivia? (2) What are the effects of climate, soil and disturbance factors on these growth variables? We expected tree growth to be highly variable due to the high heterogeneity of environmental conditions in Bolivia (Navarro & Maldonado 2002, Ibisch & Mérida 2003). Considering that growth increases with resource availability we predicted that growth rates would be higher in moist than in dry sites, higher in nutrient-rich than nutrient-poor forests, and higher in disturbed than non-disturbed forests (Swaine *et al.* 1990, Carvalho *et al.* 2004, Dauber *et al.* 2005).

Material and Methods

Study area

For this study a total of 165 1-ha plots were selected from the Network of Permanent Plots in lowland Bolivia. These plots were established in old growth forests by various projects and forestry concessionaries (see Acknowledgements for more details). To date this network and its database is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots are located between 10 – 18° S and 59 – 69° W, in upland forests (*terra firme;* only 5% of the plots were found in areas of seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from 100 – 500 masl. These plots are distributed over the main environmental gradients of climate and soil and 52% of them have been affected by logging.

Lowland Bolivia is characterized by two climatic gradients: a south-north gradient with *mean* annual precipitation ranging from 1100 to 1900 mm and an east-west gradient ranging from 1600 to 2200 mm. However, the precipitation in individual years can vary from 600 to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, 1970 – 2007, Servicio Nacional de Meteorología e Hidrología-SENAMHI, unpublished data). In general, the lowlands in Bolivia experience a 4 to 7 months long dry season (i.e. precipitation < 100 mm/month), mostly from April to September, corresponding to the austral winter. Mean annual temperature is between 24 and 26°C. Additionally lowland Bolivia is also characterized by differences in geomorphology and geological history (Montes de Oca 1997, Suárez-Soruco 2000), leading to strong gradients in soil characteristics. The soils vary largely in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003).

Data collection and analysis

The 165 selected plots were all established between 1995 and 2005 and measurement periods vary between 2 and 11 years, with the last measurements taking place in 2007. Plots were typically square (100 x 100 m), with only 11 of them being rectangular (20 x 500 m). In each plot, every tree ≥10 cm diameter at breast height (DBH; measured at 130 cm or higher height when buttresses were present) was measured with diameter tape, painted at the measurement point, tagged and identified, following standard protocols (Alder & Synnott 1992, Contreras *et al.* 1999). Re-censuses were mostly carried out in the same season or month as when the plots were established, thus minimizing intra-annual variation in DBH growth. Logging activities started in most of the plots immediately after their establishment. A total of 85 plots were affected by logging activities (i.e. logging occurred in the plot) and 80 plots were not logged.

The annual diameter growth per individual was calculated by regression as: $(D_f - D_i)/t$ where D_f is the final diameter at the end of the interval and D_i is the initial diameter at the start of the interval. Based on this diameter growth rate (hereafter DGR) we calculated five variables per plot, representing the growth rate at the individual level: average (DGR_{avg}), median (DGR_{50}), 90th, 95th and 99th percentile (DGR_{99}) of annual diameter growth. The 90th (DGR_{90}) and 95th (DGR_{95}) diameter growth rate percentile are not included in the results because they were highly correlated with the DGR_{avg}, DGR_{99} and between themselves (Appendix 1). The DGR_{50} and DGR_{99} were calculated to know lower and upper levels of growth rate. Additionally, we calculated the basal area growth rate at the stand level (hereafter $BAGR_{stand}$) as the net yearly basal area change per plot. The $BAGR_{stand}$ was calculated as: $(BA_f - BA_i)/t$, where BA_f is the total plot basal area at the end of the measurement interval and BA_i is the initial plot basal area at the start of the measurement interval or just right after logging. In both formulas t is the time interval between the two measurement dates, in terms of years. Note that $BAGR_{stand}$ includes the effects of growth, recruitment and mortality, while DGR are based upon individuals that survived the whole monitoring period only.

For each plot we obtained five climatic variables, interpolated from available data from weather stations, and 12 edaphic variables obtained from sampled soils. To summarize these environmental variables we performed two independent Principal Component Analyses, (PCAs). The climatic PCA considered annual temperature, annual precipitation, precipitation of the three driest months, length of the dry period (# months < 100 mm), and length of the drought period (# months < 50 mm). The first two axes of the climatic PCA explained 94% of the variation. The first axis (65%) correlated positively with annual precipitation and negatively with dry period length (henceforth referred to as the rainfall axis). The second axis (29%) correlated positively with mean annual temperature and negatively with the precipitation of the driest months (hereafter temperature axis). The edaphic PCA considered Cation Exchange Capacity (CEC), cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), Phosphorous (P), Organic Matter (OM), Nitrogen (N), acidity and percentage of particles content (sand, silt and clay). The first two axes of the edaphic PCA explained 68% of the variation. The first axis (48%) correlated positively with variables related with soil fertility (CEC, Ca, Mg, Na, K, P, OM, and N), and negatively with acidity (hereafter soil fertility axis). The second axis (20%), represented variation in soil texture and correlated positively with clay and silt and negatively with sand (hereafter soil texture axis) (see details on Chapter 2).

Four logging related variables were used to describe forest disturbance in each plot. Two dummy variables were created: one to describe whether or not logging was present in the plots (LP) and another one to describe whether the logging impact (LI) was high (1) or low (0), based on the number and location of logged trees and number of dead trees by logging. Other continuous disturbance variables were the amount of logged basal area (LBA, in m^2 ha^{-1}) and the time after logging (TAL, in years).

The four growth variables were first correlated (Pearson correlation) with the individual environmental variables to evaluate what components of these composite axes were most important. The four main environmental axes and the four disturbance variables (including interactions and their quadratic terms, when necessary) were regressed on the growth rate variables using a series of multiple backward regressions. Quadratic terms were included in the models because non-linear relationships between growth rates and predictors were observed in scatter plots. Because the increases in explained variation in models that included the interaction effects were very low, we re-run the analyses without the interactions. Here we only present the latter results. For each variable the Kolmogorov-Smirnov test for normal distribution was applied, and if necessary, the data were logarithmic ($\log_{10}$), square root or arcsine - transformed. All statistical analyses were performed with SPSS 15.0 for Windows (SPSS Inc.).

Results

Variation in tree and forest growth rates

Growth variables had relatively high variation across plots, with the largest variation in DGR_{50} and $BAGR_{stand}$ (Table 1). On average, $BAGR_{stand}$ was 0.49 m^2 ha^{-1} $year^{-1}$ (range from 0.17 to 1.22). Mean DGR_{avg} was 0.31 cm $year^{-1}$, with the lowest value (0.12) in a plot with low rainfall and the highest value (0.70) in a plot of intermediate amount of rainfall (Table 1, Appendix 2). In relation to the lower and upper growth rate limit, both the highest DGR_{50} (0.59 cm $year^{-1}$) and DGR_{99} (3.82 cm $year^{-1}$) were found in plots of higher rainfall and both the lowest DGR_{50} (0.07 cm $year^{-1}$) and DGR_{99} (0.63 cm $year^{-1}$) were found in plots of lower rainfall (Appendix 2). Although low DGR_{avg} was found mostly in plots with lower rainfall (Figs. 1a and 2a) low $BAGR_{stand}$ was found in plots with both low and high amount of rainfall (Figs. 1b and 2b).

Table 1. Mean ± standard deviation (SD) and ranges (minimum – maximum) of tree and forest growth variables from 165 1-ha permanent plots across lowland Bolivia. The ratio was calculated by dividing the maximum value by the minimum value. DGR = Diameter growth rate, BAGR = basal area growth rate, Avg= average, DGR_{50} = median, DGR_{99} = 99 percentile.

Variables	Mean	SD	Minimum	Maximum	Ratio
DGR_{avg} (cm $year^{-1}$)	0.31	± 0.10	0.12	0.70	5.8
DGR_{50} (cm $year^{-1}$)	0.20	± 0.08	0.07	0.59	8.0
DGR_{99} (cm $year^{-1}$)	1.77	± 0.63	0.63	3.82	6.1
$BAGR_{stand}$ (m^2 ha^{-1} $year^{-1}$)	0.49	± 0.21	0.17	1.22	7.2

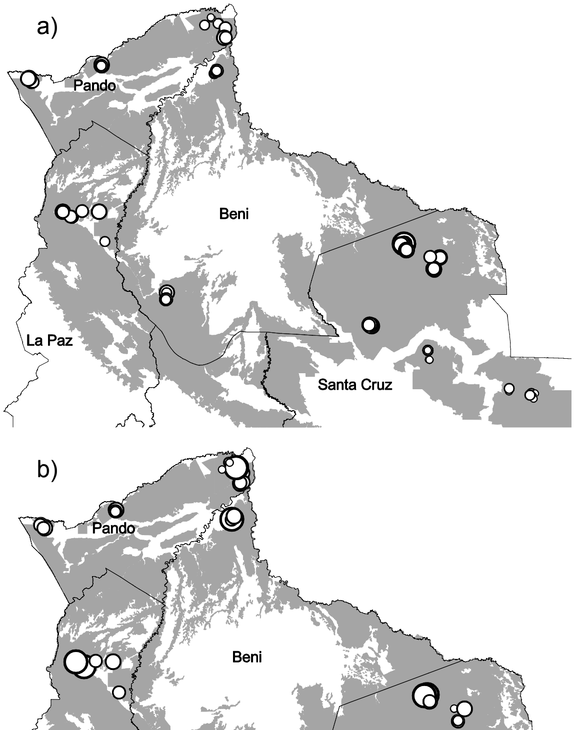

Figure 1. Variation in a) diameter (DGR_{avg}) and b) stand basal area ($BAGR_{stand}$) growth rates of 165 1-ha permanent plots located in four departments (Pando, La Paz, Beni and Santa Cruz) of lowland Bolivia.

Factors affecting tree and forest growth

All four growth variables had in general qualitatively similar relationship to the environmental axes and variables, except for texture axis, drought period, Olsen P, acidity, and LBA (Table 2). Most of the significant relationships were found for DGR_{avg}, DGR_{50} and $BAGR_{stand.}$ However, DGR_{99} showed a stronger positive response to temperature axis, precipitation, and P, and a stronger negative response to Mg and K, than DGR_{avg}. Growth variables were always positively and significantly correlated with climate axes and in most of the cases negatively and non-significantly to the soil axes.

Table 2. Pearson correlation coefficients of four tree growth variables with four environmental axes, 18 environmental and four disturbance variables from 165 1-ha plots located in Bolivian lowland forests. * $P \leq 0.05$, ** $P \leq 0.01$. DGR= diameter growth rate, BAGR = basal area growth rate, CEC = Cation Exchange Capacity, Avg = average.

Environmental axes and variables	DGR_{avg}	DGR_{50}	DGR_{99}	$BAGR_{stand}$
Rainfall axis	0.35**	0.22**	0.33**	0.27**
Temperature axis	0.26**	0.21*	0.29**	0.26**
Fertility axis	-0.14	-0.16	-0.17	-0.25**
Texture axis	-0.04	-0.02	-0.04	0.10
Annual precipitation (mm)	0.41**	0.22**	0.48**	0.37**
Driest months (mm)	0.12	0.04	0.09	0.06
Temperature (°C)	0.44**	0.35**	0.40**	0.39**
Dry period (# of months < 100 mm)	-0.48**	-0.31**	-0.46**	-0.33**
Drought period (# of months < 50 mm)	-0.06	-0.04	0.02	-0.02
Ca (cmol kg^{-1})	-0.12	-0.16	-0.14	-0.23**
Mg (cmol kg^{-1})	-0.15	-0.12	-0.26**	-0.33**
Na (cmol kg^{-1})	0.05	0.03	-0.03	-0.09
K (cmol kg^{-1})	-0.08	-0.01	-0.25**	-0.19*
CEC (cmol kg^{-1})	-0.21*	-0.28**	-0.12	-0.14
Acidity (cmol kg^{-1})	-0.03	-0.05	0.13	0.30**
P (cmol kg^{-1})	0.09	0.08	0.17*	-0.03
Organic matter (%)	-0.33**	-0.27**	-0.26**	-0.23**
N (%)	-0.15	-0.15	-0.15	-0.17*
Sand (%)	0.06	0.05	0.09	0.01
Silt (%)	-0.18*	-0.24**	-0.09	-0.02
Clay (%)	0.05	0.14	0.08	0.02
Logging (yes/no)	0.28**	0.34**	0.08	0.06
Logging impact (yes/no)	0.31**	0.31**	0.14	0.12
Logged basal area (m^2 ha^{-1})	0.26**	0.30**	0.09	-0.01
Time after logging (year)	-0.16	-0.08	-0.09	-0.05

Particularly, $BAGR_{stand}$ had a negative and significant relationship with soil fertility axis. Growth variables increased significantly with annual precipitation and temperature and decreased with the dry period (Table 2). Most of the soil variables had negative relationships to growth variables but only few relations were significant. Unexpectedly, OM content was the only soil variable significantly and negatively related to the growth variables. All disturbance variables were positively related to the four growth variables except TAL (Table 2, Figs. 2e and 2f).

The backward regression models obtained the relative importance and explained the effects of environmental axes and disturbance variables on growth rates (Table 3). The total variation explained by the models ranged between 23-54%. Variation in DGR_{avg} was explained best (54%) and was affected by most of the predictors while variation in $BAGR_{stand}$ was explained least (23%) and was affected by fewer predictors. Rainfall was the most important axis affecting significantly and positively all growth rates. Similarly, temperature and soil fertility had positive effects (Figs. 2c and 2d). In contrast, the soil texture axis had significant negative effects only on growth rates at tree level. Disturbance variables only significantly affected DGR_{avg} and DGR_{50} (Table 3).

Table 3. Backward multiple regression analysis of forest and tree growth variables on environmental (climatic and soil axes and their quadratic terms) and disturbance variables for 165 1-ha permanent plots in lowland Bolivia. Only for significant predictors the standardized regression coefficient (B) are included into the model, F-value, and coefficient of determination (R^2) are provided. Significance levels are shown * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. DGR = Diameter growth rate, BAGR = basal area growth rate, DGR_{50} = median, DGR_{99} = 99 percentile, Avg = average, L = logging, LI = logging impact, TAL = Time after logging.

	Environmental axes							Disturbance variables				
Variables	Rainfall		Temperature		Soil fertility		Soil texture					
	Rain	$Rain^2$	Temp	$Temp^2$	Ferti	$Ferti^2$	Text	L	LI	TAL	F	R^2
DGR_{avg}	0.89***	-	0.61***	-0.33**	0.61***	-0.27**	-0.28**	0.37**	0.18**	-0.39***	16.53	0.54
DGR_{50}	0.38***	-	0.34**	-	0.24*	-	-0.26**	0.53***		-0.29*	10.25	0.32
DGR_{99}	1.03***	-0.78***	-	-	0.15*	-	-0.29***	-	-	-	26.09	0.44
$BAGR_{stand}$	0.38***	-	0.29***	-	-	-0.23**	-	-	-	-	13.28	0.23

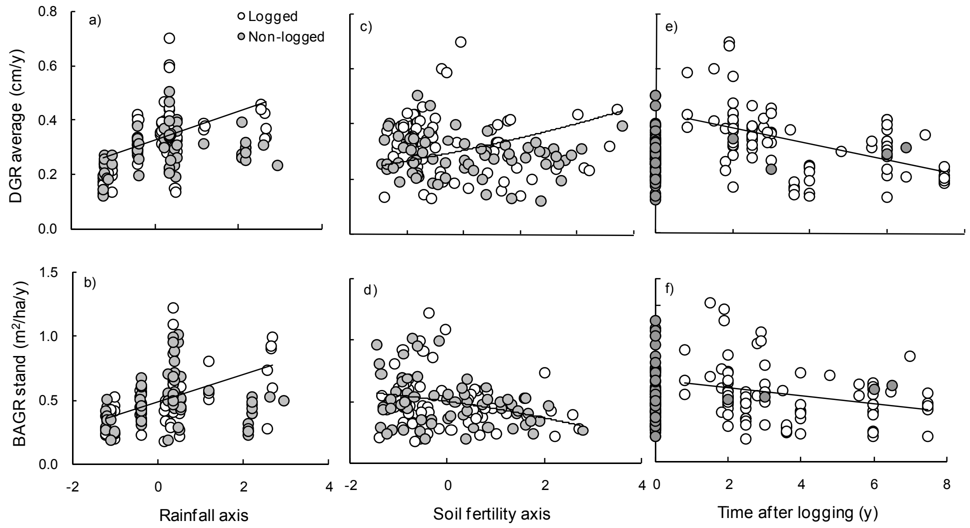

Figure 2. Relationships between average tree diameter growth rate (DGR_{avg}) and average stand basal area growth rate ($BAGR_{stand}$) with environmental axes: a) rainfall, b) soil fertility and c) time after logging (TAL) of 85 1-ha logged (white circles) and 80 1-ha non-logged (grey circles) permanent plots. Environmental axes are multivariate composite PCA axes with high scores indicating plots with high rainfall and high soil fertility. Regression lines are according to the backward multiple regression models and were done by keeping all other variables constant (at the mean value across the all plots), while varying along the variable of interest. Coefficient of determination and significance levels, from this backward analysis, are shown in Table 3. Grey dots in the relationship with TAL were plots with low impact of logging (surrounded by logging effects but non-logged plots).

Discussion

This study describes how tree growth at individual and stand level differ among Bolivian forests, shows that both environmental and disturbance factors have effects on growth rates and that climate is the strongest driver. Climate and soil fertility generally had positive effects and disturbances related to logging generally had positive effects.

