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 mesoscale. We examined floristic composition and its relationship with environmental factors across 220 1-ha permanent plots in tropical lowland Bolivia. For each plot, abundance of 100 species (93 tree and 7 palm species ≥ 10 cm diam) was obtained. Climatic data, related to rainfall seasonality and temperature, were interpolated from all available weather stations in the region, and soil properties, related to texture and fertility, were obtained for each plot. Floristic variation was strongly associated with differences in water availability and temperature, and therefore the climatic gradient shaped floristic variation more strongly than the edaphic gradient. Detrended correspondence analysis ordination divided lowland Bolivia primarily into two major groups (Southern Chiquitano region vs. the Amazon region) and a multiple response permutation procedure distinguished five floristic regions. Overall, the tested environmental variables differed significantly among the five regions. Using indicator species analysis, we distinguished 82 strong indicator species, which had significant environmental preferences for one floristic region. These species can be used as indicators of environmental conditions or to determine which floristic region a certain forest belongs. Given the predicted decreases in rainfall and increases in temperature for tropical lowland forests, our gradient approach suggests that species composition may shift drastically with climate change.

Key words: climate; environmental gradient; floristic composition; species distribution; species indicator; soil.

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.* 1999, Vormisto 2002, Phillips *et al.* 2003; but see Newbery & Proctor 1984, Pitman *et al.* 1999) affect floristic composition. Few studies in the tropics, 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 soil fertility (Swaine 1996, Bongers *et al.* 2004). Contrastingly, 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 1988, Lewis 1991, 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 they are sessile and because many species have widespread distribution (Bakker 2008). Species are considered as bioindicators of their environment when their frequency or abundance within sites of a particular habitat is high compared with other habitats (Dufrêne & Legendre 1997).

Lowland forests 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 particularly the case for Bolivia where three biogeographical regions of South America, Amazonian, Brazilian-Paranense, and Chaco converge in the lowlands (Navarro & Maldonado 2002). The most recent classification for lowland Bolivia 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; Ibisch & Mérida 2003). However, factors affecting the floristic variation in Bolivia are poorly understood due to studies linking vegetation and explanatory environmental variables being 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 analyze plant species composition across 220 1-ha plots in Bolivian tropical lowland forests. Plots are located in forests for timber production, including the humid

forests in the Amazon to the dry forests in the Chiquitano region. 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, geographical location, and observable differences in floristic composition 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 expect a large percentage of species to have significant habitat preferences due to the high habitat heterogeneity (Phillips *et al.* 2003); and (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 SITE.—A total of 220 1-ha plots were selected from the network of permanent sample plots in tropical lowland forests of Bolivia. The plots were established in old growth forests by various research projects and forestry concessionaires (before logging activities), between 1995 and 2007 (Fig. 1; see Acknowledgments for more detail). All plots were established in forests for timber production except four, which were located in an ecological reserve (Reserva Ecológica El Tigre – RET). To date this network and its data base is being coordinated and managed by the Instituto Boliviano de Investigación Forestal (IBIF). The plots are located between
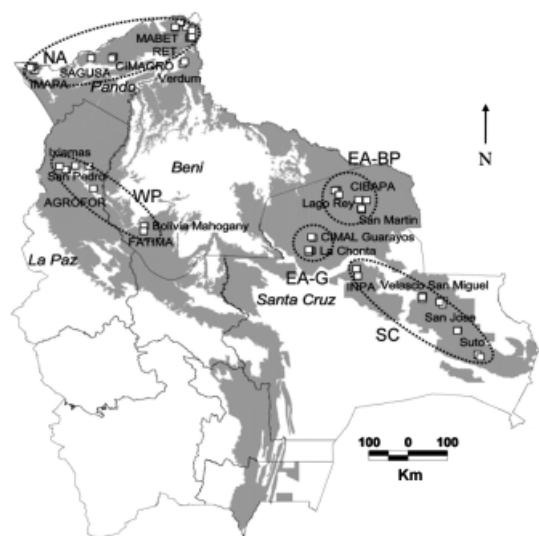

FIGURE 1. Location of the 220 1-ha plots in the five floristic regions of lowland Bolivia: WP, Western pre-Andean (Ixiamas, San Pedro, Agrofor, Bolivia Mahogany, Fátima); NA, Northern Amazon (Imapa, Sagusa, Cimagro, Mabet, RET, Verdum); EA_BP, Eastern Amazon-Bajo Paraguá (Cibapa, Lago Rey, San Martin);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

10–18° N and 59–69° W, mostly in upland areas (*terra firme*; only 5% of the plots were located in areas of seasonal flooding), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from 100 to 500 m asl. Most of the plots are typically square (100×100 m), with 17 of them being rectangular (20×500 m). The plots were selected to represent the gradient in lowland Bolivia, thus covering a wide range of environmental conditions (Table 3).

