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

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Summary

1. The analysis of species distribution patterns along environmental gradients is important for understanding the diversity and ecology of plants and species responses to climate change, but detailed data are surprisingly scarce for the tropics.

2. Here, we analyse the distribution of 100 woody species over 220 1-ha forest plots distributed over an area of c. 160 000 km², across large environmental gradients in lowland Bolivia and evaluate the relative importance of climate and soils in shaping species distribution addressing four multivariate environmental axes (rainfall amount and distribution, temperature, soil fertility and soil texture).

3. Although species abundance was positively related to species frequency (the number of plots in which the species is found), this relationship was rather weak, which challenges the view that most tropical forests are dominated at large scales by a few common species.

4. Species responded clearly to environmental gradients, and for most of the species (65%), climatic and soil conditions could explain most of the variation in occurrence ($R^2 > 0.50$), which challenges the idea that most tropical tree species are habitat generalists.

5. Climate was a stronger driver of species distribution than soils; 91% of the species were affected by rainfall (distribution), 72% by temperature, 47% by soil fertility and 44% by soil texture. In contrast to our expectation, few species showed a typical unimodal response to the environmental gradients.

6. *Synthesis.* Tropical tree species specialize for different parts of the environmental gradients, and climate is a stronger driver of species distribution than soils. Because climate change scenarios predict increases in annual temperature and a stronger dry season for tropical forests, we may expect potentially large shifts in the distribution of tropical trees.

Key-words: climate, environmental filters, gradients, plant-climate interactions, response curve, soil, species distribution, temperature, tropical forest, unimodal response

Introduction

Overlapping plant species distributions determine the species diversity of temperate and tropical communities. 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

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that is actually occupied: the realized niche (Hutchinson 1959). How species are distributed across spatial scales is, therefore, affected by several factors, such as climate, soil, disturbances and biotic interactions. These factors act as filters at different spatial scales and determine which species from the regional species pool are filtered into the local community (Whittaker 1967; Keddy 1992; ter Steege & Zagt 2002).

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 (and especially species combinations) 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). Finally, for successful ecological restoration and the establishment of plantations, better insight into the environmental requirements of the species is needed (Swaine 1996).

One of the general patterns in ecology is that widespread species are more abundant than species of restricted occurrence (Brown 1984; Gaston 1996; Gaston et al. 2000), although many combinations of spread and abundance are possible (Rabinowitz 1981). Pitman et al. (2001) found in western Amazonia that species common at local scale tend to have both high abundance and high frequency (i.e. a high number of plots in which a species is found), and consequently, there might be oligarchies consisting of a few species dominating vast areas of forest. Where environmental heterogeneity is high, however, areas dominated by such predictable oligarchies are expected to be much smaller. Most of our current insights into species distribution come from studying specieshabitat associations at small local scales (Newbery & Proctor 1984; He, Legendre & LaFrankie 1997; Harms et al. 2001; Baltzer et al. 2005). However, most of the climatic variation and much of the geological variation in the lowland tropics occurs at regional scales $> 100 \text{ km}^2$. Quantitative data of species distributions at this scale in relation to climate (McKenzie et al. 2003; Killeen et al. 2006) and soils (Schulz 1960; Ashton 1964; Phillips et al. 2003; Tuomisto 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 environmental requirements, and each species shows therefore an individualistic response to environmental gradients. 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, although many species may occupy the ends of the gradients. Species response curves should differ in shape, amplitude, width and optimum (Huisman, Olff & Fresco 1993; Austin & Gaywood 1994; Jongman, ter Braak & van Tongeren 1995; Oksanen & Minchin 2002).

Most studies have focused on environmental response curves of temperate species (Ejrnæs 2000; Lawesson & Oksanen 2002; Rydgren, Okland & Okland 2003). 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). Only two response curve studies were carried out in the tropics (Bongers *et al.* 1999; Duque 2004). A study in north-west Amazonia found that 88% of the 24 studied tree species responded to the large soil fertility gradient (Duque 2004). A study in West Africa found that 75% 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; Markesteijn *et al.* 2010) 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, Dray & Sabatier 2002). There is also evidence that soil nutrient availability influences species distribution and community composition (Potts *et al.* 2002; John *et al.* 2007).