Variation in tree and forest growth

We found high variation in tree growth rates at individual and at stand level in lowland Bolivia, in line with our hypothesis. The DGR_{avg} of 0.31± 0.10 cm year^{-1}

and its range (0.12 – 0.70 cm year^{-1}) is within the range (0.08 – 0.80 cm year^{-1}) of diameter growth rates reported for other tropical forests (Manokaran & Kochummen 1987, Chambers *et al.* 1998, Finegan & Camacho 1999, Alder *et al.* 2002, Pereira da Silva *et al.* 2002). The average of $\text{BAGR}_{\text{stand}}$ was similar (0.49 ± 0.21 m^2 ha^{-1} yr^{-1}), but the range (0.17 – 1.22 m^2 ha^{-1} yr^{-1}) was larger than other tropical forests (0.25 – 0.92 m^2 ha^{-1} yr^{-1}) (Lieberman *et al.* 1990, Nebel *et al.* 2001b, Lewis *et al.* 2004). While several factors may be responsible for this variation in growth rates, we considered that climatic, edaphic and disturbance factors have an important role in explaining this variation.

Climatic effects on growth rates

In general, our study supports the hypothesis that growth rates increase with water availability (Table 2, Fig. 2a). In lowland Bolivia, the lowest annual growth rate at tree level occurred at the drier end of the rainfall gradient (Fig. 2a, Appendix 2), and these dry forest values are in line with studies on tropical dry forests (Swaine *et al.* 1990, Uslar *et al.* 2004). Tropical dry forests are likely to have lower annual growth rates than moist forests due to their shorter growing period occasioned by lower rainfall (Murphy & Lugo 1986, Condit *et al.* 2004). In addition, studies focusing on temporal variation in rainfall have shown that lower annual rainfall or a more intense drought period decrease growth rates and affect forest dynamics (Condit *et al.* 1995, Williamson *et al.* 2000, Nath *et al.* 2006). This also has been clearly demonstrated by experiments in mature old-growth Amazonian forests (Nepstad *et al.* 2002). Water availability thus influences tree growth rates, particularly in seasonal forests, where it determines both the inter- and intra-annual growth patterns (Baker *et al.* 2003b, Vieira *et al.* 2004).

While research on growth rates related to temporal variation (Swaine *et al.* 1987, Manokaran & Kochummen 1987, Felfili 1995) and at species level (Finegan *et al.* 1999, Clark *et al.* 2003) has received considerable attention, spatial patterns in growth rates among forests with different rainfall patterns have been less investigated (Condit *et al.* 2004, Viera *et al.* 2004, Dauber *et al.* 2005). In addition, much research on tropical forest dynamics has focused on moist forests rather than on dry forests (e.g. Swaine *et al.* 1990, Bullock 1997, Uslar *et al.* 2004, Nath *et al.* 2006). While basal area growth was positively correlated with rainfall, some lower values in drier and moister forests were found as well (Fig. 2b). The lower growth values in these forests could be due to lower stem density or to a high abundance of slow-growing species. Differences in species composition and successional status among the plots might be a relevant factor to explain these findings (Condit *et al.* 2004).

The positive basal area growth, given that basal area can be directly translated into biomass (Phillips *et al.* 1998, Chave *et al.* 2001), agrees with the general finding that biomass has increased in tropical forests of South America (Phillips *et al.* 1998, Baker *et al.* 2004, Laurance *et al.* 2004, Lewis *et al.* 2004). In contrast, Costa Rican forests showed decreasing growth rates at species level (Clark *et al.* 2003) and at stand level (Feeley *et al.* 2007). In addition to rainfall effects, we also found positive and significant effects of temperature on all growth rates (Table 2). In La Selva forest, Clark and co-workers (2003) studied annual diameter increment of six species linked to inter-annual temperature during 16 years and found a decreasing growth in drier years. The authors concluded that tropical forest productivity is reduced in warmer years. Feeley *et al.* (2007) used long-term data from 50-ha tree plots located in Panama and Malaysia to examine changes in relative basal area growth rates excluding mortality and recruitment data. They found that growth rates in these two forests had decelerated dramatically, with negative effects of temperature, over the past two decades. Temperature increases over the past several decades have been more pronounced in Southeast Asia and Central America than through much of the Amazon basin, where some regions have actually experienced a net cooling since 1960 (Malhi & Wright 2004). Whether these findings, opposite to our positive growth rates, reflect regional differences in climate change remains to be studied. Differences in rainfall gradient, design and analyses used may be a source, at least partially, of the different findings as well.

Our results highlight the importance of comparisons of forests under a wide range of climatic regimes for documenting the range of growth rates and for understanding responses to environmental variation. Such a comparison deserves attention given that climate change is not only predicted but also is experienced already in some tropical forests (Malhi & Wright 2004, Boisvenue & Running 2006, Phillips *et al.* 2009). The negative effects of predicted increased seasonality, however, may be partly offset by the positive effects of temperature on tree growth. To be able to mitigate adverse impacts of reduced rainfall it is therefore important to determine and to understand the response of trees and forests to potential climate change, through annual and long-term monitoring of ecosystem performance.

Edaphic effects on growth rates

We hypothesized that growth rates would increase with soil fertility, as found in other forests (Swaine *et al.* 1990, Russo *et al.* 2005). Instead, non-significant or weak negative correlations were found between growth rates and individual and composite soil variables (Table 2). This result may be due to the fact that our soil fertility gradient is not large enough to detect strong effects on tree growth. Probably, it might also be due to the confounding effects of water availability. In our study, some plots with highly weathered and nutrient poor soils, and higher growth rates, are found in high rainfall areas. The multiple regression analysis accounted for this confounding effect and showed that soil fertility had positive effects on plant growth (Table 3). While no clear effects of soil fertility were found, positive trends at tree level and negative trends at stand level were observed (Figs. 2c and 2d). Variation in nutrients and water availability can have complex interacting effects on tree growth at spatial and temporal scales. For example, Baker *et al.* (2003a) studied tree diameter growth in semi-deciduous and evergreen forests in Ghana and found that with relatively high soil water availability, growth was higher in semi-deciduous than in evergreen forest. This difference between the two forests was only apparent under sufficient rainfall levels, and was attributed to the higher soil nutrient availability in the semi-deciduous forest. While variation in soil fertility appears to be important for determining variation in the growth rates of some species (Veenendaal *et al.* 1996, Davies *et al.* 2001, Baker *et al.* 2003b), its role in controlling growth patterns at stand-level is smaller than the role of water availability. This warrant future studies using combined analyses of both climate and soil.

Most lowland forest soils have relatively large amounts of N but relatively small amounts of available P (Vitousek & Sanford 1986, Sollins 1998). It is generally assumed that P should limit plant growth in tropical forests but we found surprisingly little relationships between growth, N and P (Table 2). One reason might be that our N and P gradients were not long enough to pick up the growth stimulator effect. Analyses on tropical ecosystems suggest that nutrient limitation might be avoided by the dynamic and fast nutrient cycling (Lathwell & Grove 1986, Vitousek & Sanford 1986). Our results are, therefore, more consistent with the hypothesis that plants in tropical forests may obtain nutrients from the litter fall before they enter to the soils (Scott *et al.* 1992), from the atmosphere (Jordan 1982) or from mycorrhizal fungi (Jordan & Herrera 1981, Onguene & Kuyper 2005).

Consequently, nutrients may also be available for plants from other sources than those that can be suggested by soil analysis alone (Clinebell *et al.* 1995). Correlations are only the first step in understanding causal relations between soil variables and plant growth rates. Fertilization experiments in tropical montane forest show that tree growth increases in response to fertilization, mainly to N and P (Tanner *et al.* 1992, 1998). However, an experimental fertilization study with large trees on nutrient-poor lowland forests found no significant increase in tree growth to fertilization of N and P, probably because montane forests are more nutrient limited than lowland forests (Mirmanto *et al.* 1999). Consequently, more experimental studies on tree growth of lowland forests are required with special emphasis on deficiency of P and other important nutrients (Lathwell & Grove 1986, Sollins 1998).

In general, individual soil variables were negatively related to growth rates with few significant relationships; organic matter (OM) showing the strongest negative correlations with all the growth rates (Table 2). Plots in the drier areas tended to have lower growth rates, at tree and stand level, and higher OM. This may be related to slow rates of litter decomposition under low rainfall (Lugo & Murphy 1986, Swaine *et al.* 1990). More variables (Ca, Mg, K, and N) were negatively and significantly related to growth rate at stand level. We expect here the confounding effect of water availability to play a role as described above. Similarly, no significant correlations between soil nutrient availability and tree growth variation were found in Borneo (Ashton & Hall 1992), Costa Rica (Clark *et al.* 1998) and Brazil (Vieira *et al.* 2004). This Brazilian study showed that Manaus, the site with slowest growth, also had the lowest amount of total base cations, while Rio Branco, the site with relatively fast growth rates, had soils with the lowest OM and cation exchange capacity. Vieira and co-workers suggested that selective logging and extractive management may have affected the differences on growth rates.

Disturbance effects on growth rates

In lowland Bolivia, growth rates increased in logged plots, especially those which had a high logging impact, and decreased with time after logging (Table 3, Figs. 2e and 2f). This is in accordance with our hypothesis that opening up of the canopy enhances light availability and hence photosynthetic carbon gain and tree growth. In tropical ecosystems, logging removes mainly larger trees, thus increasing canopy openness with associated changes in micro-environmental conditions that affect forest growth rates (Bazzaz & Pickett 1980, Lang & Knight 1983). Our analyses show that significantly higher DGR_{avg} occurred in logged plots (0.34 ± 0.12; range 0.13 – 0.70) than in non-logged plots (0.28 ± 0.08; range 0.12 – 0.51; $t = 13.7$ $P = < 0.05$) (Fig. 2a). These results are consistent with higher growth rates in logged versus non-logged plots in Brazilian (Carvalho *et al.* 2004) and Peruvian Amazonian forests (Nebel *et al.* 2001b).

Our average $BAGR_{stand}$ (0.49 ± 0.21 m^2 ha^{-1} yr^{-1}) across the 165 plots was very similar to the average value (0.51 ± 0.04 m^2 ha^{-1} yr^{-1}) found across 50 plots in Amazonian forests (Lewis *et al.* 2004). Both basal area growth rates increased through time. However, the variation in our plots was larger, probably due to the larger environmental gradient considered or due to the logging effects. Plots in logged forests had relatively higher, but not significantly different, $BAGR_{stand}$ (0.51 ± 0.21 $m^2 ha^{-1} yr^{-1}$) than non-logged plots (0.48 ± 0.20 $m^2 ha^{-1} yr^{-1}$). This increasing $BAGR_{stand}$ suggest that recruitment exceeds mortality or just higher growth of the remaining trees. This result can also occur because lower intensity of logging usually leads to lower mortality (Finegan & Camacho 1999, Nebel *et al.* 2001b). These results, however, must be confirmed through long-term research.

The amount of basal area logged (LBA) did not affect $BAGR_{stand}$ because conventional logging intensity in Bolivia usually is low (1 – 3 trees per ha) compared to other countries: in Costa Rica 4 – 15 trees per ha are felled (Finegan *et al.* 1999), in French Guiana ca. 10 trees per ha (Gourlet-Fleury & Houllier 2000), and in Borneo more than 10 trees per ha (Sist *et al.* 2003), and because of the small variation in logging intensity among our plots. Logging creates different clearing sizes which to some extent positively affect growth rates, especially of trees around or next to logged areas. Indeed, our results found a positive and significant relationship between LBA and growth rates at tree level (Table 2). Logging affected mainly the DGR_{avg} and DGR_{50} (Table 3), which emphasizes the effects on the small and suppressed trees that directly benefit from canopy opening that result from logging. In contrast, DGR_{99} was not affected by logging probably because these fast-growing individuals receive high light conditions and/or are already in the forest canopy.

Time after logging (TAL) had negative effects only on growth rate at tree level (Table 3). This result is most likely because the forest canopy closes again with time. Silvicultural experiments in Brazilian Amazon found that the stimulus of logging in growth lasts for only 3 years, as tree growth declined following canopy closure (Silva *et al.* 1995). Similar results were found in plots with silvicultural experiments of increasing logging intensity, in Costa Rica (Finegan & Camacho 1999), Surinam (De Graaf *et al.* 1999), Brazil (Carvalho *et al.* 2004) and in Bolivia (Licona-Vasquez *et al.* 2007, Peña-Claros *et al.* 2008a).

We have found current disturbances as an important source explaining the variation of growth rate, but it is likely that there are others. Field observations found that past logging affected some plots in the Bolivian network, which led to an opening up in the canopy and the establishment of pioneer species. Plots that showed the highest growth rate had also high density of pioneer species. Higher growth rates due to higher abundance of pioneer species have also been reported in Ghana (Hall & Swaine 1981) and Panama (Condit *et al.* 1999). Fast-growing species complete their life cycle more rapidly and they have higher mortality rates, resulting in higher gap formation rates, which in turn creates suitable conditions for the establishment of light-demanding species (Van der Meer *et al.* 1998, Peña-Claros *et al.* 2008b) and competitive lianas (Schnitzer & Bongers 2002). Lowland forests of Bolivia vary considerably in liana density (Pérez-Salicrup *et al.* 2001, Toledo *et al.* 2008); thereby lianas can overtop trees and reduce light availability for tree growth (Putz 1984). It has been demonstrated that trees without lianas have higher growth rates (Licona-Vasquez *et al.* 2007, Peña-Claros *et al.* 2008a, Villegas *et al.* 2009). Thus variation in floristic composition and forest structure, related at some extent with disturbances, can also affect forest growth.

Concluding remarks

Results from this study demonstrated that both environment and disturbance significantly contribute to explain the growth rate variation in Bolivian lowland forests. This variation was most strongly determined by water availability. More rainfall and a shorter and less intense dry period lead to higher growth rates. Soil fertility and soil texture alone, however, did not show clear effects. Probably our soil fertility was not large enough to detect effects on tree growth or nutrients may also be available for plant growth from other sources than soil. In some cases individual variables had stronger relationships with growth than multivariate axes. Individual climatic variables such as temperature, annual precipitation and length of the dry period showed stronger correlations to growth rates than the multivariate climatic axes. Similarly, Mg, CEC and OM were more strongly correlated to growth rates than soil axes. While growth rates increased with logging related disturbances, they decreased with time after logging. The positive stimulus of logging in growth seems to last only a short period following canopy closure, if logging intensity is low. Future decreases in rainfall and increases in temperature due to climate change can also affect growth rates. The negative effects of increased seasonality, however, may be partly offset by the positive effects of temperature on tree growth. Finally, from a forest management perspective, forest managers should take into account the high variation in growth rates occurring in the different lowland forests of Bolivia. Dry forests, for instance, have the lowest growth rates and harvest cycle length and silvicultural treatments needed for these seasonal forests may thus differ from those applied to faster growing rain forests. Based on our results we advocate that management guidelines to be developed are specific to each forest and are in line with its characteristic and conditions.

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Appendix 1. Pearson correlations between tree growth variables in Bolivian lowland forests. n=165 plots * $p \leq 0.05$, ** $p \leq 0.01$. DGR= Diameter growth rate, BAGR = basal area growth rate, avg= average, DGR_{50} = median, DGR_{90} = 90 percentile, DGR_{95} = 95 percentile, DGR_{99} = 99 percentile.

	DGR_{50}	DGR_{90}	DGR_{95}	DGR_{99}	$BAGR_{stand}$
DGR_{avg}	0.88**	0.95**	0.89**	0.65**	0.52**
DGR_{50}		0.74**	0.61**	0.33**	0.41**
DGR_{90}			0.96**	0.66**	0.55**
DGR_{95}				0.78**	0.55**
DGR_{99}					0.44**

Appendix 2. Average and range (minimum – maximum) of growth rates, at tree and stand level, of 165 1-ha plots distributed in lowland Bolivia. Regions are distinguished with different rainfall pattern (mean ± SD) based on the floristic regions (see Chapter 3): WP = Western Pre-andean, NA = Northern Amazon, EA_{BP} = Eastern Amazon-Bajo Paraguá, EA_G = Eastern Amazon-Guarayos, SC = Southern Chiquitano. DGR = Diameter growth rate, BAGR = basal area growth rate, avg= average, DGR_{50} = median, DGR_{99} = 99 percentile.

	Ecoregions				
	WP	NA	EA_{BP}	EA_G	SC
Rainfall (mm)	2075 ±91	1935 ±44	1696 ±37	1472 ±12	1170± 23
DGR_{avg}	0.31 (0.23-0.46)	0.29 (0.13-0.40)	0.41 (0.28-0.70)	0.35 (0.20-0.57)	0.20 (0.12-0.27)
DGR_{50}	0.20 (0.11-0.32)	0.18 (0.09-0.29)	0.27 (0.15-0.59)	0.21 (0.12-0.50)	0.16 (0.07-0.23)
DGR_{99}	1.71 (1.15-2.76)	1.96 (1.09-3.82)	2.14 (1.48-3.23)	2.07 (1.27-3.23)	0.95 (0.63-1.45)
$BAGR_{stand}$	0.47 (0.23-0.99)	0.58 (0.21-1.07)	0.58 (0.17-1.22)	0.49 (0.30-0.81)	0.33 (0.19-0.53)

Chapter 5

Distribution patterns and response curves of tropical woody species to climatic and edaphic gradients

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Marisol Toledo, Lourens Poorter, Marielos Peña-Claros, Alfredo Alarcón, Julio Balcázar José Chuviña, Claudio Leaño, Juan Carlos Licona and Frans Bongers

Abstract

Plant species differ in their tolerance to and requirements of the environment. As a result each species is expected to show an individualistic response to environmental gradients. Ecologists have found different response curve shapes, mostly for temperate species, but data in tropical species responses are surprisingly scarce. Using 220 1-ha permanent plots along tropical lowland forests we examined the relative importance of climatic and edaphic gradients that could affect the distribution patterns and response curve shapes of 100 woody species. We found a positive trend between species abundance and occurrence but some abundant species were also narrow distributed. Species responded differently to each environmental factor and they were more strongly affected by climatic than by edaphic factors. While 91% of the species were affected by climatic factors, only 47% of the species were affected by edaphic factors. While 25 species showed unimodal response curves to the rainfall gradient, and 10 species to temperature, only three species showed such response to soil fertility and none to soil texture. Given that virtually all species were affected by rainfall, and the large climatic changes predicted for the tropics, it is important to quantify and to monitor species distributions in relation to climate. Our results agree with the notion that species response types to environmental gradients will differ among species and among factors considered. Thus, we conclude that multiple, rather than single, environmental factors must be used to explain the species distribution in tropical forests.