In tropical lowland Bolivia the precipitation can vary from 600 to 3000 mm/yr from the driest to wettest areas (based on at least 30 yr data, 1970–2007, Servicio Nacional de Meteorología e Hidrología – SENAMHI, unpubl. data). In general, the lowlands in Bolivia experience a 4–7 mo long dry season (with precipitation < 100 mm/mo), 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, to Acrisols and Luvisols in the center, and 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 analysis (PCA). The climatic PCA considered mean annual temperature, mean annual precipitation, total precipitation of the three driest months, length of the dry period (number of months < 100 mm), and length of the drought period (number of months < 50 mm). The first two axes of the climatic PCA explained 94 percent of the variation. The first axis (65%) correlated positively with mean 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 percent 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). More details of soil analysis and climate interpolation can be found in Toledo (2010).

RECORDING OF SPECIES.—In each plot all stems ≥ 10 cm diameter at breast height (dbh, measured at 130 cm height or higher if buttresses were present) were evaluated and identified with a common name by local experts. When necessary, botanical collections were made to verify 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 (*i.e.*, 5% of all plots). The use of frequent 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 (Chave 2008). Two variables per species were considered: the occurrence (*i.e.*, 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 analyses were 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 lengths because its axes are scaled in units of the mean standard deviation of species turnover (Jongman *et al.* 1995).

We contrasted the species composition of plots using a multiple response permutation procedure (MRPP), which is a nonparametric 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 and geological 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 (ISA). This analysis allows for the detection of nonrandom 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 (percentage of average abundance of a given species in a given group over the average abundance of that species in all plots), the relative frequency (percentage of plots in a given group where a given species is present), and the indicator value (IV, in percentage, calculated by multiplying relative abundance with relative frequency). Species with an IV > 25 percent 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 more frequently 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 as defined above. To account for nonlinear 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 but exclude the interaction terms as they 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.

To test whether environmental variables among the five a priori regions were statistically different ($P < 0.05$), 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 carried out using SPSS for Windows 15.0. MRPP and ISA were carried out using PC-ORD 5.12 (McCune & Mefford 1999) and the CA and DCA ordinations were carried out using Canoco for Windows 4.5.

RESULTS

FLORISTIC OVERVIEW.—The 220 plots contained *ca* 89,200 stems ≥ 10 cm dbh and the 100 selected species represent on average 56 percent (range 25–93%) of the stems. For these 100 species, the number of species per plot ranged from 12 to 39. The 100 species represent 36 families and 86 genera (Table S1). Fabaceae (19 species; 29% of all stems) and Arecaceae (seven species; 10%) had the highest number of species and also the highest number of stems, along with Moraceae in the case of stem abundance (18%) (Table S1).

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 together 27 percent 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. S1A). On the DCA axis 2 (8% of explained variation), plots located in Eastern Amazon-Bajo Paraguá were more closely related to the Northern Amazon, and plots located in Eastern Amazon-Guarayos were more closely related to the Western pre-Andean. However, three plots from Western pre-Andean were clustered nearer to Northern Amazon and Eastern Amazon-Guarayos due to very similar floristic compositions. 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 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

TABLE 1. *Relative similarity (Jaccard's index) of floristic composition among all five a priori recognized floristic regions. Pair-wise comparison is based on species occurrence. WP, Western pre-Andean; NA, Northern Amazon; EA_{BP}, Eastern Amazon-Bajo Paraguá; EA_G, Eastern Amazon-Guarayos; SC, Southern Chiquitano.*

Floristic regions	WP	NA	EA_{BP}	EA_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

(Fig. S1B). 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 (Myracrodruon) 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 S1; Fig. S1B).

When species occurrence was related to each floristic region, only ten 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 S1). The ISA test, combining the relative abundance and the relative frequency of each species (Table S2), allowed identification of species that were significant indicators of a particular region (Table S1). 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 *P. 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 2), but their relative importance varied (Fig. 2). While both climatic axes had positive effects, the rainfall axis accounted for 93 percent of the variation in DCA axis 1 and the temperature axis accounted for 54 percent of the variation in DCA axis 2. 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 3). The floristic DCA axis 1 was strongly positively related to annual precipitation (Fig. 3A) 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. 3B), CEC, Ca^{2+}, silt content, and annual temperature.