The aim of this study is to evaluate the relative importance of environmental factors in determining species distributions in tropical lowland forests. We analysed the distribution, in terms of frequency and abundance, of 100 woody species over 220 1-ha forest plots distributed over an area of c. 160 000 km^2 across large environmental gradients in lowland Bolivia. Specifically, we question (i) how species' frequency and abundance are related; (ii) how climate and soil affect the distribution of tropical woody species; and (iii) what is the shape of species response curves to environmental gradients? To our knowledge, this is the largest tropical 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, and 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). Third, as our environmental gradients are long, we hypothesize that the majority of the species will show unimodal response curves to these gradients (Gauch & Whittaker 1972; Huisman, Olff & Fresco 1993).

Materials 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 (Fig. 1). 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 Acknowledgments 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, and these plots were included in the analysis), generally on flat terrain (20% in slopes of hilly areas), and in an altitude range from 100 to 500 m a.s.l. Most of the plots were typically square $(100 \times 100 \text{ m})$, with 11 of them being rectangular (20×500 m). The 220 plots cover a wide range in environmental conditions (Table 1). For a description of the composition, structure and dynamics of these forests, see the study of Toledo et al. (2011a), Toledo et al. (2011b), Toledo et al. (2011c).

Lowland Bolivia is characterized by two rainfall gradients: a south-north gradient where rainfall increases towards the equator with mean annual precipitation ranging from 1100 to 1900 mm and an east-west gradient where mean rainfall increases from 1600 to 2200 mm owing to orographic uplift towards the Andes. However,



Fig. 1. Location of 220 1-ha permanent sample plots in lowland Bolivia. Grey areas indicate the subset of forest area gazetted as permanent production forests. Different number of plots were established in areas under forest management located in four departments: La Paz [(Ixiamas (5 plots), San Pedro (2) and AGROFOR (1)]; Pando [IM-APA (8), SAGUSA (16), CIMAGRO (3) and 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)]. Not all Bolivian forests are included here; for example, the white areas in Pando belong to flooded forests. The white areas in Beni pertain mostly to edaphic savannas, and the white area in Santa Cruz pertains mostly to Chaco shrubland.

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 Hidrología – SENAMHI, unpubl. data). The lowlands in Bolivia experience a 4- to 7-month-long dry season (with precipitation < 100 mm month⁻¹), 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 1-ha plot, 20 soil samples were collected from the first 30 cm of soil with an auger, and a pooled sample of 500 g was analysed within a week after collection at the Center of Tropical Agricultural Research (CIAT-Santa Cruz, Bolivia). The analyses included 12 edaphic variables: particle size (percentage of clay, silt and sand content) using the Bouyoucos hydrometer; exchangeable Ca, Mg, Na, K (in 1 mol L^{-1} ammonium acetate at pH 7); cation exchange capacity (CEC, sum of exchangeable cations plus acidity); acidity (in 1 mol L^{-1} KCl); plant available phosphorus (P, Olsen method); total nitrogen (N, micro-Kjeldahl method); and organic matter (OM, Walkley–Black method). In line with many forest studies, we

Environmental responses of tropical trees 3

measured exchangeable bases rather than total bases, although total bases might provide a better indicator of long-term site productivity.

Climatic data came 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 obtained from SENAMHI. Data from an additional 21 weather stations located in Brazil, Paraguay and Peru were obtained from Agrotecnologia Amazonica (http://www.agteca. com). For each plot, we obtained five climatic variables [annual temperature, annual precipitation, total precipitation of the three driest months, dry period length (no. of months < 100 mm) and drought period length [no. of months < 50 mm], interpolated from the 45 weather stations. Interpolations were made with Surfer 8.0 (Golden Software, Golden, CO, USA) using the kriging interpolation method and nearest-neighbour statistics.

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, Okland & Okland 2003). To summarize the environmental data, we performed, therefore, two independent principal component analyses (PCAs): one for climate and one for soils. The climatic PCA included five climatic variables, and the first two axes 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 included the 12 edaphic variables, and the first two axes explained 68% of the variation. The first axis (48%) correlated positively with variables related to soil fertility (CEC, Ca, Mg, Na, K, P, OM and N) and negatively to 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).