Key words: Bolivia, climate, environmental filters, gradients, individualist response, response curve shape, soil, species distribution, tropical lowland forests, unimodal response, woody species.

Introduction

Overlapping plant species distributions determine the high species diversity of tropical forests. The distribution of a species is largely determined by the multidimensional ecological niche space it occupies (MacArthur 1972). The theoretical range that a species may occupy (i.e. the fundamental niche) is often modified by interactions with other species (e.g. competitors, predators or parasites) and restricted by historical factors (e.g. dispersal opportunities, catastrophic events, land configuration) that reduce its fundamental niche to the fraction that is actually occupied - the realized niche (Hutchinson 1959). Thus how species are distributed across spatial scales is affected by several factors, such as climate, soil, disturbances, and biotic interactions. These factors act as environmental filters at different spatial scales, and determine what species from the regional species pool are filtered into the local community (Whittaker 1967, Keddy 1992, ter Steege & Zagt 2002).

One of the general patterns in ecology is that widespread species are more abundant than species of restricted occurence (Brown 1984, Wright 1991, Gaston 1996, Gaston *et al.* 2000). The issue of scale is important because it allows the understanding of how species are spatially distributed (Crawley & Harral 2001). Pitman *et al.* (2001) found that common species at local scale tend to have high frequency and high abundance and thus may constitute species oligarchies consisting of a few species that may dominate vast areas of forest. But where environmental heterogeneity is high, the areas dominated by such predictable oligarchies may be much smaller (Ruokolainen & Tuomisto 1998).

Most of our current insights in species distribution have come from studying species-habitat associations at small local scales (Newbery & Proctor 1984, He *et al.* 1997, Harms *et al.* 2001, Baltzer *et al.* 2005). However, most of the climatic and geological variation in the tropics occurs at regional scales (> 1000 km^2). Quantitative data of species distributions at this scale in relation to climate (McKenzie *et al.* 2003, Killeen *et al.* 2006) and soils (Tuomisto *et al.* 2003, Phillips *et al.* 2003) are scarce and studies considering the effects of both climate and soils are even scarcer. Such studies show that the occurrence of most species is strongly linked to rainfall, whereas for some species it is related to soil fertility (Swaine 1996, Holmgren & Poorter 2007).

Plant species differ in their tolerance to and requirements of the environment, thus each species shows an individualistic response to environmental gradients (Bongers *et al.* 1999, Duque 2004). Theoretically, plant species should exhibit a unimodal response at some point along a large environmental gradient (Gauch & Whittaker 1972). Indeed, the unimodal curve has been generally accepted as a fundamental response shape to environmental gradients. Species response curves should differ, however, in shape, amplitude, width and optimum (Austin & Smith 1989, Huisman *et al.* 1993, Austin & Gaywood 1994, Jongman *et al.* 1995, Oksanen & Minchin 2002).

Some studies, mostly in temperate regions, have focused on the response of individual species along gradients (Ejrnæs 2000, Lawesson & Oksanen 2002, Oksanen & Minchin 2002, Rydgren *et al.* 2003, McKenzie *et al.* 2003; but see Bongers *et al.* 1999 and Duque 2004 for the tropics). For example, Ejrnæs (2000) found that 53% of temperate species, from grassland vegetation samples located in Denmark, responded to a pH gradient (3.8 – 8.6). The only study in north-west Amazonia found that of the 24 studied tree species nearly all (21) responded to the large soil fertility gradient (Duque 2004). A study on West African species found that eight of 12 tree species responded to annual rainfall and length of dry season but not to cumulative water deficit (Bongers *et al.* 1999). Responses of tropical woody species to seasonal drought are complex because the impact of low rainfall can be mitigated by soil water reserves influenced by topography, soil texture, and soil depth (Itoh *et al.* 2003) and a variety of drought avoidance mechanisms in trees (Nepstad *et al.* 1994, Engelbrecht *et al.* 2007, Poorter & Markesteijn 2007). As a result, many species responses are not well correlated with climate alone (Corlett & LaFrankie 1998). For example, soil drainage was the main factor structuring species distribution in French Guiana (Pélissier *et al.* 2002). Moreover, there is also evidence that soil nutrient availability influences species distribution and community composition (Potts *et al.* 2002, Phillips *et al.* 2003, John *et al.* 2007).

Focusing on plant species distribution patterns along environmental gradients is important for several reasons. First, clarifying these patterns in relation to environmental variation enhances our understanding of the diversity and ecology of tropical forests. Second, by knowing species-environment relationships species can then be used as indicators of environmental conditions (Diekmann 2003). Third, by identifying the ecological niches of plant species we can predict their potential response to climate change (Borchert 1998, McKenzie *et al.* 2003). Finally, for successful ecological restoration and the establishment of plantations a better insight is needed in the environmental requirements of the species (Swaine 1996).

The aim of this study is to evaluate the relative importance of environmental factors determining the plant species distribution in tropical lowland forests. We analyzed the distribution, in terms of frequency and abundance, of 100 woody species over 220 one-hectare forest plots across a large environmental gradient in lowland Bolivia. Specifically we question (1) how species' frequency and abundance are related; (2) how climate and soil affect the distribution of tropical woody species and (3) how species response curves are shaped along climatic and edaphic gradients in tropical lowland forests. To our knowledge this is the largest study so far to address such questions including both climate and soil factors. We have three corresponding hypotheses: First, species frequency and abundance will be positively correlated, thus widespread species will be locally abundant (Gaston 1996, Pitman *et al.* 2001). Second, because of the hierarchy in environmental filters, species will respond stronger to climate than to soil (Swaine 1996, Díaz *et al.* 1998). Third, as our environmental gradients are very long, we hypothesize that the majority of the species will show unimodal response curves to these gradients (Gauch & Whittaker 1972, Huisman *et al.* 1993).

Material and Methods

Study area

For this study a total of 220 1-ha plots were selected from the Network of Permanent Sample Plots in lowland Bolivia. These plots were established in old growth forests by various research projects and forestry concessionaires, before logging activities took place, between 1995 and 2007 (see Acknowledgements for more details). To date this network is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots are located between 10 – 18° S and 59 – 69° W, mostly in upland forests (*terra firme;* only 5% of the plots were found in areas of seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from 100 – 500 masl. Most of the plots were typically square (100 x 100 m), with 11 of them being rectangular (20 x 500 m). The 220 plots cover a wide range in environmental conditions (Table 1).

The Bolivian lowlands are characterized by two climatic gradients: a south-north gradient with *mean* annual precipitation ranging from 1100 to 1900 mm and an east-west gradient ranging from 1600 to 2200 mm. However, the precipitation in individual years can vary from 600 to 3000 mm per year from the driest to wettest areas (based on at least 30 years data, 1970 – 2007, Servicio Nacional de Meteorología e Hidrología – SENAMHI). The lowlands in Bolivia experience a 4 to 7 months long dry season (with precipitation < 100 mm/month), mostly from April to September, corresponding to the austral winter. Mean annual temperature is between 24 and 26°C. Lowland Bolivia is also characterized by differences in geomorphology and geological history (Suárez-Soruco 2000) leading to strong gradients in soil characteristics. The soils vary largely in fertility, from acid Acrisols in the Amazon forest in the north, via Acrisols and Luvisols in the centre, to Cambisols and Arenosols in the south (Gerold 2003).

Environmental data

Species generally do not respond to single environmental variables but to complex gradients consisting of varying environmental variables (Whittaker 1967). Thus, ordination techniques are important for summarizing these environmental variables and their axes are used as substitutes for complex gradients (Rydgren *et al.* 2003). To summarize the environmental data we performed, therefore, two independent Principal Component Analyses (PCAs).

For each plot we obtained five climatic variables, interpolated from available data from 45 weather stations, and 12 edaphic variables obtained from sampled soils in each of the 220 plots. The climatic PCA included annual temperature, annual precipitation, total precipitation of the three driest months, dry period length (# months < 100 mm), and drought period length (# months < 50 mm). The first two axes of the climatic PCA explained 94% of the variation. The first axis (65%) correlated positively with annual precipitation and negatively with dry period length (henceforth referred to as the rainfall axis) (Table 1). The second axis (29%) correlated positively with mean annual temperature and negatively with the precipitation of the driest months (hereafter temperature axis). The edaphic PCA considered Cation Exchange Capacity (CEC), cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), Phosphorous (P), Organic Matter (OM), Nitrogen (N), acidity, and percentage of particles content (sand, silt and clay). The first two axes of the edaphic PCA explained 68% of the variation. The first axis (48%) correlated positively with variables related with soil fertility (CEC, Ca, Mg, Na, K, P, OM, and N), and negatively with acidity (hereafter soil fertility axis). The second axis (20%) represented variation in soil texture and correlated positively with clay and silt and negatively with sand (hereafter soil texture axis) (Table 1, see details on Chapter 2).

Table 1. Mean and range (minimum and maximum) of climate and soil variables of lowland Bolivian forest plots and their correlations (Pearson) with the environmental PCA axes. n=220 * $P \leq 0.05$, ** $P \leq 0.01$. CEC = Cation Exchange Capacity, OM = organic matter.

Variables	Mean	Range	Environmental factors			
			Climatic PCA		Edaphic PCA	
			Rainfall	Temperature	Fertility	Texture
Climate						
Annual precipitation (mm)	1592	1113 - 2198	0.93**	0.26**	-0.35**	0.49**
Driest months (mm)	100	68 - 262	0.74**	-0.63**	0.33**	0.31**
Dry period (< 100 mm)	5.6	4 - 7	-0.95**	-0.24**	0.31**	-0.45**
Drought period (< 50 mm)	2.8	0 - 4	-0.81**	0.54**	-0.16*	-0.45**
Annual temperature (°C)	25.3	24.2 - 26.4	0.55**	0.78**	-0.57**	0.36**
Soil fertility						
Ca^{2+} (cmol kg^{-1})	3.25	0.2 - 13.8	-0.26**	-0.52**	0.91**	-0.22**
Mg^{2+} (cmol kg^{-1})	1.35	0.1 - 7	-0.10	-0.49**	0.73**	0.04
Na^{+} (cmol kg^{-1})	0.08	0.03 - 0.19	0.05	-0.58**	0.83**	0.08
K^{+} (cmol kg^{-1})	0.27	0.05 - 0.79	-0.18**	-0.59**	0.84**	0.08
CEC (cmol kg^{-1})	5.8	1.5 - 20.1	-0.11*	-0.50**	0.92**	0.06
Acidity (cmol kg^{-1})	0.9	0 - 6.1	0.41**	0.46**	-0.52**	0.61**
P (cmol kg^{-1})	5.5	1 - 51	0.13*	-0.39**	0.63**	-0.11*
OM (%)	2.7	0.9 - 5.2	-0.46**	-0.43**	0.69**	-0.09
N (%)	0.2	0.05 - 0.4	-0.45**	-0.41**	0.78**	-0.20**
Soil texture						
Sand (%)	56.3	2 - 83	-0.42**	0.19**	-0.33**	-0.93**
Silt (%)	22.5	3 - 68	0.39**	-0.41**	0.50**	0.61**
Clay (%)	21.2	6 - 50	0.24**	0.17*	-0.03	0.82**

Recording of species

We selected 100 species that were reliably identified in each plot (Table 2) and that occurred in at least 11 of the 220 plots (i.e. 5% of the total). To explore species distribution across the 220 permanent plots we considered two variables: the occurrence (based on presence-absence in the plot) and the abundance (the number of stems ≥ 10 cm diameter at breast height, DBH measured at 130 cm height or higher height when buttresses were present) in each plot.

Data analysis

For each species the relative frequency (the percentage of 220 plots where a species occurs) and the average abundance (the average density of stems per ha of a species in the plots in which it occurs) were calculated and are given in Table 2. We distinguished four types of distribution patterns based on the relative frequency (low/high) and the average abundance (low/high). These groups were defined using the average of $\log_{10}$ transformed variables as class breaks.

Species distribution models may use data on presence-only, presence-absence or abundance (Guisan *et al.* 2007). In this study, presence-absence data over abundance was preferred because variation in the abundance data can be caused by a wide range of processes (competition), species traits (ecological guild, dispersion type) or sampling effects (plot position). Thus, we constructed species response curves for each species against each of the four environmental gradients using logistic regression analysis on the presence-absence data. The power of logistic regression lies in the simultaneous analysis of the effect of several environmental variables (ter Braak & Looman 1986). We built a logistic model for each species by including the four environmental axes from the PCA analyses, their quadratic terms and products as predictor variables, using the forward likelihood ratio method (Field 2000). The model with the highest Nagelkerke R^2 was considered the best model from a statistical point of view. We present results from models excluding the interaction terms as for most of the species (85%) the interactions did not improve the final models (results not shown). The partial variation explained from the logistic regression analysis by each of the four environmental factors was calculated as the increase in variation when that variable was included in the model. In case that both a simple and squared variable were included in the model (e.g., rainfall axis and its quadratic term), then their individual explained variances were summed to calculate the total amount of explained variance by that environmental factor. We used the area under the curve (AUC) of a receiver operating characteristic (ROC) to measure the overall model accuracy (Pearce & Ferrier 2000). AUC values were interpreted on the scale proposed by Swets (1988): good = AUC > 0.9, useful = 0.9 > AUC > 0.7 and poor = AUC < 0.7. In general, the model performance was very good; 95 species obtained the AUC > 0.7. All the statistical analyses were done using SPSS version 15.0 for Windows.

Results

Frequency, abundance and species distribution patterns

On average the species occurred in 24% of the plots (range 5 – 86%). Most of the 100 studied species had relatively a low frequency, 97 species were present in less than 50% of the plots (Table 2). Only three species, *Sweetia fruticosa* (in 86% of the plots), *Pseudolmedia laevis* (74%) and *Casearia gossypiosperma* (60%) occurred in more than half of the plots. Average density of the species, in the plots where they occurred, ranged from 1.3 – 106 ind/ha. *Acosmium cardenassi,* the most abundant species (106 ind/ha), was found in only 26% of the plots while *P. laevis,* the second most abundant species (44 ind/ha), was found in 74% of the plots.

More common species also had higher abundance, but the relation was weak (Pearson's r = 0.31, $P < 0.001$). We determined four groups of species distribution patterns based on combinations of frequency and abundance. The four groups had different numbers of species; group I (low abundance and low frequency) had 28 species, group II (low frequency and high abundance) had 16 species, group III (high abundance and high frequency) has 31 species and group IV (high frequency and low abundance) had 25 species (Fig. 1).

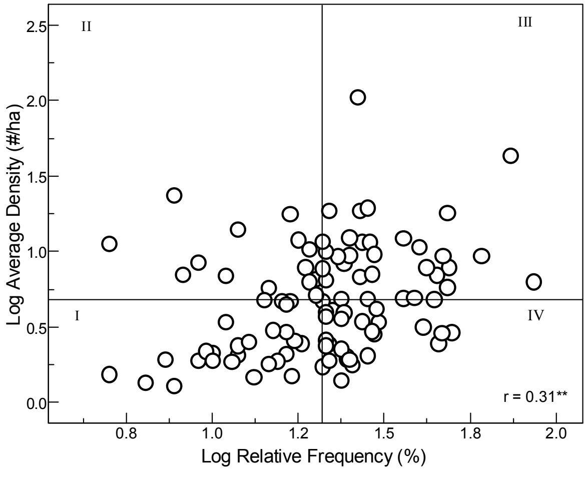

Figure 1. Four types of distribution patterns of 100 species studied across 220 1-ha permanent plots in lowland Bolivia. The four groups are based on the frequency - abundance (log transformed data) of each species and defined using the average (gray line) of each parameter: I = low frequent/low abundant species (n=28); II = low frequent/high abundant (n=16); III = high frequent/high abundant (n=31) and IV = high frequent/low abundant (n=25). See Table 2 for identity of plant species.

Table 2. Distribution data and environmental factor effects on 100 woody species across lowland Bolivia. Relative frequency (Rel. Freq. in %) is based on the occurrence of each species in 220 1-ha plots. Density (mean ± SD) is based on the stem abundance per ha of a species in the plots in which it occurs. Each species belongs to one of four distribution groups based on the frequency-abundance relationship (see Fig. 1). Environmental factors (summarized as PCA axes) are rainfall (R), temperature (T), soil fertility (F) and soil texture (Tx). Total variation (R^2) explained by the logistic models and the shape of the response curve to each factor (1 = no response, 2 = increasing, 3 = decreasing, 4 = unimodal) are given. The list is alphabetically ordered by scientific name of the plant species.

