Soil Effects on Forest Structure and Diversity in a Moist and a Dry Tropical Forest

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ABSTRACT

Soil characteristics are important drivers of variation in wet tropical forest structure and diversity, but few studies have evaluated these relationships in drier forest types. Using tree and soil data from 48 and 32 1 ha plots, respectively, in a Bolivian moist and dry forest, we asked how soil conditions affect forest structure and diversity within each of the two forest types. After correcting for spatial effects, soil-vegetation relationships differed between the dry and the moist forest, being strongest in the dry forest. Furthermore, we hypothesized that soil nutrients would play a more important role in the moist forest than in the dry forest because vegetation in the moist forest is less constrained by water availability and thus can show its full potential response to soil fertility. However, contrary to our expectations, we found that soil fertility explained a larger number of forest variables in the dry forest (50 percent) than in the moist forest (17 percent). Shannon diversity declined with soil fertility at both sites, probably because the most dominant, shade-tolerant species strongly increased in abundance as soil fertility increased.

TROPICAL TREE SPECIES DIVERSITY IS DETERMINED BY A VARIETY OF FACTORS that operate at different spatial scales. At the continental scale, plant diversity is determined largely by annual rainfall and dry season length (*e.g.*, Gentry 1988, Clinebell *et al.* 1995, ter Steege *et al.* 2003, 2006) with tree species richness typically increasing with increasing annual rainfall and decreasing seasonality (Pitman *et al.* 2002, ter Steege *et al.* 2003, 2006). At regional or local scales, in contrast, plant diversity may be determined by dispersal limitation and/or environmental conditions. Dispersal limitation refers to the fact that a limited ability to disperse seeds may affect species distributions, and hence, community composition and diversity (Tuomisto *et al.* 2003a). Among environmental conditions, soil type and topography play an important role in shaping diversity as both of them influence water and nutrient availability (Potts *et al.* 2002, Miyamoto *et al.* 2003, Philips *et al.* 2003, Tuomisto *et al.* 2003a, b). Huston (1979) predicted that as nutrient availability increases, species richness should decrease because a few competitive species should exclude the other species. Indeed, Huston (1980) found that diversity decreases with soil fertility in Costa Rica, perhaps because many Costa Rican soils are rather fertile due to their volcanic origin. Other studies, in contrast, report that species diversity does not vary (Clinebell *et al.* 1995, Tuomisto *et al.* 2002 for Pteridophytes) or even increases with soil fertility (Duivenvoorden

1996, Poulsen *et al.* 2006). Given these contrasting results, there is obviously still much to learn about how soils, and other factors (*e.g.*, climate), affect tree species diversity in the tropics.

Studies examining the effect of soil variables on tree diversity and species distribution have mostly used proxy variables such as soil types and topography to describe soil conditions (*e.g.*, Duivenvoorden 1996, Clark *et al.* 1999, Harms *et al.* 2001, Gunatilleke *et al.* 2006). It is clear, however, that plants do not respond to soil proxy variables *per se* but to the physical and chemical characteristics that underlie them (Sollins 1998). Studies that have measured specific soil characteristics (*e.g.*, nutrient availability and texture) suggest that species richness, distribution, and composition are mostly influenced by cation availability (measured as Ca, Mg, K), cation exchange capacity, Al concentration, and by the percentage of sand in the soil (Hall & Swaine 1981, Clinebell *et al.* 1995, Swaine 1996, Potts *et al.* 2002, Tuomisto *et al.* 2002, 2003b, Philips *et al.* 2003, Hall *et al.* 2004, Vormisto *et al.* 2004, Paoli *et al.* 2006, Poulsen *et al.* 2006).

Most studies published to date have focused on the relationship between soil characteristics, diversity, and composition in wet forests (> 1800 mm/y; but see Clinebell *et al.* 1995, Swaine 1996, ter Steege *et al.* 2003). Here, we present new data to evaluate whether the same relationships between forest characteristics and soil conditions hold for drier tropical forests. Consequently, the objective of this study was to determine how soil texture and fertility affect forest structure and tree diversity *within* two forest types

receiving < 1600 mm/y of rainfall. To this end, we took advantage of a large dataset (80 1 ha plots) available for a moist semi-evergreen (*sensu* Hall & Swaine 1981) and a dry deciduous forest in lowland Bolivia. For each forest type, we evaluated soil-vegetation relationships at the mesoscale (1–100 km^2) because, in this way, a broad range of soil conditions is sampled, thus increasing the power to detect significant relationships (Paoli *et al.* 2006). We predicted that (1) soil characteristics will have qualitatively similar effects on forest characteristics within each forest type; and (2) soil fertility-vegetation relationships will be stronger in the moist forest than in the dry forest because moist forest trees are less constrained by water availability and can thus more fully express their potential responses to soil nutrient conditions. This study may provide a first important step in addressing these predictions, although we realized that the ultimate test requires a large number of plots in several replicated forest sites.