RECORDING OF SPECIES

Plots were established in different forest types in Bolivia and by different field crews. First, we selected 195 species that occurred in at least 11 of the 220 plots (i.e. 5% of the total). This minimum number of occurrences is needed to reliably model species responses to environmental gradients using logistic regression analysis because at least a certain number of presences are needed. We acknowledge that some extremely rare species may be rare because they have strong habitat preferences, but unfortunately, they are too rare to test this hypothesis statistically. Because we were not sure about the consistent identification of these species, we selected for this analysis a subset of 100 species for which we checked their identification and concluded that they were reliably identified in each plot (see Appendix S1 in Supporting Information). The selected 100 species represent 56% of all trees in the 220 plots. 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 [d.b.h., 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

4 M. Toledo et al.

Table 1. Mean, range (minimum and maximum) and ratio (maximum divided by the minimum) of climatic and soil parameters of lowland Bolivian forest plots and their Pearson's correlations with the environmental principal component analysis (PCA) axes. The climatic PCA is based on five climatic variables, and the first climatic PCA axis ('Rainfall axis') explains 65% of the variation, and the second climatic PCA axis ('Temperature axis') explains 29%. The edaphic PCA is based on 12 soil-fertility- and texture-related variables, and the first edaphic PCA axis ('Fertility axis') explains 48% of the variation and the second edaphic PCA axis ('Texture axis') explains 20%

Parameters	Mean	Range	Ratio	Environmental factors	
				Axis 1	Axis 2
				Rainfall axis	Temperature axis
Climate					
Annual precipitation (mm)	1592	1113-2198	2.0	0.93**	0.26**
Driest months (mm)	100	68-262	3.9	0.74**	-0.63**
Annual temperature (°C)	25.3	24.2-26.4	1.1	0.55**	0.78**
Dry period (mo)	5.6	4–7	1.8	-0.95**	-0.24**
Drought period (mo)	2.8	0–4	∞	-0.81**	0.54**
				Fertility axis	Texture axis
Soil fertility					
Ca^{2+} (cmol kg ⁻¹)	3.25	0.2-13.8	69.0	0.91**	-0.22**
Mg^{2+} (cmol kg ⁻¹)	1.35	0.1 - 7	70.0	0.73**	0.04
Na^+ (cmol kg ⁻¹)	0.08	0.03-0.19	6.3	0.83**	0.08
K^+ (cmol kg ⁻¹)	0.27	0.05-0.79	15.8	0.84**	0.08
$CEC \pmod{kg^{-1}}$	5.8	1.5-20.1	13.4	0.92**	0.06
Acidity (cmol kg^{-1})	0.9	0-6.1	∞	-0.52**	0.61**
P (cmol kg^{-1})	5.5	1-51	51.0	0.63**	-0.11*
OM (%)	2.7	0.9-5.2	5.8	0.69**	-0.09
N (%)	0.2	0.05-0.4	8.0	0.78**	-0.20**
Soil texture					
Sand (%)	56.3	2-83	41.5	-0.33**	-0.93**
Silt (%)	22.5	3–68	26.7	0.50**	0.61**
Clay (%)	21.2	6–50	8.3	-0.03	0.82**

n = 220. * $P \le 0.05$, ** $P \le 0.01$. CEC, cation exchange capacity; OM, organic matter. Dry and drought periods refer, respectively, to the number of months with < 100 or 50 mm rainfall month⁻¹.

calculated and are given in Appendix S1. We distinguished four types of distribution patterns based on the relative frequency (low/high) and the average abundance (low/high) in the plots where the species was found. These groups were defined using the median of log_{10} -transformed variables as class breaks.