No.	Scientific name	Family	Rel.	Density		Group	PCA		Curve shape			
			Freq.	(ind/ha)	SD		Axes	R^2	R	T	F	Tx
1	*Acosmium cardenassi*	Fabaceae	26	106.3	74.3	III	R	1.00	3	1	1	1
2	*Amburana cearensis*	Fabaceae	19	7.9	8.9	II	R,T,F	0.80	3	4	3	1
3	*Ampelocera ruizii*	Ulmaceae	40	10.8	10.6	III	R,T,F,Tx	0.72	4	3	2	3
4	*Anacardium occidentale*	Anacardiaceae	8	1.3	0.6	I	T,F,Tx	0.57	1	3	3	2
5	*Anadenanthera colubrina*	Mimosaceae	27	18.8	15.5	III	R	0.99	3	1	1	1
6	*Apuleia leiocarpa*	Caesalpinaceae	30	2.8	2.0	IV	R,T,F,Tx	0.73	2	2	4	3
7	*Aspidosperma cylindrocarpon*	Apocynaceae	49	7.9	12.5	III	R,T,Tx	0.68	3	2	1	3
8	*Astrocarium aculeatum*	Arecaceae	24	8.4	18.7	III	R,T,Tx	0.53	2	2	1	3
9	*Astronium fraxinifolium*	Anacardiaceae	8	7.1	4.5	II	T,Tx	0.36	1	2	1	3
10	*Astronium lecontei*	Anacardiaceae	18	2.5	1.7	I	R,T,F	0.60	2	2	3	1
11	*Astronium urundeuva*	Anacardiaceae	15	5.8	6.7	II	R,T	0.72	3	2	1	1
12	*Attalea phalerata*	Arecaceae	28	4.9	9.7	III	R,T	0.51	4	3	1	1
13	*Bellucia grossularioides*	Melastomataceae	12	2.1	2.1	I	T	0.12	1	2	1	1
14	*Bertholletia excelsa*	Lecythidaceae	17	2.6	1.7	I	T,F,Tx	0.67	1	2	3	2
15	*Caesalpinia pluviosa*	Caesalpinaceae	28	19.5	17.9	III	R,Tx	0.82	3	1	1	3
16	*Capirona decorticans*	Rubiaceae	27	6.8	7.4	III	R,F	0.71	2	1	3	1
17	*Capparis prisca*	Capparidaceae	9	8.5	12.3	II	R	0.41	2	1	1	1
18	*Cariniana domestica*	Lecythidaceae	10	2.1	3.0	I	R	0.22	4	1	1	1
19	*Cariniana estrellensis*	Lecythidaceae	21	1.7	1.2	I	R,F,Tx	0.46	4	1	2	3
20	*Cariniana ianeirensis*	Lecythidaceae	22	4.1	3.7	IV	R,T,F,Tx	0.69	2	4	2	3
21	*Cariniana micrantha*	Lecythidaceae	7	1.9	1.0	I	R,T	0.77	2	2	1	1
22	*Casearia gossypiosperma*	Flacourtiaceae	60	9.4	13.0	III	R,F,Tx	0.41	3	1	3	3
23	*Castilla ulei*	Moraceae	9	1.9	0.9	I	R,T,F	0.62	2	2	3	1
24	*Cavanillesia hylogeiton*	Bombacaceae	17	1.5	0.7	I	R,F	0.17	4	1	2	1
25	*Cecropia concolor*	Cecropiaceae	16	2.1	2.6	I	R,T,F	0.50	4	3	2	1
26	*Cecropia membranacea*	Cecropiaceae	17	4.7	8.3	I	R,T,F,Tx	0.51	2	2	2	3
27	*Cedrela fissilis*	Meliaceae	25	1.9	2.0	IV	R,Tx	0.13	3	1	1	3
28	*Cedrela odorata*	Meliaceae	15	1.9	1.1	I	R,T	0.52	2	2	1	1
29	*Cedrelinga catenaeformis*	Mimosaceae	10	2.2	1.4	I	T	0.55	1	2	1	1
30	*Ceiba pentandra*	Bombacaceae	25	1.8	0.9	IV	R,T	0.27	2	2	1	1
31	*Celtis schipii*	Ulmaceae	29	7.1	8.3	III	R,T,F,Tx	0.79	2	4	3	3
32	*Centrolobium microchaete*	Fabaceae	18	12.0	14.1	II	R,T	0.82	3	3	1	1
33	*Chorisia speciosa*	Bombacaceae	45	7.0	7.0	III	R,T,Tx	0.51	3	2	1	3
34	*Combretum leprosum*	Combretaceae	14	4.8	5.2	I	R,T,Tx	0.36	3	3	1	3
35	*Copaifera chodatiana*	Caesalpinaceae	21	4.7	4.7	I	R	0.83	3	1	1	1
36	*Cordia alliodora*	Boraginaceae	50	2.9	2.3	IV	R,T	0.13	3	3	1	1
37	*Couratari macrosperma*	Lecythidaceae	12	2.4	1.1	I	R,T,F,Tx	0.55	2	4	3	2
38	*Dendropanax arboreus*	Araliaceae	36	4.9	4.0	III	R,F,Tx	0.70	2	1	2	3
39	*Dialium guianense*	Caesalpinaceae	16	4.7	5.7	I	R,T,F,Tx	0.70	2	4	3	2
40	*Didymopanax morototoni*	Araliaceae	27	3.5	3.0	IV	R,T,Tx	0.40	2	2	1	3
41	*Erisma uncinatum*	Vochysiaceae	20	6.6	6.4	II	R,T	0.82	4	4	1	1
42	*Euterpe precatoria*	Arecaceae	48	18.2	20.5	III	R	0.95	2	1	1	1
43	*Galipea jazminiflora*	Rutaceae	11	6.9	5.0	II	R,T	0.60	2	4	1	1
44	*Gallesia integrifolia*	Phytolaccaceae	24	4.9	5.9	III	R,T,F,Tx	0.54	2	4	2	3

Table 2. Continued

No.	Scientific name	Family	Rel.	Density		Group	PCA Axes		Curve shape			
			Freq.	(ind/ha)	SD			R^2	R	T	F	Tx
45	*Guazuma ulmifolia*	Sterculiaceae	25	2.0	1.4	IV	R,T,F,Tx	0.53	2	2	2	3
46	*Hevea brasiliensis*	Euphorbiaceae	16	4.5	4.0	I	R,T,F	0.74	4	3	2	1
47	*Himatanthus sucuuba*	Apocynaceae	10	1.9	1.5	I	R,T,F	0.57	4	3	2	1
48	*Hura crepitans*	Euphorbiaceae	25	9.5	5.6	III	R,T	0.80	4	3	1	1
49	*Hymenaea courbaril*	Caesalpinaceae	24	1.4	0.7	IV	R,F	0.13	3	1	3	1
50	*Hymenaea parvifolia*	Caesalpinaceae	11	1.9	1.5	I	F	0.30	1	1	3	1
51	*Iriartea deltoidea*	Arecaceae	17	17.8	36.8	II	R,F	0.62	2	1	3	1
52	*Jacaranda copaia*	Bignoniaceae	22	2.5	2.2	IV	R,T,F,Tx	0.68	4	4	3	2
53	*Jacaratia spinosa*	Caricaceae	30	3.4	4.1	IV	R,T,F,Tx	0.58	2	2	2	3
54	*Licaria triandra*	Lauraceae	23	9.3	8.9	III	R,T	0.97	3	3	1	1
55	*Luehea paniculata*	Tiliaceae	21	2.6	3.3	IV	T,F,Tx	0.22	1	3	3	3
56	*Machaerium acutifolium*	Fabaceae	27	11.6	12.5	III	R,F	0.83	3	1	3	1
57	*Machaerium scleroxylon*	Fabaceae	21	6.5	7.4	III	R,T	0.86	3	2	1	1
58	*Maclura tinctoria*	Moraceae	13	1.5	0.8	I	R,T	0.44	4	2	1	1
59	*Metrodorea flavida*	Rutaceae	21	10.1	11.4	III	R,T	0.48	2	2	1	1
60	*Neea hermaphrodita*	Nyctaginaceae	47	9.4	11.2	III	R,T	0.73	3	3	1	1
61	*Ocotea guianensis*	Lauraceae	30	4.2	3.6	IV	R,T,F	0.73	4	3	3	1
62	*Oenocarpus bataua*	Arecaceae	19	6.3	10.1	II	R,T,F,Tx	0.78	2	2	3	2
63	*Pausandra trianae*	Euphorbiaceae	39	5.0	6.1	III	R,T	0.49	4	3	1	1
64	*Peltogyne heterophylla*	Caesalpinaceae	5	11.4	4.4	II	R,T	0.89	2	2	1	1
65	*Peschiera arcuata*	Apocynaceae	28	2.0	1.5	IV	R,T	0.29	4	3	1	1
66	*Phyllostylon rhamnoides*	Ulmaceae	25	12.4	26.4	III	R	0.27	3	1	1	1
67	*Poulsenia armata*	Moraceae	8	23.7	29.9	II	R,T	0.86	4	2	1	1
68	*Pourouma cecropiifolia*	Cecropiaceae	36	12.3	16.6	III	R,T,F,Tx	0.53	4	3	3	3
69	*Pouteria lucuma*	Sapotaceae	48	5.8	6.2	III	R,F,Tx	0.66	2	1	2	3
70	*Pouteria nemorosa*	Sapotaceae	44	4.8	3.3	III	R,T,F,Tx	0.80	4	3	3	2
71	*Pseudolmedia laevigata*	Moraceae	22	18.7	31.8	III	R,T,Tx	0.62	2	2	1	3
72	*Pseudolmedia laevis*	Moraceae	74	43.6	47.8	III	R	1.00	2	1	1	1
73	*Pseudolmedia macrophylla*	Moraceae	16	2.9	2.5	I	R,T	0.59	2	2	1	1
74	*Psidium sartorianum*	Myrtaceae	41	3.2	4.0	IV	R,T,Tx	0.31	3	3	1	3
75	*Pterogyne nitens*	Caesalpinaceae	6	1.4	0.7	I	R	0.10	3	1	1	1
76	*Qualea paraensis*	Vochysiaceae	21	7.7	9.5	II	R,T,F,Tx	0.64	2	2	4	3
77	*Quiina florida*	Quiinaceae	21	4.0	9.3	IV	R,T,Tx	0.39	4	3	1	3
78	*Sapindus saponaria*	Sapindaceae	21	3.7	2.6	IV	R,T	0.87	4	3	1	1
79	*Schinopsis brasiliensis*	Anacardiaceae	13	2.5	2.7	I	R,T	0.67	3	3	1	1
80	*Schizolobium parahyba*	Caesalpinaceae	24	2.3	1.7	IV	R,F,Tx	0.23	2	1	2	3
81	*Simarouba amara*	Simaroubaceae	24	3.9	4.1	IV	R,T,F,Tx	0.51	2	3	2	3
82	*Siparuna decipiens*	Monimiaceae	21	11.7	10.3	II	R,T,F,Tx	0.92	2	2	3	2
83	*Socratea exorrhiza*	Arecaceae	29	11.6	16.9	III	R,T,F	0.54	2	2	3	1
84	*Spondias mombin*	Anacardiaceae	45	2.5	2.1	IV	T,F	0.36	1	3	2	1
85	*Sterculia apetala*	Sterculiaceae	25	1.9	1.3	IV	R,T	0.39	2	2	1	1
86	*Swartzia jorori*	Fabaceae	21	2.4	2.2	IV	R,T,Tx	0.51	4	3	1	3
87	*Sweetia fruticosa*	Fabaceae	86	6.3	7.5	III	R	0.21	3	1	1	1
88	*Swietenia macrophylla*	Meliaceae	15	1.8	1.3	I	R,F,Tx	0.20	2	1	2	3
89	*Syagrus sancona*	Arecaceae	22	1.9	1.4	IV	R,T,F	0.55	4	3	2	1
90	*Tabebuia impetiginosa*	Bignoniaceae	20	5.2	6.9	II	R,T,F	0.34	3	2	3	1
91	*Tabebuia serratifolia*	Bignoniaceae	46	2.9	2.7	IV	R,F	0.20	3	1	3	1
92	*Tachigali paniculata*	Caesalpinaceae	19	10.4	9.1	II	R,T	0.92	4	3	1	1
93	*Terminalia amazonica*	Combretaceae	24	3.6	4.0	IV	R,T,Tx	0.46	2	2	1	3
94	*Terminalia oblonga*	Combretaceae	42	7.9	7.0	III	R,T	0.83	4	3	1	1
95	*Trema micrantha*	Ulmaceae	15	3.0	3.3	I	R,T,Tx	0.36	4	3	1	2
96	*Trichilia pallida*	Meliaceae	12	14.2	13.8	II	T,F,Tx	0.53	1	2	4	3
97	*Triplaris americana*	Polygonaceae	11	3.4	3.8	I	R,F,Tx	0.45	2	1	2	3
98	*Urera baccifera*	Urticaceae	30	9.6	9.0	III	R,T,F,Tx	0.77	2	4	2	3
99	*Vitex cymosa*	Verbenaceae	5	1.5	1.0	I	R,T	0.32	2	2	1	1
100	*Zanthoxylum sprucei*	Rutaceae	29	3.0	3.0	IV	R,F,Tx	0.28	3	1	3	3

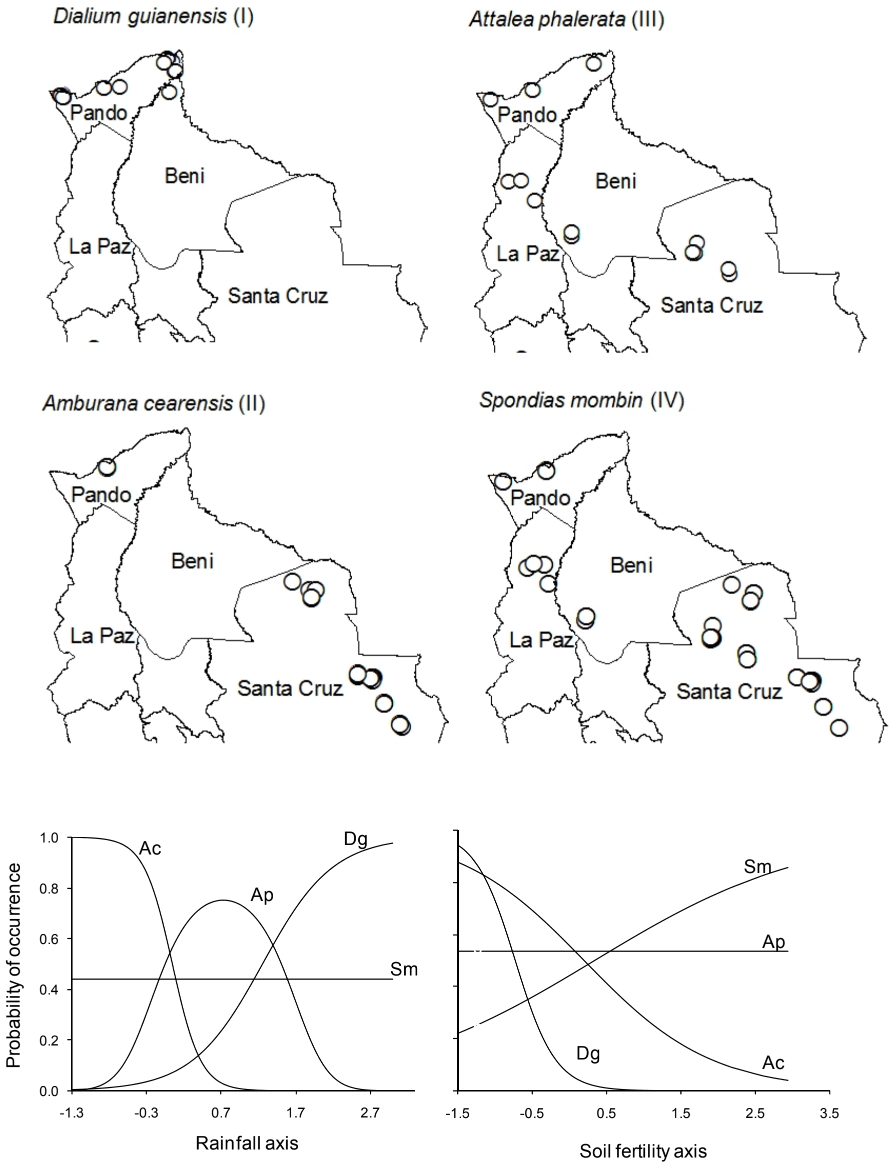

Figure 2. Selected woody species as examples of the four distribution patterns (I = low frequent/low abundant, II = low frequent/high abundant, III = high frequent/high abundant, and IV = high frequent/low abundant) based on frequency-abundance relationship and their response curves in relation to rainfall and soil fertility gradients (as summarized by the PCA axes) in lowland Bolivia. Dot in the map is the species presence across 220 1-ha permanent plots. Curves give the probability of occurrence from logistic regression for each species (Initials from scientific name).

Examples of species belonging to each of the four groups (Fig. 2) are *Dialium guianense* (group I), a species restricted to the northern Amazonian forests; *Amburana cearensis* (group II), more frequently found in the southern Chiquitano dry forests; *Attalea phalerata* (group III), a widely distributed palm from sub-humid to humid areas; and *Spondias mombin* (group IV), a very frequent species from moist to dry areas.

Environmental factors affecting plant species distribution

The logistic regression models predicted the probability of occurrence of a species along the environmental factors studied (Fig. 3). All 100 species were significantly related to at least one of the four environmental factors and the total variation explained by the logistic models ranged between 10 −100% (average ± SD, 0.53 ± 0.23; Table 2). Species occurrence was explained by a single environmental factor (13 species), by a combination of two to three environmental factors (69 species), or by all four factors (18 species). Overall, for 99% of the species, the occurrence was affected by at least one of the climatic factors, but for less than 50% of the species the occurrence was affected by at least one of the edaphic factors. Of the 13 species affected by one environmental factor only *Hymenaea parvifolia* was affected by soil fertility and the other 12 species were affected by climatic factors (Table 2). Rainfall was the most important environmental factor, being significant for 91 of the 100 species studied, followed by temperature (72), soil fertility (47) and soil texture (44). Rainfall was also the environmental factor that explained, on average, most of the variation in species occurrence (30%, Table 3).