All five a priori regions were also characterized with respect to their environmental conditions. Overall, the environmental variables tested differed significantly among the five regions (Table S3). 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 a similar percentage of clay except Eastern Amazon-Guarayos.

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 analyses

TABLE 2. *Forward multiple regression of the floristic detrended correspondence analysis (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) both single and squared values are used to account for nonlinear 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.*

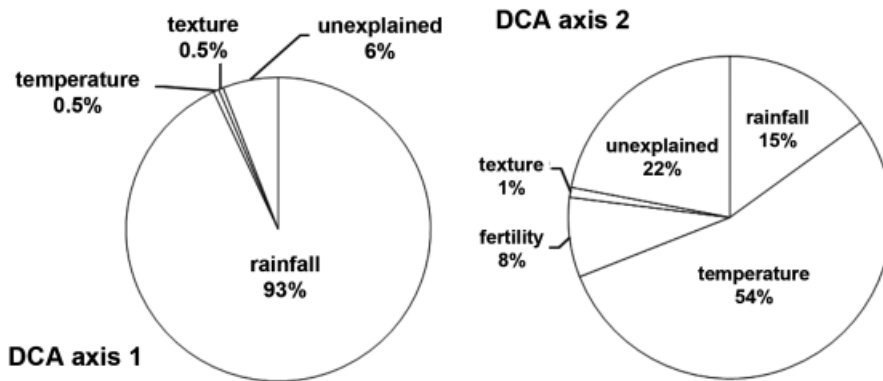|	Climatic axes				Soil axes			*F*	*R^2*
	Rain	Rain^2	Temp	Temp^2	Ferti	Text	Text^2		
DCA 1	1.15***	− 0.81***	− 0.15**	0.07*	–	0.06*	–	661.5***	0.94
DCA 2	− 0.57***	0.50***	0.84***	0.18**	− 0.38***		− 0.16**	121.5***	0.78

FIGURE 2. Percentage of the variation in the detrended correspondence analysis (DCA) floristic axes explained by the environmental principal component analysis (PCA) axes. PCA axes are rainfall, temperature, soil fertility, and soil texture.

divided the lowland forests of Bolivia primarily into two major groups (Southern Chiquitano region vs. the rest; Fig. S1A) and the MRPP analysis distinguished five floristic regions as suggested by our hypothesis. Our results therefore, 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, López *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 1988, 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 S1). 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 (Table S2). *Ceiba* (*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 are most probably related to the environmental differences among the regions (Table S3), 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. These species had a 'narrow' distribution in the country but were highly abundant and frequent in the region they occur. All these ten 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 tropical lowland Bolivia had a relatively wide distribution thus covering different floristic regions (Table S1). *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, *Euterpe precatoria*, *Iriartea 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).

On the basis of the results of this study it can be stated that the 100 woody species provided a good representation of the floristic composition in Bolivian tropical 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, 2000; Terborgh & Andresen 1998) 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 axes explained the most floristic variation while soil axes explained only a very minor part of the variation (Table 2; Fig. 2). 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. The climatic seasonality

TABLE 3. *Range (minimum and maximum) and Pearson correlation of environmental axes and environmental variables with the first and second axis of a floristic detrended correspondence analysis (DCA) analysis on composition and abundance of 100 species across lowland Bolivia. n = 220 plots, *P ≤ 0.05, **P ≤ 0.01. CEC, cation exchange capacity; OM, organic matter; TEB, total exchangeable bases.*

| | | | 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**
Annual temperature (°C)	24.2	26.4	0.61**	0.53**
Dry period	4	7	− 0.90**	− 0.01
(number of month				
< 100 mm)				
Drought period	0	4	− 0.36**	0.44**
(number of month				
< 50 mm)				
Soil fertility				
pH	3.3	7.8	− 0.36**	− 0.60**
Ca^{2+} (cmol/kg)	0.20	13.80	− 0.41**	− 0.70**
Mg^{2+} (cmol/kg)	0.10	7.00	− 0.46**	− 0.54**
Na^{+} (cmol/kg)	0.03	0.19	− 0.21**	− 0.57**
K^{+} (cmol/kg)	0.05	0.79	− 0.50**	− 0.39**
TEB (cmol/kg)	0.4	20.0	− 0.31**	− 0.68**
CEC (cmol/kg)	1.5	20.1	− 0.19**	− 0.73**
Acidity (cmol/kg)	0.0	6.1	0.55**	0.37**
P (cmol/kg)	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**