Species distribution models may use data on presence-only, presence-absence or abundance. In this study, presence-absence was preferred over abundance because variation in the abundance data can be caused by a wide range of processes (competition), species traits (ecological guild, dispersal type) or sampling effects (plot position). We used a multiple logistic regression analysis to construct species response curves to the environmental gradients, using presenceabsence data as the dependent variable. The power of a multiple 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. The inclusion of a quadratic term allows to model bell-shaped response curves. Only those variables that significantly improved the fit of the model were included. The Nagelkerke R^2 indicates the explained variation of this logistic regression model (Nagelkerke 1991) and is analogous to the coefficient of determination in least-squares regression models. 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). The AUC of the ROC plot offers a quantitative, cut-offfree assessment of model performance based entirely on predicted probability values. AUC values were interpreted on the scale proposed by Swets (1988): good = AUC > 0.9, useful = 0.9 > AUC > 0.7and poor = AUC < 0.7. In general, the model performance was good; 95 of 100 species obtained an AUC > 0.7. All the statistical analyses were conducted using spss version 15.0 for Windows (SPSS Inc., Chicago, IL, USA).

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, and 97 species were present in <50% of the plots (Appendix S1). Only three species, *Sweetia fruticosa* (in 86%)



Fig. 2. 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 or abundance (log-transformed data) of each species and defined using the median (grey line) of each parameter: I = low-frequent/low-abundant species (n = 29); II = low-frequent/high-abundant (n = 21); III = high-frequent/ high-abundant (n = 29) and IV = high-frequent/low-abundant (n = 21). See Appendix S1 for species identity.

of the plots), *Pseudolmedia laevis* (74%) and *Casearia gossypio-sperma* (60%), occurred in more than half of the plots. Average density of the species, in the plots where they occurred, ranged from 1.3 to 106 ind. ha⁻¹. *Acosmium cardenasii*, the most abundant species (106 ind. ha⁻¹), was found in only 26% of the plots, while *P. laevis*, the second most abundant species (44 ind. ha⁻¹), was found in 74% of the plots (Appendix S1).

More common (i.e. frequent) species also had higher abundance, but the relation was weak (Pearson's r = 0.31, P < 0.001, Fig. 2). 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 29 species, group II (low frequency and high abundance) had 21 species, group III (high abundance and high frequency) had 29 species, and group IV (high frequency and low abundance) had 21 species (Fig. 2). Because of our species selection criterion (i.e. a species should be present in at least 5% of the plots), we have underestimated the percentage of species found in the low frequency groups (I and II). Examples of species belonging to each group (Fig. 3) are Couratari macrosperma (group I), a species restricted in Bolivia to the wetter 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 subhumid 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. 4). 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% and 100% (average \pm SD, 53 \pm 23; Appendix S1). 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 < 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 (Appendix S1). Rainfall was the most important environmental factor, being significant for 91 of the 100 species studied (Table 2), 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 2).

SPECIES RESPONSES TO THE ENVIRONMENTAL GRADIENTS

Species showed different response curves to the four environmental factors studied (Fig. 4). In general, we distinguished four responses types: a flat curve (indicating no response), a monotonically increasing curve, a monotonically decreasing curve and a unimodal curve (Appendix S1). Of the 91 species responding to rainfall, 40 showed an increasing response curve, 26 a decreasing response and 25 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. Of the 48 species responding to soil fertility, 20 showed an increasing response curve, 25 a decreasing response and only 3 a unimodal response curve. Finally, of the 44 species that responded to the soil texture, nine had an increasing, 35 a decreasing and no species a unimodal response curve (Table 3). Examples of different species responses are given in Fig. 2. Attalea phalerata shows a 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. Amburana cearensis and C. macrosperma showed an opposite response to the rainfall gradient but responded similarly to the soil fertility gradient.

Discussion

In this study, we analysed large-scale distribution patterns of tropical tree species in relation to climatic and edaphic gradients. We show that there is indeed a positive relationship between species frequency and abundance, although the explained variation is surprisingly low, indicating species with highly deviating patterns. Climate was a stronger driver of species distribution patterns than soils, and, in contrast to our expectations, typical unimodal response curves were rare, despite the large environmental gradients considered.