Table 3. Number of species with significant response curves and the mean (± SD) and range (minimum and maximum) of the partial variation explained by each of the four environmental factors affecting the occurrence of 100 plant species distributed across lowland Bolivia. The mean is based only on the species that significantly responded to the environmental factors.

Environmental factors	#	Mean	± SD	Range
Rainfall	91	0.30	± 0.26	0.02 – 1.00
Temperature	72	0.20	± 0.18	0.02 – 0.75
Soil fertility	47	0.19	± 0.17	0.02 – 0.58
Soil texture	44	0.10	± 0.06	0.02 – 0.27

Species responses to the environmental gradients

Species showed different response curves to the four environmental factors studied (Fig. 3). In general, we distinguished four responses types: a flat curve (indicating no response), a monotonically decreasing curve, a monotonically increasing curve and a unimodal curve (Table 4). Of the 91 species responding to rainfall, 40 showed an increasing response curve, 26 a decreasing response and 25 had a unimodal response curve. Similarly, of the 73 species that responded to the temperature axis, 34 had an increasing response curve, 29 had a decreasing response and 10 had a unimodal response curve. While more species had an increasing response to climatic factors, more than 50% of the species showed no response to soil factors. Thus of the 48 species responding to soil fertility, 20 showed an increasing response curve, 25 a decreasing response and only 3 had a unimodal response curve. Finally, of the 44 species that responded to the soil texture, 9 had an increasing response curve, 35 had a decreasing response and no species had a unimodal response curve (Table 4). Examples of different species responses are given in Figure 2. *A. phalerata,* shows an unimodal response to rainfall but no response at all to soil fertility; *S. mombin,* shows no response to rainfall and an increasing response to soil fertility. *A. cearensis* and *D. guianensis* showed an opposite response to the rainfall gradient but responded similarly to the soil fertility gradient.

Table 4. Number of Bolivian lowland forest species with specified shapes of response curves, based on occurrence data, to the four environmental factors.

	Response curve shape			
Environmental factors	No response	Increasing	Decreasing	Unimodal
Rainfall	9	40	26	25
Temperature	27	34	29	10
Soil fertility	52	20	25	3
Soil texture	56	9	35	0

Discussion

This study describes the positive relationship between frequency and abundance of 100 woody species and analyzes how climatic and edaphic factors affect their distribution in tropical lowland forests. The distribution patterns, described by the response curves, show that species responded different to each environmental factor and that they were more strongly affected by climatic than by edaphic factors.

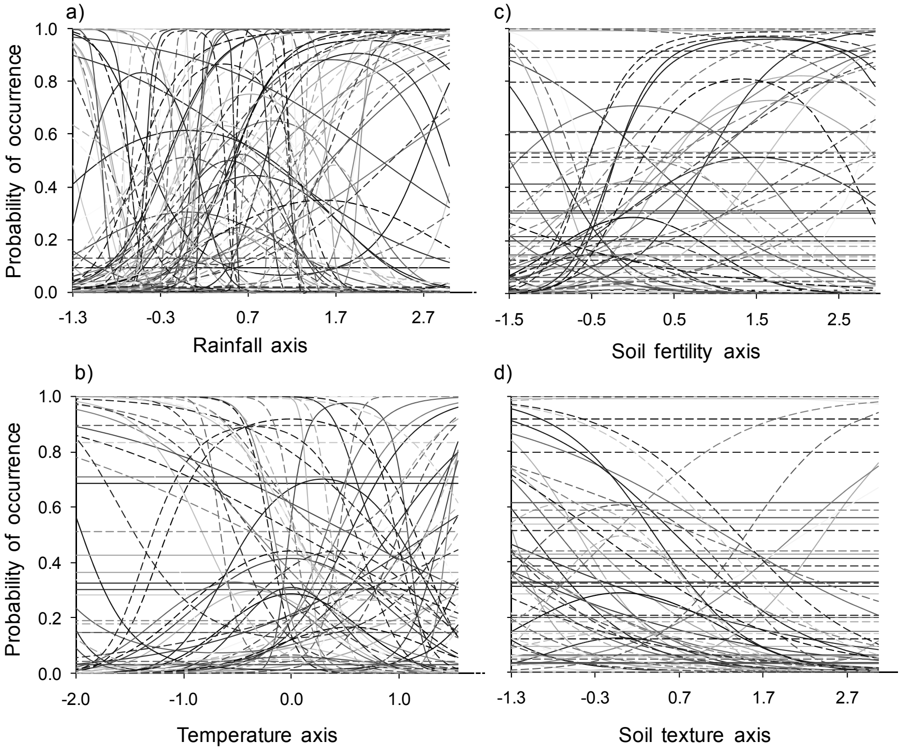

Figure 3. Response curves and probability of occurrence (0 – 1) of 100 tropical plant species in relation to four environmental gradients, as summarized by the four PCA axes: (a) rainfall, (b) temperature, (c) soil fertility and (d) soil texture, across 220 1-ha plots distributed in lowland Bolivia.

Species distribution: frequency-abundance relationship

We found a positive relationship between occurrence and abundance of species (Fig. 1), in line with the first hypothesis. Following Pitman *et al*. (2001), we predicted that widespread species would be locally abundant. Although some species showed this pattern (i.e. *Pseudolmedia laevis*), other species deviated from this general trend (Table 2). *Acosmium cardenasii*, for example, was the most abundant in our study, but had only an intermediate frequency (in 26% of the 220 plots). Similarly, the third most abundant species *Poulsenia armata* (23.7 ind/ha) had a very low frequency (8%). In contrast, the more frequent species, *S. fruticosa* (86%) and *C. gossypiosperma* (60%) were hardly abundant with 6.3 and 9.4 ind/ha, respectively. Because our regional study encompassed longer environmental gradients than the study by Pitman *et al.* (2001) we found different patterns, with some species specializing for specific parts of the environmental gradient, thus combining a high abundance with a low frequency.

In lowland Bolivia, species density per plot was more than 1.3 ± 0.6 ind (Table 2), while in western Amazonian most species showed landscape-scale densities of < 1 ind/ha (Pitman *et al.* 2001). Although our study was based on 100 selected “common” species we realized that these differences are partially a consequence on how average density was obtained. Whereas we considered average of abundance taking into account only plots where each species occurred, other studies on species distribution considered relative abundance (Pitman *et al.* 2001, Phillips *et al.* 2003). Although a higher relationship ($r = 0.70$, $P < 0.001$) was obtained between relative frequency and relative abundance, our species density was lower when relative abundance was considered instead of average abundance. A literature review by Gaston (1996) on the frequency-abundance relationship showed that data sets differed enormously in the scales, sample size and the way in which abundance was measured, thus making comparison sometimes difficult.

Environmental factors affecting the species distribution

Climate was a more important factor than soil in affecting the species distribution in line with the second hypothesis. Whereas over 91 of our species were affected by the climatic factors, only 47 were affected by soil factors (Fig. 3; Tables 2 and 3). Similar results have been obtained by other studies in Africa (Swaine 1996, Holmgren & Poorter 2007). Although several studies have documented the strong relationship of species distribution with water availability, i.e. rainfall and seasonality (Borchert 1998, Bongers *et al.* 1999, McKenzie *et al.* 2003, Killeen *et al.* 2006) these results do not exclude the possibility that edaphic conditions, such as nutrient availability are involved in regulating the distributions of woody species. Indeed, edaphic conditions have been documented as important factors affecting the species distribution, especially at smaller spatial scales (Newbery & Proctor 1984, ter Steege *et al.* 1993, Sollins 1998, Clark *et al.* 1998, 1999, Harms *et al.* 2001, Tuomisto *et al.* 2003, John *et al.* 2007). However, these studies considered only one factor, and those studies that do evaluate both climatic and edaphic factors (Swaine 1996, Holmgren & Poorter 2007) found that species distributions are more related to climatic than soil characteristics.

In terms of number of species responding to environmental factors the factors rank in importance as rainfall > temperature > soil fertility > soil texture. In mountain forests, conifer species distributions were also more frequently (79%) related to climatic variables than to other biophysical variables (40 – 50%) (McKenzie *et al.* 2003) Similarly, 73% of rare and endemic plant species studied in Western African forests was related to rainfall and only 11% of the species was related to available cations (Holmgren & Poorter 2007). In addition, at a 573-ha landscape on La Selva Biological Station, Costa Rica, only 30% of the species were significantly associated to certain habitat types characterized by edaphic differences (Clark *et al.*1999). Given that virtually all species are affected by rainfall, and the large climatic changes predicted for the tropics (Borchert 1998, Malhi & Wright 2004, IPCC 2007), it is important to quantify and to monitor species distributions in relation to climate.

Experimental studies in the shadehouse (Poorter & Markesteijn 2007) and the field (Engelbrecht *et al.* 2007, Brenes-Arguedas *et al.* 2009) also conclude that seasonal drought has a stronger effect on growth and survival over other factors. Plant water availability and drought sensitivity are therefore important determinants in the distribution of tropical species. However, as most of the woody species (87%) were significantly affected by more than one environmental factor (Table 2), we consider that multiple, rather than single, environmental factors must be used to explain the species distribution in tropical forests (cf. Swaine 1996).

Shapes of the species response curves

While unimodal response curves were relatively frequent (25% of the species) along the rainfall gradient they were rarely found for the edaphic factors, with only three species having this response to soil fertility and none to soil texture (Fig. 3, Table 4). Our hypothesis that most of the plant species would have unimodal responses to the large gradients studied is, therefore, rejected. Theoretically, plant species should exhibit a unimodal response when large environmental gradients are considered (Gauch & Whittaker 1972, Austin & Smith 1989, Oksanen & Minchin 2002).

The only two studies on species response curves in tropical forests obtained contrasting results. In West Africa, for example, only one of 12 species showed a unimodal response curve to the cumulative water deficit, indicating that the main factors explaining their distribution should be found outside water availability (Bongers *et al.* 1999). In contrast, 10 of 24 species showed unimodal responses to soil fertility gradient in northwestern Amazonia (Duque 2004). Comparison of cations concentrations and the soil fertility index, expressed by the PCA scores (from -6 to + 3), show that the soil gradient in NW Amazonia was longer than ours (PCA scores from -1.5 to + 3), which may explain the differences in unimodal responses. These results confirm that our sampled climatic gradient was larger than the edaphic one. In addition, we found 11 species with a truncated unimodal response to the rainfall gradient, suggesting that a larger gradient for both dry and wet extreme would be needed to increase the number of unimodal responses. On the other hand, soils in tropical lowland forest are very heterogeneous, and they are spatially distributed in a patchy system reflecting a mosaic instead of a gradient (Sollins 1998, John *et al.* 2007), suggesting that more areas may need to be sampled for getting all the soil variation.

Even though we sampled large environmental gradients a considerable proportion of species (62%) showed non-unimodal responses, indicating that the probability of occurrence of these species increased or decreased along the sampled gradient, or that the species did not respond at all (Tables 2 and 4, Fig. 3). Such response patterns of vascular plants, increasing, decreasing and non-response, were also found along environmental gradients in temperate forests (Ejrnæs 2000, Oksanen & Minchin 2002, Lawesson & Oksanen 2002, McKenzie *et al.* 2003). Increasing and decreasing responses are likely caused by an incomplete gradient sampled or by species of which their optima fall outside the sampled portion of the gradient (ter Braak & Looman 1986, Jongman *et al.* 1995, Rydgren *et al.* 2003).

We found lack of species responses to the environmental gradients mostly for edaphic factors (around 50% of the species). Thus, it is also probable that some of the selected species are soil generalists growing in any soil conditions or that within the plots the soil heterogeneity was very high. Other studies considering wide environmental conditions also obtained some species with no response to edaphic conditions (Ejrnæs 2000, Duque 2004). It is also possible that woody species respond at specific environmental factor or that other factor determine the response curve shapes (Grime 1979, Austin & Gaywood 1994, Duque 2004). In summary, although most of our species were affected by climate and half of the species by soil conditions, we found that each plant species might have different response curves to the different environmental factors considered (Table 2). Thus, our results agree with the notion (Huisman *et al*. 1993, Bongers *et al*. 1999, Oksanen & Minchin 2002) that species response types to environmental gradients will differ among species and among factors considered.

While for most of the species (65%), climatic and soil conditions could explain most of the variation in occurrence ($R^2 > 0.50$), other factors, such as disturbance, may be of high importance in explaining species distribution patterns (Clark *et al*. 1999, Holmgren & Poorter 2007). In lowland Bolivia around 50% of the selected woody species are partially or totally light demanding (Mostacedo *et al*. 2001, Justiniano *et al*. 2004). These species, belonging to typical pioneer genera such as *Astronium, Cecropia, Cedrela, Cedrelinga, Ceiba, Jacaratia, Jacaranda, Pourouma, Swietenia, Tabebuia, Trema, Urera,* and *Zanthoxylum*, are common and abundant to some extent due to the past logging activities that occurred in these forests.

Concluding remarks

The positive abundance-occurrence relationship in species distribution is common in nature, but a large gradient allowed to find different species distribution patterns. For example, abundant species would be widespread or of restricted distribution. This study indicates that most of the species had an increasing response to climatic factors whereas half of the species showed no response to soil factors. Our results suggest that larger gradients, for both rainfall and soil fertility, may be needed to find a higher number of unimodal responses. Specifically, distribution of most species was strongly linked to rainfall whereas for some species it was related to soil fertility. Thus this study supports the notion that species responses to environmental gradients are different among species and among factors considered. In summary, multiple, rather than single, environmental factors must be used to explain the species distribution in tropical forests. Results from this study showed that virtually all species were affected by rainfall seasonality. Consequently, given the large climatic changes predicted for the tropics, efforts to monitor species distribution will be necessary to predict and understand their potential responses to climate changes.

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Chapter 6

Synthesis

Approximately half of the world's tropical forest is in the Neotropics (Gentry 1992). The Neotropics feature an extraordinary display of vegetation types related to both geomorphological complexity and climatic variation (Hueck 1978, Daly & Prance 1988). This variation in vegetation types is especially the case for Bolivia, where three biogeographical regions (Amazonian, Brazilian-Paranaense and Gran Chaco) meet in the lowland areas (Navarro & Maldonado 2002). Although it is widely recognized that Bolivia is one of the world's most important biodiversity spots (Pottes 1991), studies on spatial patterns of plant communities in lowland forests and their underlying factors have started only recently (e. g. Killeen *et al.* 2006).

In this dissertation, I examined the effects of climate and soil on structure, composition, and dynamics of forest ecosystems across lowland Bolivia. In this chapter, I summarize and discuss the main results obtained. Finally, I consider the implications of my results for forest management and the probable effects of climate change on the region.

Effects of climate and soil on plant communities

Data for forest structure, floristic composition and species distribution were obtained from 220 1-ha plots where I recorded and evaluated all stems $\geq$ 10 cm diameter at breast height (DBH at 130 cm height or higher height when buttresses were present). Data for tree growth were obtained from 165 plots, of which 52% of the plots have been selectively logged after plot establishment. For each plot, climatic data were interpolated from available stations and soil samples were collected and analyzed in a soil laboratory in Bolivia. A set of five climatic variables [annual temperature, annual precipitation, total precipitation of the three driest months, length of the dry period (# months < 100 mm), and length of the drought period (# months < 50 mm)] and 12 edaphic variables [cation exchange capacity (CEC), cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), Olsen phosphorous (P), organic matter (OM), nitrogen (N), acidity and percentage of different particles (sand, silt and clay)] were summarized using Principal Component Analyses (PCAs). I used the two main climatic PCA axes (named after the most important factors they represent as rainfall axis and temperature axis) and the two soil PCA axes (named as soil fertility axis and soil texture axis) to reduce the number of highly correlated variables and to have composite variables that summarize the main environmental gradients. Rainfall axis, for example, represents a rainfall seasonality gradient. I used a stepwise selection approach to identify what environmental factors were important and how these factors, climate, soil and disturbance, affected forest attributes. Individual environmental variables were also correlated to forest attributes to evaluate what components of these composite environmental axes were the most important ones.

In this research I evaluated: 1) forest structure, divided into vertical (e. g. height) and horizontal structure (e. g. basal area), and density of life-forms (trees, palms and lianas; 2) floristic composition, based on the abundance of 100 woody species (93 trees and 7 palms); 3) tree growth rates, at individual and at stand level, based on the tree diameter increment and 4) species distribution, based on the occurrence of the 100 selected species and modeled with logistic regression along environmental gradients.

Forest structure

While rainfall affected practically all the forest structural attributes, surprisingly soil texture played a more important role than temperature or soil fertility (Chapter 2, Table 3). Forest height increased with rainfall and the water holding capacity of the soils (e.g. silt content). This result confirms the hypothesis of Ashton & Hall (1992) that canopy height is mostly related to soil water supply. Temperature had negative effects in the emergent layer of trees. Plots located in northern and southern sites with higher annual temperature tended to have a higher percentage of trees in the canopy layer and a lower tree percentage in the sub-canopy layer (Chapter 2, Appendix 3).

Palm density significantly increased with rainfall (cf. Vormisto 2002). The seven palm species included in this dissertation had higher density in humid forests than in dry forests (Chapter 5, Table 2). Although palm occurrence was explained by rainfall, no clear effects of soil fertility were found consequently, palms occurred in both poor and fertile soils (cf. Ruokolainen & Vormisto 2000, Vormisto *et al*. 2004) (Chapter 2, Figs. 5c and 5f).