in southern Neotropics, with a well-defined dry season of variable length, can determine the physiognomy of the vegetation types from semi-deciduous to strongly deciduous. Temperature gradients can also exert a strong control on forest structure and composition along an altitudinal gradient (Takyu *et al.* 2005, Sesnie *et al.* 2009). 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). The floristic variation can be also associated with the effects of lower temperature during the austral winter, with the occasional cold fronts that occur in the region (Prado 2000, Killeen

et al. 2006), or the altitude (100–480 m asl). Although small differences were found between temperature and altitude, they were negatively and highly correlated (Pearson $r = - 0.91$, $P < 0.001$). 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 mean annual precipitation or phosphorous showed stronger correlations with the floristic DCA axes (Pearson $r = 0.94$ and 0.79, respectively) than the multivariate rainfall and temperature axes (Pearson $r = 0.79$ and 0.73, respectively), suggesting that they might be the strongest underlying drivers of floristic variation (Table 3; Figs. 3A and B). In addition, Ca was also strongly correlated with the DCA axis 2 (Pearson $r = 0.70$). 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 periods, as expected (Fig. S1A; Table S3). 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 partially located in the Precambrian shield, while the Western pre-Andean region has geologically younger soils with recently deposited rich sediments (Richter & Babbar 1991, Lips & Duivenvoorden 1996, 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 S3). 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). Although these forests are under the same geological substrate of the Precambrian Shield, soils in the Guarayos region have been subjected to human influences that have resulted in the creation of anthropogenic soils; terra preta (Paz-Rivera & Putz 2009). Our analysis based on floristic composition (Fig. S1A) and environmental conditions has clearly shown that these two areas represent two different floristic regions and are at the same time notoriously different from the Southern Chiquitano forests.

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
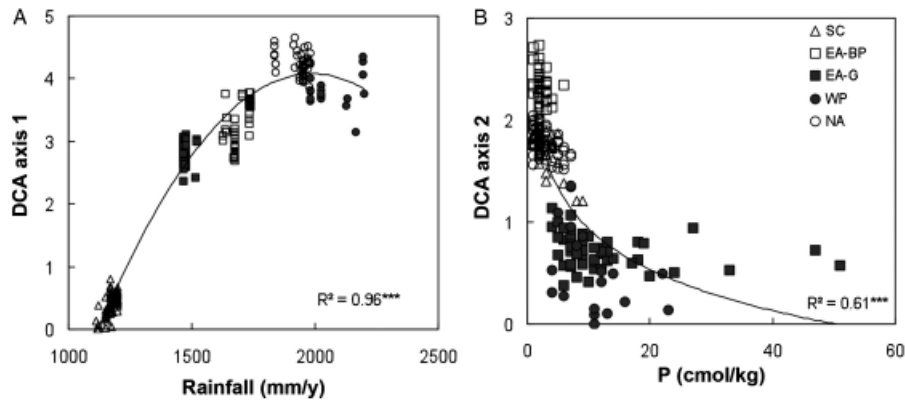
FIGURE 3. Relationships between detrended correspondence analysis (DCA) floristic axes and (A) annual precipitation and (B) phosphorous concentration. Symbols indicate the five floristic regions: WP, Western pre-Andean; NA, Northern Amazon; EA$_G$, Eastern Amazon-Guarayos; EA$_{BP}$ (Bajo Paraguá); SC, Southern Chiquitano. Regression lines, corresponding coefficient of determination (R^2) and significance level are shown (***$P < 0.001$).

soil characteristics and the different sample size. 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.

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 contemporary 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 (see Mayle *et al.* 2000). The effects of historical processes such as past climate and geographic changes are, however, still controversial. It has been suggested that both ancient and recent diversification of species processes could explain current species composition (Gentry 1982, Prance 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 a 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.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Floristic DCA axes scores, floristic region (number of region where the species is indicator), indicator value (IV), significance level (P) and occurrence (x) of the 100 plant species in five floristic regions.*

TABLE S2. *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.*

TABLE S3. *Differences of environmental variables between plots belonging to the five floristic regions.*

FIGURE S1. Scatterplots of the first two axes of a species-site Detrended Correspondence Analysis (DCA) ordination. (A) Plot scores (B) Species scores.

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