6 M. Toledo et al.



Fig. 3. Examples of the four species distribution patterns in lowland Bolivia: (a) *Couratari macrosperma* (Cm), (b) *Attalea phalerata* (Ap), (c) *Amburana cearensis* (Ac) and (d) *Spondias mombin*. The modelled probability of occurrence of each species in relation to (e) the rainfall gradient, and (f) soil fertility gradient are also shown. The gradients are summarized by the principal component analysis axes, with high axis values indicating a high rainfall and a high soil fertility. Distribution patterns are based on the frequency–abundance relationship: I = low frequency/low abundance, II = low frequency/low abundance, and IV = high frequency/low abundance. Filled dots on the map indicate species presence and open dots indicate species absence across 220 1-ha permanent plots.

SPECIES DISTRIBUTION: FREQUENCY-ABUNDANCE RELATIONSHIP

We found a positive relationship between occurrence and abundance of species (Fig. 2), 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 (e.g. *P. laevis*), other species deviated from this general trend (Appendix S1), and the average explained variation was low (Fig. 2, $r^2 = 0.09$). *Acosmium cardenasii*, for example, was the most abundant species 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⁻¹), 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⁻¹, respectively. Hence, although Pitman *et al.*'s (2001) statement that most Amazonian forests are dominated at large scales by oligarchies of a small number of common species is intellectually appealing, it seems to be an oversimplification based on 24 plots in two sites only. Because our regional study of 220 1-ha plots encompassed longer environmental



Fig. 4. Response curves and probability of occurrence (0-1) of 100 tropical plant species in relation to four environmental gradients (as summarized by the four principal component analysis axes): (a) rainfall, (b) temperature, (c) soil fertility and (d) soil texture across 220 1-ha plots distributed in lowland Bolivia.

Table 2. Number of species with significant response curves and the mean $(\pm SD)$ 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 environmental factors refer to the multivariate principal component analysis axes. The mean is based only on the species that significantly responded to the environmental factors

Environmental factors	No.	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

gradients (and drier forests) than studied by Pitman *et al.* (2001), we found different patterns. Using longer gradients enhances the possibility to detect that some species specialized for specific parts of the environmental gradient, thus combining a high abundance with a low frequency.

ENVIRONMENTAL FACTORS AFFECTING SPECIES DISTRIBUTION

Climate was a more important factor than soil in affecting the species distribution in line with the second hypothesis.

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 Table 3. Number of Bolivian lowland forest species with specified shapes of response curves, based on occurrence data, to the four environmental factors. The environmental factors refer to the multivariate principal component analysis axes

Environmental factors	Response curve shape					
	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		

Whereas over 91 of our species were affected by the climatic factors, only 47 were affected by soil factors (Fig. 4; Table 2). Similarly, 59% of 89 rare and endemic West-African rain-forest plant species responded to rainfall, whereas only 9% of the species were related to available cations (Holmgren & Poorter 2007). In mountain forests, conifer species distributions were also more frequently (79%) related to climatic variables than to other biophysical variables such as soils and hydrology (40–50%) (McKenzie *et al.* 2003). Several reasons might explain the higher importance of climate over soils in this and other studies. First, climate varies over larger spatial scales and acts, therefore, as an environmental filter at these scales, whereas soils show smaller-scale variation and act as an additional filter under homogeneous climatic conditions at smaller spatial scales. Second, our tropical forests are at the drier end of the rainfall gradient (1100–2200 mm year⁻¹), and water availability is clearly a more limiting factor here than for forests at the wetter part of the rainfall gradient, where nutrient availability might become a limiting factor. Third, the climate was based on long-term data and averaged out over large spatial scales and might, therefore, have been more reliably estimated than soil conditions, which were sampled at a small scale at one point in time. Fourth, nutrient pool sizes, as measured in this study, might not be a good indicator of the nutrients that are available to plants, and plant responses might be more tightly related to nutrient mineralization rates (Ordoñez et al. 2009). Of course, soils can be very variable, and extreme soils such as limestone karsts, granitic outcrops and white sands can have a dramatic effect on species occurrence. But such extreme soil types are rare in our sampled forests and may be also relatively rare in the lowland tropical forest zone.

In terms of number of species responding to environmental factors, the factors rank in importance as rainfall > temperature > soil fertility > soil texture. Several studies that evaluated only climatic variables 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; Engelbrecht *et al.* 2007). Experimental studies in the shadehouse (Poorter & Markesteijn 2007) and the field (Engelbrecht, Kursar & Tyree 2005) also conclude that seasonal drought has a stronger effect on growth and survival over other factors, as it immediately affects cellular processes and plant physiology (Chaves, Maroco & Pereira 2003). Plant water availability and drought sensitivity are, therefore, important determinants of the distribution of tropical tree species.