Research in tropical forests show that lianas are extremely abundant and tend to decrease with rainfall (Putz 1984, Gentry 1991, Pérez-Salicrup *et al*. 2001, Schnitzer 2005, DeWalt *et al*. 2009) but their relationship with soil fertility is still not clear (but see Laurance *et al.* 2001, DeWalt *et al.* 2006). In our study, lianas were more abundant in drier than in moister forests, with a trend to be more abundant on more fertile soils (Chapter 2, Table 3, Fig. 4c). It has been proposed that lianas would have higher densities at low water availability due to their capacity for taking water from deep soils layers (Schnitzer 2005). Liana abundance was indeed higher on coarse soils which have a low water holding capacity (Chapter 2, Figs. 4c and 4f).

In contrast to palms or lianas, the variation of basal area and tree density were not explained by the environmental factors; probably because these structural variables were highly variable among both moist and dry forests (Chapter 2, Table 3, Figs. 4b and 5e). This result can be due to variation in stem density combined with variation in tree thickness as a high basal area can be the result of many slender stems or few thick stems (Bongers *et al.* 1988). Other factors like disturbances (natural e.g. tree fall, wind or fire or anthropogenic e. g. logging) could also have a direct or indirect effect to tree density through changes in the floristic composition (Spies 1998, Richards 1996). For example, several plots with lower tree density and basal area had massive abundance of non-tree species (e.g. *Phenacospermum guianense, Erythrochyton fallax* and *Pausandra trianae*).

Floristic composition

The questions on how and why floristic variation varies across forests in lowland Bolivia were addressed in Chapter 3. I have shown that species composition is not evenly distributed over Bolivia and also that clear floristic regions with important ecological correlates can be identified. These floristic regions were strongly determined by rainfall and temperature and at a lesser degree by soil fertility (Chapter 3, Table 3). Rainfall seasonality increased from north to south with the consequence that floristic similarity of forests decreased from the northern Amazon to the southern Chiquitano region (Chapter 3, Fig. 2a, Table 2). The rainfall gradient thus was linked to a gradual change from wet evergreen forests to dry deciduous forests, as has been found for other tropical forests (Swaine 1996, Bongers *et al.* 2004). As there is generally a strong positive relation between annual rainfall and soil nutrient leaching, particularly in sandy soils (Sánchez 1976, Lathwell & Grove 1986, Baillie 1996), rainfall and soil characteristics tend to strongly covary at regional scales. For example, drier forests have more fertile soils (Hall & Swaine 1981). In lowland Bolivia, however, this is not the case as some plots in moister areas were also fertile due to parent material (e.g. foothills of the Andean mountains) or past anthropogenic activities in the Guarayos region (e.g. *terra preta*) (Chapter 2, Fig. 3a).

Studies considering both factors, i.e. rainfall and soil, have found that either rainfall (Gentry 1988, Clinebell *et al*. 1995, Bongers *et al*. 2004) or soil (ter Steege *et al*. 2006, Réjou-Méchain *et al.* 2008) is the most important factor explaining the floristic composition of a region. Clearly a consensus has not still been reached, probably because the different methods used for sampling soil characteristics and the different sample size. These methodological differences complicate comparisons among studies and may prevent the elucidation of solid patterns. Also, the relative importance of climate and soil in shaping species composition may depend on the part and length of the environmental gradient that has been studied.

Tree growth

Water, nutrients and light are essential resources for growth and their availability vary over spatial and temporal scales. As a result tree growth varies with resource availability (Chapter 4, Table 1; Baker *et al.* 2003b). I found that rainfall and temperature were the most important factor affecting positively the growth rate variables while the soil factors had a much smaller effect (Chapter 4, Tables 2 and 3). In general tree and stand growth rates increased with rainfall (Chapter 4, Figs. 2a and 2b). Effects of temperature may partly be exerted through water relations because rates of evaporation and transpiration are correlated with temperature (Walsh 1996). If there is no water deficiency, higher temperatures stimulate water and nutrient transportation thus contributing to higher growth rates. On the other hand, an indirect consequence of high annual rainfall is that solar radiation tends to decline with increased cloudiness. This can lead to reduced rates of photosynthesis, transpiration and evaporation (Walsh 1996, Lambers *et al.* 2006). These environmental conditions probably can explain why humid regions had intermediate growth rates.

Most terrestrial plants absorb the nutrients required for growth predominantly from the soil (Lambers *et al.* 2006). I found no clear effects of soil fertility on growth rate (Chapter 4, cf. Baker *et al.* 2003b). This result may be due to the fact that our soil fertility gradient is not large enough to detect strong effects on tree growth. Similarly, no significant correlations between soil nutrient availability and tree growth variation were found in Borneo (Ashton & Hall 1992), Costa Rica (Clark *et al.* 1998) and Brazil (Vieira *et al.* 2004). Forests on poor mineral soils show a highly efficient nutrient cycling (Chapin III *et al.* 1986), as demonstrated, for example, in central Amazonian forests (Jordan 1985). Such findings could be more consistent with the hypothesis that plants in tropical forests may obtain nutrients from the litterfall before they enter to the soils (Vitousek 1984, Scott *et al.* 1992), from the atmosphere (Jordan 1982), or from mycorrhizal fungi (Jordan & Herrera 1981, Barea *et al.* 2002). Consequently, nutrients may also be available for plants from other sources than those that can be suggested by soil analysis alone (Clinebell *et al.* 1995).

Species distribution

Theoretically, plant species should exhibit a unimodal response when large environmental gradients are considered (Gauch & Whittaker 1972, Austin & Smith 1989). Several studies have, however, shown that plant species have different responses to environmental gradients both in temperate forests (Ejrnæs 2000, Oksanen & Minchin 2002, Lawesson & Oksanen 2002, McKenzie *et al.* 2003) and tropical forests (Bongers *et al.* 1999, Duque 2004). It is worth mentioning that to my best knowledge only these two studies were carried out in tropical forests.

For 100 tropical woody species I investigated the response curves to climate and soil factors (Chapter 5, Fig. 3). While unimodal response curves were relatively frequent (25% of the species) along the rainfall gradient, 10 species showed a unimodal response to temperature, only three species to soil fertility and none to soil texture (Chapter 5, Table 4). These results suggest that the sampled environmental gradient is not sufficiently large to increase the number of unimodal responses. It is also possible that woody species respond to specific environmental factor, or that factors not studied here determine the response curve shapes (Grime 1979, Austin & Gaywood 1994, Duque 2004). In general, 91% of species were strongly affected by rainfall whereas 47% of species were affected by soil fertility (Chapter 5, Table 3). Although most of our species were affected by climate and half of the species by soil conditions, each plant species might have different response curves to the different environmental factors considered (Chapter 5, Table 2). Thus these findings agree with the general notion (Huisman *et al.* 1993, Bongers *et al.* 1999, Oksanen & Minchin 2002) that species response types to environmental gradients will differ among species and among factors considered.

How do climate and soil affect lowland tropical forests?

The main results in this dissertation were obtained by stepwise multiple selections using each of the four environmental axes (rainfall, temperature, soil fertility and soil texture). The direction of effects of the environmental factors on the forest structure, composition and dynamics (positive, negative and no-effect) are given in Table 1.

Table 1. Effects of four environmental factors (PCA axes) on forest attributes. Coefficient of determination (R^2) and positive (+), negative (-) or no effects (0) as obtained in the stepwise multiple regression are given. For tree growth, models include the effects of logging variables.

Forest attributes	Environmental factors (PCA axes)				
	Rainfall	Temperature	Soil fertility	Soil texture	R^2
Forest structure					
Vertical structure					
Height_{max} (m)	+	+	0	+	0.57
Emergent layer (%)	-	-	-	+	0.09
Canopy layer (%)	+	+	0	0	0.13
Sub-canopy layer (%)	-	-	0	-	0.13
Horizontal structure					
Total basal area ($m^2\,ha^{-1}$)	+	0	0	+	0.15
Tree basal area ($m^2\,ha^{-1}$)	0	0	0	+	0.07
Palm basal area ($m^2\,ha^{-1}$)	+	0	-	+	0.69
Size class distribution (slope)	+	+	+	-	0.29
DBH_{50} (cm)	-	0	0	0	0.15
DBH_{99} (cm)	+	+	+	0	0.21
Density of life-forms					
Total density (# ha^{-1})	+	-	-	+	0.24
Tree density (# ha^{-1})	-	-	-	+	0.06
Palm density (# ha^{-1})	+	0	-	+	0.82
Liana “density” (# ha^{-1})	-	0	0	-	0.15
Mean liana infestation	0	+	+	-	0.31
Floristic composition					
DCA axis 1	+	+	0	+	0.94
DCA axis 2	-	+	-	0	0.78
Tree and forest growth					
DGR_{avg} (cm $year^{-1}$)	+	+	+	-	0.54
DGR_{50} (cm $year^{-1}$)	+	+	+	-	0.32
DGR_{99} (cm $year^{-1}$)	+	0	+	-	0.44
$BAGR_{stand}$ ($m^2\,ha^{-1}\,year^{-1}$)	+	+	0	0	0.23

I expected that climate plays a more important role than soil in affecting lowland forests. The results of my studies indeed show that rainfall is the most important factor followed by soil texture, temperature and soil fertility (Table 1). In general, rainfall had more significant positive effects, soil texture more significant negative effects and soil fertility had the most non-significant effects. Overall, rainfall affected nearly all the forest variables except two structural variables. Similarly, temperature affected strongly the floristic composition, tree growth and species distribution. Effects of soil factors were more variable with some important effects of soil texture in some structural variables and some important effects of soil fertility in floristic composition. As discussed in the previews paragraphs, the rainfall gradient, which is related to seasonality and soil water availability, is one of the most decisive factors for spatial patterns of tropical lowland forests. Rainfall seasonality presents changes in availability of abiotic factors such as heat, moisture and nutrients, which determine not only the growth of plants but also the species composition and distribution.

The main environmental gradients were summarized into two main climatic PCA axes and two soil PCA axes. These composite variables thus represent a subset of the most important independent or predictor variables. The stepwise selection method is used frequently for exploratory research (Field 2000). In addition, this selection approach avoids over fitting the regression models with several predictor variables. While the stepwise selection method gave the most important environmental factors, I also correlated the individual environmental variables with the forest attributes to evaluate what components of these composite environmental axes were important.

In general, individual climatic variables like annual precipitation, dry period length and annual temperature were highly correlated with most of the structural, floristic composition and tree growth variables. Soil variables showed diverse correlations; acidity, Ca, OM, N and P were best correlated to the forest's structural variables and floristic composition. Tree growth variables were highly correlated to OM, CEC, K, and Mg. In some cases, correlations of individual environmental variables with forest attributes were higher than correlations of environmental axes with forest attributes. Specifically, these higher correlations were found with floristic and tree growth variables. While the stepwise approach allowed determining what environmental factors (e.g climate, soil) are most important, simple correlations revealed particularly strong relationships of individual environmental variables (e.g. annual precipitation) with the forest attributes.

Effects of disturbance on lowland forests

Disturbance is an important factor affecting community structure and dynamics at different levels, from individual to ecosystem and landscape scale (Pickett *et al.* 1989). In tropical forests, disturbances initiate the forest growth cycle through the creation of canopy gaps (Whitmore 1989) which are hotspots for regeneration. In this dissertation I analyzed the effects of logging as a disturbance factor on the growth rates at tree and stand level. Logging removes mainly larger trees, thus increasing canopy openness with associated changes in micro-environmental conditions, especially higher levels of light, that affect tree growth rates (Bazzaz & Pickett 1980, Lang & Knight 1983, Peña-Claros *et al.* 2008a). Disturbance created by logging activities had clear positive effects on tree growth; growth rates were higher in logged plots than non-logged plots, were highest just after logging and decreased with time after logging (Chapter 4, Fig. 2). Silvicultural experiments of increasing logging intensity have also found that the growth-stimulating effect of logging lasts for only 3 years, as tree growth declines following canopy closure (Silva *et al.* 1995, Finegan & Camacho 1999, Carvalho *et al.* 2004, Peña-Claros *et al.* 2008a, De Graaf *et al.* 1999).

The high light conditions and soil disturbance created by logging do not only stimulate growth of established trees but also allow for the germination and establishment of new species. Around 50% of the selected woody species studied in this dissertation are partially or totally light-demanding (Mostacedo *et al.* 2001, Justiniano *et al.* 2004). These species belong to typical pioneer genera such as *Astronium, Cecropia, Cedrelinga, Jacaratia, Pourouma, Trema, Urera, and Zanthoxylum*, were common and abundant in these logged forests (Chapter 5, Table 2). Plots that showed the highest growth rate had also high density of pioneer species. Higher growth rates due to higher abundance of pioneer species have also been reported in Ghana (Hall & Swaine 1981) and Panama (Condit *et al.* 1999). Thus, logging can have both direct effects (through enhanced light availability) and indirect effects (through changed species composition and stand dynamics).

Fast-growing species complete their life cycle more rapidly and they have higher mortality rates, resulting in higher gap formation rates, which in turn creates suitable conditions for the establishment of light-demanding species (Jans *et al.* 1993, Peña-Claros *et al.* 2008b) and competitive lianas (Schnitzer & Bongers 2002). Lianas can overtop trees, and reduce light availability and tree growth (Putz 1984, Peña-Claros *et al.* 2008a, Van der Heijden & Phillips 2009). The role of lianas in tropical forest dynamics warrants special attention, especially in lowland Bolivia where liana dense forests are common (Pérez-Salicrup *et al.* 2001, Toledo *et al.* 2008).

Logging not only allows the establishment of pioneer species and lianas, but also increases the flammability of the forests (Blate 2005, Cochrane & Laurance 2002), and once burnt a forest becomes more vulnerable to further burns (Nepstad *et al.* 1999, Malhi *et al.* 2008). Logging also alters the physical, chemical and biological properties of the soils (Grigal 2000), and causes a disruption of the nutrient cycle (Jordan 1985). In relation to nutrient cycling, selective logging has been classified as a disturbance of moderate intensity (Jordan 1985). Compared to cattle grazing or mechanized agriculture (Steininger *et al.* 2001), however, logging produces relatively low impact to the forests (Verissimo *et al.* 1992, Fredericksen & Putz 2003). Loggers often harvest a few species only. Selective logging impact thus depends on the abundance of the commercial species and the logging intensity used (Panfill & Gullison 1998). Current logging rates in Bolivia are relatively low (1 – 3 trees per ha) compared to other countries: in Costa Rica 4 – 15 trees per ha (Finegan *et al.* 1999), in French Guiana ca. 10 trees per ha (Gourlet-Fleury & Houllier 2000), and in Borneo more than 10 trees per ha (Sist *et al.* 2003). Increased logging intensities, however, could easily become unsustainable, especially when growth rates are very low as is the case in the Bolivian dry forests (Chapter 4, Appendix 2). Logging impacts vary between regions because of the different biotic and abiotic characteristics. This dissertation provides insight into the ecological differences among regions, which have to be taken into account when developing forest-specific management plans.

Implications for forest management

This research provided also insight in the differences in floristic composition, forest structure and dynamics among forests, which have to be taken into account when developing forest-specific management plans. The analysis of floristic composition, based on the woody species abundance, gave five floristic regions

(Chapter 3, Fig. 2a). These floristic regions were different not only in species composition but also in environmental conditions (Chapter 3, Table 5). Thus these regions could be used as a basis for the development of a stratified forest management. Most of the selected species, including several timber species, were of wide distribution and therefore were present in different floristic regions across the country (Chapter 3, Table 1). Because the regions have different environmental conditions (Chapter 3, Table 5) and growth varies with climatic factors (Chapter 4, Fig. 2), it is expected that species will have site or region specific growth rates. Forest specific species growth rates have been shown earlier for lowland Bolivia (see Dauber *et al.* 2003). In this sense, forest managers need to consider not only species-specific growth rates and other life history characteristics (regeneration requirements, but possibly also pollination and seed dispersal strategies) but also the variation of these characteristics within each floristic region when designing management practices.

Several studies have shown that diameter increments vary widely not only among tree species but also among diameter size classes, guilds and plots (Lieberman *et al.* 1985, Swaine *et al.* 1990, Felfili 1995, Laurence *et al.* 2004, Peña-Claros *et al.* 2008a). Results of the present research show that lowland forests also as a whole differ in their growth rates, varying from 0.12 cm diameter growth per year in the dry forest up to 0.7 cm per year in sub-humid forests; which confirm preliminary analyses in the region (Chapter 4, Table 1; cf. Dauber *et al.* 2003). This variation has tremendous consequences for the multiple-species based forest-wide cutting cycle that should be applied to the different forest types (cf. Dauber *et al.* 2005). Here I showed that tree and forest growth is generally slow, which would warrant longer cutting cycles to be in line with sustainable yield principles. However, from an economic point of view increasing the cutting cycle is for many concession holders not feasible. One of the alternatives to increasing cutting cycles is the stimulation of tree and forest growth. Species specific silvicultural treatments could be necessary to enhance growth of commercial tree species. These treatments may also need to be based on specific characteristic of each forest (species-site or species-region specific treatments). Liana load, for example, is exceptionally high in drier forests (Chapter 2, Fig. 4c; cf. Dauber *et al.* 2003, Pérez-Salicrup *et al.* 2001, Toledo *et al.* 2008). It has been demonstrated that lianas have a large negative impact on tree growth (Van der Heijden & Phillips 2009). Liana cutting on future crop tree (see Peña-Claros *et al.* 2008a, Verwer *et al.* 2008, Villegas *et al.*

2009) could, therefore, be seen as a promising silvicultural treatment to enhance growth rates of these forests.

Implications for climate change

Climate change is one of the most serious global challenges having a large impact on ecosystems (Vergara *et al.* 2007). Malhi &Wright (2004) analyzed for tropical forests rainfall and temperature changes over a 38 year period from 1960-1998. They found that tropical rainforests have experienced a decrease in rainfall and an increase in temperature, but they did not find a significant trend in Amazonia. Recent analyses on climate change predict that tropical droughts may be more frequent and intense this century (Malhi *et al.* 2008), although the increases in drought will be strongest in Mediterranean, West African, central Asian and central American regions (Sheffield & Wood 2008). Another modeling study predicts even that rain forests could disappear entirely from Bolivia, Paraguay and Argentina and most of Brazil and Peru (Cook & Vizy 2008). Predictions of future precipitation change vary, however, according to the particular climate model (Füssel 2009).

A closer inspection of the climatic data for the last 30 years in lowland Bolivia show that annual rainfall tends to decrease and temperature tends to increase above the average in the observed regions (Fig. 1). Consequently ongoing and continued drying patterns might have a dramatic effect on Bolivian forests, especially since these forests are located across a climatic transition between the Amazonian and Gran Chaco regions. Transitional ecosystems are more likely to be impacted by climate change as many species are at the extreme limits of their ecological requirements (Killeen *et al.* 2006). Although I did not evaluate climatic change effects on forest attributes, the climatic gradient approach considered in this dissertation allowed evaluating how forests are shaped by different climatic conditions. I found strong effects of rainfall and temperature on floristic composition (Chapter 3), tree growth (Chapter 4), and species distribution (Chapter 5). If current rainfall patterns change, the distribution of individual species will change and as a consequence the community composition of forests will change as well. Based on my findings that rainfall seasonality and temperature strongly affected the forest attributes, and the observed climatic trends, I can hypothesize that a decrease in rainfall and an increase in temperature would eventually lead to loss of forest ecosystem integrity.

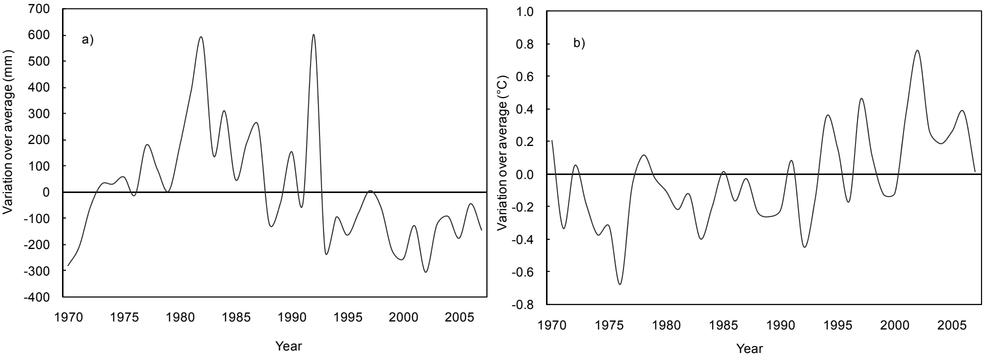

Figure 1. Temporal trends of a) annual precipitation and b) annual temperature calculated from 1970-2007. Trends plotted are above and below the average from 20 weather stations occurring in lowland Bolivia. Data were provided by the Servicio Nacional de Meteorología e Hidrología-Bolivia (SENAMHI).

The interaction between global climate change and regional deforestation may make tropical forests more vulnerable to large-scale degradation (Malhi *et al.* 2008). Observations suggest that extensive deforestation often reduces cloud formation and rainfall, and accentuates seasonality (Bonan 2008). What happens to the water cycle if big trees are harvested? Forests transpire water and through the recycling of rainwater back into the atmosphere, forests may also influence their own regional climate (Sheil & Murdiyarso 2009). Climate change in tropical regions thus could be critical to global climate change. In this dissertation I have shown that forests, in terms of structure, species composition and tree growth, strongly depend on water availability and temperature. Human activities affect both the rainfall amount and distribution and the temperature, therefore, the functioning of tropical forests. As a result it will be difficult in the near future for forests to continue providing the functions and ecosystem services that forests provide currently.

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Summary

Neotropical lowlands feature an extraordinary display of vegetation types. This is especially the case for Bolivia where three biogeographical regions, Amazonian, Brazilian-Paranaense and Gran Chaco meet in the lowland areas, providing thus an ideal setting to study vegetation-environment relationships. Understanding spatial patterns of tropical forests and the environmental factors determining these patterns is important for forest management and for predicting responses of forests to climate change. Thus, the main objective of this dissertation was to evaluate how environmental factors shape tropical lowland forests in Bolivia. Specifically it assessed how climatic and edaphic factors affect 1) forest structure, 2) floristic composition, 3) tree growth rates, and 4) species distribution. Additionally, it assessed how disturbance factors affect tree growth rates.

For this research, I used a network of 220 1-ha permanent sample plots distributed along environmental gradients. For each plot, all stems ≥ 10 cm diameter were identified, evaluated and monitored; climatic data were interpolated from weather stations and soil samples were collected. In lowland Bolivia, seasonality increased from north to south. Rainfall decreases, and dry season length increases, along this gradient. Although in general the drier forest had more fertile soils than moister forests, some plots in moister forests were also fertile. A set of five climatic variables [annual temperature, annual precipitation, total precipitation of the three driest months, length of the dry period (# months < 100 mm), and length of the drought period (# months < 50 mm)] and 12 edaphic variables [cation exchange capacity, cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), Olsen phosphorous, organic matter, nitrogen, acidity and percentage of different particles (sand, silt and clay)], were summarized into four environmental gradient axes using a Principal Component Analysis (PCA). I used the two main climatic PCA axes (named after the most important factors they represent as “rainfall” and “temperature”) and the two soil PCA axes (named as “soil fertility” and “soil texture”) to reduce the number of highly correlated variables and to have composite variables that summarize the main environmental gradients. Rainfall axis, for example, represents a seasonality gradient. Finally, a stepwise selection approach was used to determine how the climatic and edaphic PCA axes affected the plant community.

Structural attributes of the tropical forests differ along gradients. In Chapter 2, I described how forest structure varies among forests across lowland Bolivia. I considered 15 forest structural variables based on height, crown position, diameter, and liana infestation of each stem. I tested the hypothesis that stem density and basal area of trees and palms will increase with water availability and liana density will increase in drier forests. My results showed that tree maximum height, palm density and basal area increased with rainfall while lianas decreased with rainfall. While forest height and lianas were more affected by soil texture, palm density was negatively affected by soil fertility. Surprisingly, tree basal area was not affected by environmental factors. I found that rainfall, temperature and soil texture were more important drivers of forest structure than soil fertility. Thus climatic and edaphic factors have strong effects on variation in forest structure at the landscape-scale.

Only recently researchers have started to examine the influence of environmental factors on species composition on a regional scale. In Chapter 3, I evaluated patterns in floristic composition using abundance and presence-absence data of 100 plant species. I predicted that climate is a more important factor than soil in shaping floristic composition. In line with my hypothesis the climatic gradient shaped the floristic variation more strongly than the edaphic gradient. Detrended Correspondence Analysis ordination divided lowland Bolivia primarily into two major groups (Southern Chiquitano versus Amazonian regions) and Multiple Response Permutation Procedure distinguished five floristic regions: Northern Amazon, Western Preandean, Eastern Amazon - Bajo Paraguá, Eastern Amazon - Guarayos, and Southern Chiquitano. In addition, all the environmental variables tested were significantly different among the floristic regions. Of the 100 species, 10 occurred in only one floristic region and 90 occurred in two or more floristic regions. I also distinguished 92 strong indicator species, which had significant environmental preferences for one floristic region, so these species can be indicators of environmental conditions. Given the predicted decreases in rainfall and increases in temperature for lowland forests, our gradient approach suggests that species composition may drastically shift with climate change.

Most of the forest dynamic studies have evaluated the effects of temporal variation of rainfall on tree growth rates, but spatial variation on growth rates along gradients is less known. Thus, in Chapter 4, I described the variation in tree growth by examining growth rates at individual level (average diameter growth) and at stand level (basal area growth) across 165 plots, of which 85 were affected by logging. I expected that growth rates would be higher in humid than in dry sites, higher in nutrient-rich than nutrient-poor forests, and higher in logged than non-logged forests because of an increase in water, nutrients and light, respectively. I found positive basal area increases at the stand level which agrees with the generally reported biomass increases in tropical forests. Multiple regression analysis demonstrated that environmental and disturbance factors significantly explained the high variation in growth rates. While rainfall and temperature had positive effects on tree growth, no clear effects with soil fertility were found. Probably our soil fertility was not large enough to detect effects on tree growth, or nutrients may also be available for plant growth from other sources than soil alone. Growth rates increased in logged plots, especially those which had a high logging impact. Future decreases in rainfall and increases in temperature due to climate change can also affect growth rates. The negative effects of increased seasonality, however, may be partly offset by the positive effects of temperature on tree growth. Forest managers should take into account the high variation in growth rates occurring in the lowland forests of Bolivia. Based on the results I advocate that management practices to be developed are specific to each forest and are in line with its characteristics and conditions.

Ecologists have found different response curve shapes for species distribution, mostly for temperate species, but data in tropical species responses are surprisingly scarce. Therefore, in Chapter 5, I analyzed the distribution patterns of the 100 selected species and constructed response curves for each species against each of the four environmental gradient axes using logistic regression analysis on presence-absence data. I hypothesized that species frequency and abundance would be positively correlated, that the majority of the species would show unimodal response curves and that species would respond stronger to climate than to soil effects. I indeed found a positive trend between species abundance and occurrence but some abundant species were also narrowly distributed. While 25 species showed unimodal response curves to the rainfall gradient, and 10 species to temperature, only three species showed such response to soil fertility and none to soil texture. Probably, the sampled environmental gradient is not sufficiently large to find a higher number of unimodal responses. In line with my hypothesis, 91% of the species were affected by climatic factors and only 47% of the species were affected by soil factors. These results agree with the notion that species response types to environmental gradients will differ among species and among factors considered. Thus, multiple, rather than single, environmental factors must be used to explain the species distribution in tropical forests.

In conclusion, this dissertation documented the high variation of tropical lowland forests in Bolivia and indicated that climate (i.e. rainfall and temperature) was the most important factor shaping forest structure, composition and dynamics. The high variation of forests and the ecological differences among regions have to be taken into account when developing forest-specific management plans. Finally, the results of the gradient approach suggest that with future decreases in rainfall and increases in temperature, due to climate change, drastic shifts can be expected in forest structure, composition and dynamics in these tropical lowland forests.

Resumen

Las tierras bajas del Neotrópico poseen una extraordinaria variedad de tipos de vegetación. Este es el caso especialmente de Bolivia donde tres regiones biogeográficas, Amazónica, Brasileño-Paranense y Gran Chaco, se encuentran en las tierras bajas, creando así un sistema ideal para estudiar la relación entre vegetación y ambiente. Es importante entender los patrones espaciales de los bosques tropicales y los factores ambientales que determinan estos patrones para definir pautas de manejo forestal y para predecir las respuestas de los bosques al cambio climático. Consecuentemente, el principal objetivo de esta disertación fue evaluar como los factores ambientales definen los bosques tropicales de las tierras bajas de Bolivia. Específicamente, se evaluó como los factores climáticos y edáficos afectan la 1) estructura del boque, 2) composición florística, 3) tasa de crecimiento de los árboles y 4) distribución de especies. Adicionalmente, se evaluó como factores de disturbio afectan las tasas de crecimiento de los árboles.

Para la investigación se usó una red de 220 1-ha parcelas permanentes de muestreo distribuidas a lo largo de gradientes ambientales. Para cada parcela, todos los tallos ≥10 cm de diámetro fueron identificados, evaluados y monitoreados; datos climáticos fueron interpolados desde estaciones meteorológicas y muestras de suelos fueron colectadas. En las tierras bajas de Bolivia, la estacionalidad de lluvias incrementa de norte a sur. La lluvia decrece y la duración de la época seca incrementa a lo largo de este gradiente. Aunque en general los bosques secos tuvieron suelos más fértiles que los bosques húmedos, algunas parcelas en bosques húmedos tuvieron también suelos fértiles. Un grupo de cinco variables climaticas [temperatura anual, precipitación anual, precipitación total de los tres meses más secos, el largo del periodo seco (# de meses < 100 mm) y el largo del periodo de sequía (# de meses < 50 mm)] y 12 variables edáficas [capacidad de intercambio de cationes, cationes (Ca^{2+}, Mg^{2+}, K^{+} and Na^{+}), Olsen fósforo, materia orgánica, nitrógeno, acidez y porcentaje de las diferentes partículas (arena, limo y arcilla)], fueron resumidas en cuatro ejes de gradientes ambientales usando un análisis de componentes principales (PCA).

Se usaron los dos principales ejes del PCA climático (denominado según los factores más importantes que ellos representan como ejes de “lluvia” y “temperatura”) y los dos principales ejes del PCA edáfico (denominado como

"fertilidad de suelos" y "textura de suelos") para reducir el número de variables altamente correlacionadas y para tener variables compuestas que resuman los principales gradientes ambientales. El eje lluvia, por ejemplo, representa un gradiente de la estacionalidad de lluvia. Finalmente se usó regresión múltiple de selección gradual para determinar como los componentes climáticos y edáficos afectaron la comunidad de plantas.

Las características estructurales de los bosques tropicales difieren a lo largo de gradientes ambientales. En el Capítulo 2 se describió como la estructura del bosque varía a lo largo de las tierras bajas de Bolivia. Se consideraron 15 variables estructurales basadas en la altura, posición de la copa, diámetro y la infestación de lianas de cada tallo. Se evaluó la hipótesis que la densidad y área basal de árboles y palmeras aumenta con la disponibilidad de agua y que la densidad de lianas incrementa en bosques secos. Los resultados muestran que la altura máxima de los árboles y la densidad y área basal de las palmeras incrementaron con la lluvia mientras que la densidad de lianas decreció. Mientras la altura del bosque y la infestación de lianas fueron más afectadas por la textura de los suelos, la densidad de palmeras fue afectada negativamente por la fertilidad de los suelos. Sorprendentemente, el área basal de los arboles no fue afectado por los factores ambientales. Se encontró que los ejes lluvia, temperatura y textura de los suelos fueron más importantes que la fertilidad de los suelos en determinar la estructura del bosque. Así, los factores climáticos y edáficos tienen un gran efecto en la variación de la estructura de los bosques a una escala de paisaje.

Sólo recientemente los investigadores han empezado a examinar la influencia de los factores ambientales en la composición de especies a una escala regional. En el Capítulo 3, se evaluaron los patrones en composición florística utilizando datos de abundancia y presencia-ausencia de 100 especies de plantas. Se predijo que el clima es más importante que el suelo para determinar la composición florística. En línea con la hipótesis el gradiente climático afectó la variación florística más fuertemente que el gradiente edáfico. El análisis de ordenación de correspondencia detrended dividió las tierras bajas de Bolivia primeramente en dos grandes grupos (la región Amazónica y la región Chiquitana) y el procedimiento permutación de respuestas múltiples distinguió cinco regiones florísticas: Amazonia norte, Pre-Andino oeste, Amazonia este - Bajo Paraguá, Amazonia este - Guarayos y Chiquitania sur. De las 100 especies, 10 ocurrieron en solo una región florística y 90 ocurrieron en 2 o más regiones florísticas. Se distinguieron también 92 especies

indicadoras, las que tuvieron preferencias ambientales significativas por una determinada región florística, así estas especies pueden ser indicadoras de condiciones ambientales. Dada las predicciones actuales de reducción de lluvias e incrementos de temperatura para los bosques tropicales, nuestro enfoque de gradiente sugiere que la composición de especies puede cambiar drásticamente con el cambio climático.

La mayoría de los estudios en dinámica de bosques han evaluado los efectos de la variación temporal de la lluvia en el crecimiento de los árboles, pero la variación espacial de las tasas de crecimiento a lo largo de gradientes es menos conocida. Así, en el Capítulo 4, se describe la variación del crecimiento de los árboles a través de la evaluación de las tasas de crecimiento a nivel de individuo (promedio del crecimiento en diámetro) y a nivel de parcela (crecimiento del área basal). Para ello se utilizaron 165 parcelas de 1 ha, de las cuales 85 fueron afectadas por aprovechamiento forestal. Se esperaba que las tasas de crecimiento fueran más altas en bosques húmedos que en bosques secos, más altas en suelos ricos en nutrientes que en suelos pobres en nutrientes y más altas en bosques aprovechados que en bosques no aprovechados, debido a un incremento de agua, nutrientes, y luz, respectivamente. Se encontró un incremento positivo del área basal a nivel de parcela lo cual concuerda con el incremento de biomasa reportado generalmente para los bosques tropicales. Los análisis de regresión múltiple demostraron que los factores ambientales y de disturbio explicaron significativamente la alta variación de tasas de crecimiento. Mientras los ejes lluvia y temperatura tuvieron efectos positivos en el crecimiento de los árboles, no se encontró efectos claros con la fertilidad de los suelos. Probablemente, nuestro gradiente de fertilidad no fue lo suficientemente amplio para detectar efectos en el crecimiento de los árboles, o los nutrientes están disponibles para el crecimiento de las plantas en otras fuentes que sólo en el suelo. Las tasas de crecimiento incrementaron en las parcelas aprovechadas, especialmente las que tuvieron un mayor impacto del aprovechamiento. Los manejadores de bosque deben tomar en cuenta la alta variación de las tasas de crecimiento reportadas en las tierras bajas de Bolivia. La futura disminución de lluvias e incremento en temperatura, debido al cambio climático, pueden también afectar las tasas de crecimiento. Los efectos negativos de una mayor estacionalidad, sin embargo, pueden ser parcialmente subsanados por los efectos positivos de la temperatura en el crecimiento de los árboles. En base a los resultados obtenidos se propone que las prácticas de manejo a ser desarrolladas

sean específicas para cada bosque y estén en línea con sus características y condiciones.