Temperature affected 72% of the species, which is surprising giving the small difference in mean annual temperature between sites (24.2-26.4 °C). Tropical tree species should be sensitive to such small temperature variation, given the fact that they experience - and are adapted to - a very small range in temperatures: within the lowland tropics, mean annual temperature ranges only from 24 to 27 °C, and seasonal monthly temperature variation is <4 °C over a band of 20° latitude around the equator (Wright, Muller-Landau & Schipper 2009). Small changes in temperature may have drastic effects on tropical species and thus on their distribution patterns (Wright 2010) as many of these species are adapted to low temperature variation and lack populations inhabiting a wider range of temperatures (Colwell et al. 2008). It is also likely that the mean annual temperature is a good proxy for the minimum temperatures faced at the sites. Bolivian forests are situated at the southern margin of the tropical forest biome and experience regular cold fronts ("surazos") coming from Patagonia in which the temperature may drop in a few hours to 6-15 °C (Montes de Oca 1997). Their frequency, duration and intensity are higher in the south than in the north, and they are even felt up to the centre of the Amazon. Across nine Bolivian lowland

weather stations, the minimum monthly temperature recorded varied from 13.8 to 17.3 °C and is highly correlated with the average annual temperature (Pearson's r = 0.87, P < 0.01, n = 9). Such cold fronts may lead to reduced photosynthetic activity and chilling injury of tropical trees (Feng & Cao 2005), thus affecting the growth, survival and distribution of tropical tree species.

Soil fertility affected, surprisingly, only 47% of the species. Soil fertility may act as a more important environmental filter at smaller spatial scales. Indeed, edaphic conditions are found to control species distribution in climatically homogeneous environments and small spatial scales (Newbery & Proctor 1984; ter Steege et al. 1993; Clark, Clark & Read 1998; Sollins 1998; Clark, Palmer & Clark 1999; Harms et al. 2001; Tuomisto et al. 2003). Soil texture was nearly as important as soil fertility and affected the distribution of 44% of the species. Soil texture may modify in an important way plant water availability through its effect on water-holding capacity, and it may also constrain species distribution, by creating waterlogged or anaerobic conditions (ter Steege et al. 1993; Kozlowski 2002). Intriguingly, most species (35) that show a significant response to soil texture have a higher probability of being present at lower values of the texture axis (Fig. 4d). These low PCA values are indicative of higher sand content and, hence, a lower water-holding capacity, suggesting that these species prefer edaphically dry soils or are better competitors there. This enforces the importance of water availability as a driver of tree distributions.

Pitman et al. (1999) concluded that the great majority of the Upper Amazonian tree species (85%) are habitat generalists. They defined a specialist as a species that can only be found in one out of four forest types, related to river dynamics (successional floodplain forest, mature floodplain forest, terra firme forest and swamp forest). This identification of habitat as a basis for identifying a specialist is rather coarse, and without doubt, many species are found occasionally in suboptimal habitats, resulting in few specialists only. However, by really measuring environmental conditions and formally analysing environmental response curves, we found that most species have clear preferences for certain environmental conditions and show that for more than 65% of the species, climatic and soil conditions could explain most of the variation in occurrence ($R^2 > 0.50$). Perhaps the higher number of responding species and the high explained variation result from the larger climatic gradient covered in our study compared to Pitman et al.'s study and from the fact that climate is a more important driver of species distribution than soils are. Additionally, most of the species (87%) were significantly affected by more than one environmental factor (Appendix S1), indicating that multiple rather than single environmental factors explain the distribution of tropical tree species (cf. Swaine 1996).

THE SHAPE OF SPECIES RESPONSE CURVES

Theoretically, plant species should exhibit a unimodal response when large environmental gradients are considered (Gauch & Whittaker 1972; Austin & Smith 1989; Oksanen &

Minchin 2002), but the question is to what extent theory meets reality. Of the species that responded significantly to the environmental axes, only 27% showed a unimodal response to rainfall, 14% to temperature, 6% to soil fertility and 0% to soil texture (Table 3). In West Africa, only 8% of the tree species evaluated showed a unimodal response curve to the cumulative water deficit (Bongers *et al.* 1999), while in north-western Amazonia, 42% of the tree species evaluated showed unimodal responses to soil fertility (Duque 2004). Unimodal responses may, therefore, be the exception, rather than the rule for tropical trees.

Several reasons may explain the relative lack of unimodal responses. First, species may show their optima outside the sampled portion of the gradient (ter Braak & Looman 1986). Although our climatic gradient was not that long (rainfall differed by a factor of two between the wettest and dries site), the length of the edaphic gradient was considerable: sand content varied a by a factor of 40, phosphorus concentration by a factor of 70 across plots (Table 1). It is, therefore, surprising that we did not find more unimodal responses to soil conditions.

Second, species may have wider environmental tolerances than expected. Species responses to soil fertility and soil texture were surprisingly wide or flat (Fig. 4c,d), and therefore, most species are relative generalists with respect to soil characteristics. They may be filtered out of the environment only under extreme abiotic soil conditions such as the extremely poor white sand soils (Bongers, Engelen & Klinge 1985, Bánki 2010). This is in line with Duque (2004) who found that extreme abiotic conditions (anoxia, toxicity) rather than differences in resource availability may underlie the bell-shaped response curves to edaphic gradients (cf. Austin 1990) in (flooded) Amazonian forests.

Third, species are not in equilibrium with the environment, because of historical contingencies (e.g. ice ages and forest refugia) and/or dispersal limitation (Svenning & Skov 2007). This is especially the case for climate, which may show strong directional changes over time (Malhi & Wright 2004) and to which long-lived tree species may lag behind in their response.

Fourth, other abiotic and biotic factors than the ones we studied, such as topography (Guillaumet 1967), fire (Hoffmann *et al.* 2009) and disturbances, shape species distribution. Time after disturbance is a good proxy for changes in multiple environmental conditions (Lebrija-Trejos *et al.* 2010). In the Bolivian Amazon, 31% of the 51 species evaluated showed a bell-shaped response in their abundance with time after shifting cultivation (Peña-Claros 2003), probably because of species differences in dispersal and differences in light-dependent growth and survival. Several species included in our study are typical pioneers (e.g. *Cecropia, Cedrela, Jacaranda, Trema, Urera* and *Zanthoxylum*), and they may respond more strongly to disturbance than to climatic or edaphic conditions.

Lastly, methodological issues may also play a role. Our analysis was based on presence–absence data, and much more complex response curves may be found when abundance data are used (Bongers *et al.* 1999).

FINAL REMARKS

We found only a weak positive relationship between species frequency and abundance, which challenges the view that most tropical forests are dominated at large scales by a few common species. Species responded clearly to environmental gradients (climate and/or soil, cf. Engelbrecht et al. 2007; Baltzer et al. 2008), and for most of the species (65%), climatic and soil conditions could explain most of the variation in occurrence $(R^2 > 0.50)$. This challenges the idea that most Amazonian tree species are generalists with respect to environmental conditions. Surprisingly, only few species-environment relations show the expected unimodal response curves, suggesting either that very long environmental gradients are needed or that other factors shape species distribution patterns as well. Based on the number of species responding and the variation explained, the environmental factors rank in importance as follows: rainfall > temperature > soil fertility > soil texture. Climate (rainfall and temperature) was, therefore, a stronger driver of species distribution patterns than soils were. As climate change scenarios predict for tropical forests an increase in annual temperature and a stronger dry season (IPCC 2007), we may expect potentially large shifts in the distribution of tropical forest trees. In Bolivia, for example, 65% of the species evaluated (i.e. species with a unimodal or an increasing response to rainfall) may decline with a stronger dry season, whereas 39% of the species may decline with a future increase in temperature (Table 3).

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Supporting Information

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

Appendix S1. Overview of the distribution of 100 woody species in lowland Bolivia with their relative frequency, density, and responses to four environmental factors (rainfall, temperature, soil fertility, and soil texture).

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