Los ecólogos han encontrado diferentes formas de curvas de respuesta en la distribución de especies a lo largo de gradientes, mayormente para especies templadas, pero datos de especies tropicales son sorprendentemente escasos. Por lo tanto, en el Capítulo 5, se analizaron los patrones de distribución de las 100 especies seleccionadas y se elaboraron curvas de respuesta para cada especie a lo largo de los cuatro gradientes ambientales utilizando datos de presencia-ausencia a través de análisis de regresión logística. Se hipotetizó que la frecuencia y la abundancia de las especies estarian correlacionada positivamente, que la mayoría de las especies mostrarian formas unimodales de curvas de respuesta y que las especies responderian más fuertemente a los efectos del clima que a los del suelo. Se encontró una tendencia positiva entre la ocurrencia y la abundancia de las especies, pero algunas especies abundantes tuvieron una distribución restringida. Mientras 25 especies mostraron curvas de respuesta unimodales al gradiente de lluvias, y 10 especies a temperatura, sólo 3 especies mostraron tal respuesta a la fertilidad de los suelos y ninguna especie a la textura de los suelos. Probablemente, el gradiente ambiental analizado no fue suficientemente largo para encontrar un número más alto de respuestas unimodales. En línea con la hipótesis, 91% de las especies fueron afectadas por factores climáticos y sólo 47% de las especies fueron afectadas por los factores edáficos. Estos resultados concuerdan con la idea que el tipo de respuesta de las especies a gradientes ambientales varía entre especies y entre factores considerados. Por lo tanto, se deben utilizar factores ambientales múltiples en lugar de factores individuales para explicar la distribución de especies en bosques tropicales.

En conclusión, la presente disertación documentó la alta variación de los bosques tropicales de las tierras bajas de Bolivia y encontró que el clima, (es decir los ejes de lluvia y temperatura) fue el factor más importante en la determinación de la estructura, composición y dinámica de estos bosques. La alta variación de bosques y las diferencias ecológicas entre las regiones deben ser tomadas en cuenta al desarrollar planes de manejo específicos para cada bosque. Finalmente, los resultados obtenidos al utilizar un enfoque de gradiente sugieren que las futuras disminuciones de lluvia e incrementos de temperatura debido al cambio climático, pueden cambiar drásticamente la estructura, composición y dinámica de estos bosques tropicales.

Samenvatting

Het neotropische laagland wordt gekenmerkt door een grote variatie aan vegetatietypen. Dit geldt in bijzondere mate voor Bolivia, waar drie biogeografische regio's samenkomen, te weten; de Amazone, de Braziliaans-Paranaense en de Gran Chaco. Tezamen bieden zij een ideale mogelijkheid om de relaties tussen vegetatie en het abiotisch milieu te bestuderen. Het begrijpen van de ruimtelijke patronen van tropische bossen, en de milieufactoren die bijdragen aan de vorming van deze patronen, is van belang voor het bosbeheer, maar ook om mogelijke reacties van het bos op klimaatverandering te kunnen voorspellen. De hoofddoelstelling van deze dissertatie was om te evalueren op welke manier abiotische milieufactoren vorm geven aan de bossen van het tropisch laagland van Bolivia. Specifiek werd bestudeerd hoe klimaat- en bodemfactoren invloed hebben op 1) bosstructuur, 2) vegetatiesamenstelling, 3) boomgroeisnelheid en 4) de verspreiding van soorten. Daarnaast werd bekeken, in hoeverre verstoringsfactoren (houtkap-activiteiten) de groeisnelheid van bomen beïnvloeden.

Voor dit onderzoek maakte ik gebruik van een netwerk van 220 permanente onderzoekspercelen van 1 hectare, verspreid langs natuurlijke milieugradiënten. Van ieder perceel werden alle stammen vanaf 10 cm diameter geïdentificeerd, geëvalueerd en gevolgd over de tijd. Klimaatgegevens werden geïnterpoleerd van weerstations en bodemmonsters werden verzameld. In het laagland van Bolivia neemt de seizoenaliteit toe van noord naar zuid: de totale regenval neemt af en de droge tijd duurt langer. Hoewel over het algemeen het drogere bos vruchtbaarder bodems had dan het nattere bos, hadden sommige percelen uit het nattere bos toch ook een hoge vruchtbaarheid. Ik heb 5 klimaatvariabelen [jaarlijkse temperatuur, jaarlijkse neerslag, totale neerslag van de drie droogste maanden, lengte van de droge periode (aantal maanden < 100 mm), en lengte van de droge periode (aantal maanden < 50 mm)] en 12 bodem variabelen [de capaciteit van kationenuitwisseling, kationen (Ca^{2+}, Mg^{2+}, K^+ en Na^+), Olsen-P fosfor, organische stof, stikstof, zuurgraad en percentage korrelgrootte (zand, leem en klei)] geëvalueerd. Met behulp van Belangrijkste Componentenanalyse (PCA, Principal Component Analysis) zijn deze 17 milieuvariabelen samengevat in vier milieu-assen. Ik gebruikte twee PCA klimaat hoofd-assen (vernoemd naar de belangrijkste factoren die zij vertegenwoordigen; neerslag en temperatuur) en twee PCA bodem-assen (bodemvruchtbaarheid en bodemtextuur genaamd), teneinde het aantal hoog gecorreleerde variabelen te verminderen, en zo samengestelde variabelen te verkrijgen die de belangrijkste milieugradiënten samenvatten. De regenval-as bijvoorbeeld, vertegenwoordigt een regenseizoengradiënt. Een stapsgewijze selectie bepaalde in welke mate klimaat- en bodem- PCA-assen invloed hadden op de plantengemeenschap.

De structuur van tropische bossen verandert langs deze milieugradiënten. In Hoofdstuk 2 beschreef ik, hoe de structuur verschilt tussen de diverse bossen in het laagland van Bolivia. Ik beschreef 15 bosstructuurvariabelen op basis van boomhoogte, kroonpositie, stamdiameter, dichtheid en lianenbegroeiing. De maximale boomhoogte, palmendichtheid en lianenbegroeiing, lieten de sterkste relatie zien met de milieuvariatie. Ik testte de hypothese dat de stamdichtheid en het grondvlak van bomen en palmen zouden toenemen met de waterbeschikbaarheid, en dat de lianendichtheid zou afnemen met waterbeschikbaarheid. Mijn resultaten laten zien dat de maximale boomhoogte, palmdichtheid en het grondvlak toenemen met regenval, terwijl lianen afnemen met regenval. Boshoogte en lianendichtheid worden meer door bodemtextuur beïnvloed, terwijl de palmdichtheid negatief beïnvloed wordt door bodemvruchtbaarheid. Verrassend was de bevinding, dat het grondvlak niet wordt beïnvloed door milieufactoren. Ik vond dat regenval, temperatuur en bodemtextuur belangrijkere sturende factoren zijn dan de bodemvruchtbaarheid. Klimaat- en bodemfactoren hebben sterke consequenties voor de variatie in bosstructuur op landschapsschaal.

Slechts recentelijk zijn onderzoekers begonnen de invloed van milieufactoren op soortensamenstellingen te bestuderen op een regionale schaal. In Hoofdstuk 3 heb ik patronen bestudeerd in de vegetatiesamenstelling, op basis van gegevens van abundantie en het voorkomen (de aan- of afwezigheid) van 100 plantensoorten (bomen en palmen). Ik voorspelde dat klimaat een belangrijkere factor zou zijn dan de bodem, voor het vormgeven van de vegetatiesamenstelling. In overeenkomst met mijn hypothese blijkt de klimaatgradiënt de vegetatiesamenstelling sterker te bepalen dan de bodemgradiënt. De ordinatiemethode Detrended Correspondentieanalyse (DCA, Detrended Correspondence Analysis), verdeelt laagland Bolivia in twee hoofdgroepen (Zuid Chiquitano versus Amazone regio's) en onderscheidt vijf vegetatieregio's. Bovendien bleken alle geteste milieuvariabelen significant verschillend te zijn tussen deze vegetatieregio's. Van de 100 soorten kwamen er 10 soorten voor in slechts één vegetatieregio, terwijl 90 soorten voorkwamen in twee of meer vegetatieregio's. Ik heb ook 92 sterke indicatorsoorten kunnen onderscheiden, die een significante voorkeur hadden voor één vegetatieregio. Hiermee kunnen deze soorten voortaan gebruikt kunnen worden als indicatoren voor milieucondities (standplaatsfactoren). Klimaatscenario's voorspellen een afnemende neerslag en toenemende temperatuur voor de laaglandbossen, en mijn gradiëntbenadering laat zien dat de soortensamenstelling in de toekomst drastisch zou kunnen wijzigen door klimaatsverandering.

Veel bosdynamiek studies hebben de effecten bestudeerd van verschillen in regenval op boomgroei in de tijd, maar de ruimtelijke variatie van groeiwaarden langs gradiënten is minder bekend. Daarom heb ik in Hoofdstuk 4 de variatie beschreven van boomgroei op individueel niveau (gemiddelde diametergroei), en op opstandniveau (grondvlaktoename) voor 165 percelen, waarvan 85 waren verstoord door houtkap. Mijn verwachting was dat de groeiwaarden hoger zouden zijn op vochtige locaties dan op droge locaties, hoger in nutriëntrijke dan -arme bossen en hoger in (door houtkap) verstoorde dan niet verstoorde bossen, vanwege respectievelijk een toenemende beschikbaarheid van water, nutriënten en licht. Ik vond een toename van het grondvlak op opstandniveau, wat overeen komt met algemeen gerapporteerde toename van biomassa in tropische bossen. Meervoudige regressieanalyse heeft aangetoond dat milieu- en verstoringsfactoren de hoge variatie in groeiwaardeverschillen significant verklaren. Terwijl regenval en temperatuur een positief effect hadden op de boomgroei, bleken er geen duidelijke effecten van de bodemvruchtbaarheid te zijn. Mogelijk waren onze bodemvruchtbaarheidswaarden niet hoog genoeg om effecten op de boomgroei waar te nemen, of kwamen nutriënten voor plantengroei ook beschikbaar via andere bronnen dan de bodem alleen. Groeiwaarden namen toe in percelen waar houtoogst had plaatsgevonden en met name in percelen met een intensievere verstoring. Dit onderzoek laat zien dat een toekomstige afname van regenval en toename van temperatuur de groeiwaarden zouden kunnen beïnvloeden. Het negatieve effect van toenemende seizoeninvloed, compenseert het positieve effect van verhoogde temperatuur op boomgroei. Bosbeheerders zouden rekening moeten houden met de hoge verschillen in groeiwaarden, die in de laaglandbossen van Bolivia voorkomen. Gebaseerd op deze resultaten, pleit ik ervoor dat er specifieke beheersrichtlijnen worden opgesteld voor ieder bostype navenant de milieukarakteristieken en condities.

Ecologen hebben verschillende vormen van responsecurven gevonden voor met name boomsoorten uit gematigde streken, maar gegevens over de milieu-respons van tropische soorten zijn verrassend schaars. Om deze reden heb ik in Hoofdstuk 5, de distributiepatronen van de 100 geselecteerde boom- en palmsoorten geanalyseerd. Per soort werden responsecurven gemaakt voor elk van de vier milieugradiënt-assen. Hiervoor maakte ik gebruik van logistische regressieanalyse en aan- en afwezigheidsgegevens. Ik veronderstelde, dat de soortenfrequentie en -abundantie positief gerelateerd zouden zijn, dat de meerderheid van de soorten een unimodale (eentoppige) responscurve zouden laten zien en dat soorten sterker op klimaat- dan op bodemfactoren zouden reageren. Inderdaad vond ik een positieve trend tussen soortenabundantie en -voorkomen, maar sommige abundante soorten hadden ook een vernauwde verspreiding. Terwijl 25 soorten een unimodale responscurve op de regengradiënt lieten zien, en 10 soorten op temperatuur; toonden slechts drie soorten een dergelijke respons op bodemvruchtbaarheid en geen enkele soort op bodemtextuur. Mogelijk waren de bestudeerde milieugradiënten niet lang genoeg geweest om een groter aantal unimodale responsen te vinden. In overeenkomst met mijn hypothese werden 91% van de soorten beïnvloed door klimaatfactoren en maar 47% van de soorten door bodemfactoren. Deze resultaten komen overeen met het idee dat soort-responsen op milieugradiënten zullen verschillen tussen soorten en tussen betrokken factoren. Om de soortenverspreiding in tropische bossen te verklaren kunnen dus beter meervoudige dan enkelvoudige milieufactoren worden gebruikt.

Samenvattend kan gezegd worden dat deze dissertatie heeft laten zien dat er een grote variatie is in tropisch laaglandbos in Bolivia. Het klimaat, d.w.z. regenpatronen en temperatuur, is de belangrijkste milieufactor die de bosstructuur, soortensamenstelling en de dynamiek bepaald. Deze grote variëteit aan bossen en milieufactoren, dienen in beschouwing te worden genomen bij de ontwikkeling van bosspecifieke beheersplannen voor elke regio. Tot slot laten de resultaten van dit onderzoek zien, dat met de toekomstige reductie in regenval en toename van temperatuur door klimaatsverandering, drastische veranderingen kunnen worden verwacht in de bosstructuur, soortensamenstelling en dynamiek van deze tropische laaglandbossen.

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Short Biography

Marisol Toledo was born in Santa Cruz, Bolivia, on June 6, 1970. In September 1995, she obtained her BSc. degree in Biology at the Universidad Autónoma Gabriel René Moreno, Santa Cruz, Bolivia. For her BSc. thesis she carried out the ethnobotanical study of the Chiquitanos of Bolivia. From 1991 to 1997 she was trained in (ethno) botany and worked as research assistant in different projects at the Museo de Historia Natural Noel Kempff Mercado. From 1998 to 2002 she was the botanist at the Forest Research Unit of the BOLFOR Project (Phase I) participating in different studies related to tropical forest management and diversity.

In June 2002, she obtained the Bascom fellowship from the Missouri Botanical Garden for participating in the MSc. program of the University Missouri of Saint Louis, USA. For her thesis, she performed quantitative plant ecology and ethnobotanical analyses on secondary forests of the indigenous Guarayos in Bolivia. She obtained her MSc. degree in Biology in September 2004 as well as her certificate in Tropical Biology and Conservation. For this latter certificate she carried out an internship at the Instituto Boliviano de Investigación Forestal (IBIF). During this internship she studied the structure and floristic composition on 152 permanent plots. This internship gave the opportunity to develop her ideas for a doctoral thesis.

In October 2005 she started her PhD program as a sandwich student at Wageningen University, the Netherlands. The doctoral research was carried out in close collaboration with the IBIF and the Forest Ecology and Forest Management Group of the university. From November 2004 to December 2008, parallel to the thesis fieldwork in lowland Bolivia, she participated in different research and training programs at IBIF. Her PhD program was interrupted for half a year in 2007 to work as the interim executive director of IBIF. Early 2009, she arrived in the Netherlands to finish her PhD thesis.

As biologist she is interested in plant diversity, forest conservation and resource management. Her main goal is to continue with applied research and training activities, including local people and students, driven by the fascination and concerns for the amazing tropical forests.

Publications

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Education certificate

PE&RC PhD Education Certificate

The C.T. De Wit
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CONSERVATION

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities).

Review of Literature (4.2 ECTS)

- Species diversity, forest structure and dynamics along environmental gradients in lowlands forests of Bolivia (2006)

Writing of Project Proposal (4.2 ECTS)

- Spatial patterns in species composition, forest structure and dynamics along environmental gradients in lowland forests of Bolivia (2005)

Laboratory Training and Working Visits (1.4 ECTS)

- Introduction to ArcGIS (Training course in Bolivia); Geosystems S.R.L. (2006)

Post-Graduate Courses (10 ECTS)

- Basic and advanced statistics; PE&RC (2005-2006)
- Multivariate analysis; PE&RC (2008)
- Competencies for integrated agricultural research; PE&RC (2009)
- iGis; PE&RC (2009)
- What’s up in tropical forest community ecology?; PE&RC (2009)

Competence Strengthening / Skills Courses (1.5 ECTS)

- PhD Competence assessment; WGS (2006)
- Techniques for writing and presenting a scientific paper; WGS (2008)

Discussion Groups / Local Seminars and Other Scientific Meetings (5 ECTS)

- Ecological theory and application; PE&RC discussion group (2006-2009)
- Network about effects of climate change in forestry ecosystems-FORCLIM; three meetings in Argentina, Colombia and México (2008-2009)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.8 ECTS)

- PE&RC- day: the truth of science (2005)
- PE&RC introduction weekend (2008)
- Tropical dry forest: regeneration, recovery and conservation; mini symposium at Wageningen University (2009)
- Tropical forest trees and climate changes; mini symposium at Utrecht University (2010)

International Symposia, Workshops and Conferences (9.8 ECTS)

- 19th Annual meeting of tropical ecology (GTO); Kaiserslautern, Germany; poster presentation (2006)
- 3rd National forest research meeting; Santa Cruz de la Sierra, Bolivia; poster presentation (2006)
- ATBC Annual meeting in Paramaribo, Surinam; oral presentation (2008)
- NERN Annual meeting in Lunteren, the Netherlands (2008)
- ATBC Annual meeting in Marburg, Germany; oral presentation (2009)

Supervision of MSc Students (2 students, 20 days)

- Dynamics in unlogged and logged rainforests in northern Bolivia; David Aparici, Utrecht University

- Structure and dynamics of semi-evergreen and deciduous lowland forests in Bolivia; Frederik Vroom, Wageningen University

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