METHODS

RESEARCH SITE.—The study was carried out in a moist semi-evergreen tropical forest (henceforth referred to as 'moist forest') and a dry deciduous tropical forest (henceforth referred to as 'dry forest') in Bolivia. The moist forest site is the 100,000 ha timber concession of La Chonta, 30 km east of the town of Ascensión de Guarayos (15°47′ S, 62°55′ W). The vegetation represents forests that are transitional between wet Amazonian forests and Chiquitano dry forest (Killeen *et al.* 2006, Toledo *et al.* 2011). Annual precipitation in the region is 1580 mm (range 1269–1871 mm, data collected at La Chonta sawmill from 1994 to 2006), with five months receiving < 100 mm precipitation (May through September) and one month (July) during which potential evapotranspiration exceeds rainfall. At the peak of the dry season, the soil water potential is − 1.6 MPa in the first 20 cm of topsoil (L. Markesteijn, unpubl. data). During the dry season, about 30 percent of the canopy trees are deciduous. The forest is situated on the southwestern border of the Brazilian Shield, characterized by rolling hills with thin soil mostly derived from gneiss, granitic, and metamorphic rocks (Crochane 1973, Navarro & Maldonado 2004). Soils have been described as ultisols with high fertility due to human influence, as *ca* 20 percent of the area is being covered by anthropogenic soils (Paz-Rivera & Putz 2009). The dry tropical forest site is about 140 km from the moist forest site on the 33,000 ha private property of the timber company INPA Parket, 50 km to the southeast of the town of Concepción (16°06′ S, 61°42′ W). The vegetation belongs to the dry Chiquitano forest formation, which is the largest area of dry forest remaining in the Neotropics (Parker *et al.* 1993). Annual precipitation in the region is 1160 mm (range 799–1859 mm, data from Administración de Aeropuertos y Servicios Auxiliares a la Navegación Aérea at Concepción, collected from 1943 to 2005), with seven months receiving < 100 mm (April through October) and four months (June through September) during which potential evapotranspiration exceeds rainfall. At the peak of the dry season the soil water potential is − 5.1 MPa in the first 20 cm of topsoil (L. Markesteijn, unpubl. data). During the dry season nearly all canopy trees are deciduous. The area is also on the southwestern border of

the Brazilian Shield (Cochrane 1973, Navarro & Maldonado 2004) but the soils are nutrient-poor oxisols. The two sites belong to different ecoregions and differ substantially in species composition (Toledo *et al.* 2011; Instituto Boliviano de Investigación Forestal [IBIF] unpubl. data).

Both sites are part of the Long-Term Silvicultural Research Program (LTSRP) of the IBIF. Plots of the LTSRP are large (21.25 ha in the dry forest and 27 ha in the moist forest), replicated (8 plots in the dry forest and 12 plots in the moist forest), and received one of four treatments varying in management intensity (Peña-Claros *et al.* 2008). In each large plot there are four 1 ha subplots in which trees ≥ 10 cm diameter at breast height (dbh) are measured, providing a total of 32 plots in the dry forest and 48 plots in the moist forest. For the current study, we used the pretreatment data (*i.e.*, before logging was applied). Minimum and maximum inter-plot distance of the 1 ha subplots range from 0.1 to 8.2 km in the moist forest, and from 0.3 to 20.7 km in the dry forest.

DATA COLLECTION.—Trees were identified to species (or assigned to morphospecies), measured for dbh, assigned to a crown exposure class, and evaluated for liana loads. Trees were assigned to one of four liana infestation classes (Adler & Synott 1992): 1 = no lianas; 2 = lianas on stem; 3 = lianas on stem and crown; and 4 = lianas completely covering crown. Crown exposure was visually estimated using a five-point scale (Clark & Clark 1992) in which 1 = no direct overhead light and little lateral light; 2 = no direct overhead light but moderate or substantial lateral light; 3 = vertical light on part of the crown; 4 = vertical light on the whole crown; and 5 = exposed emergent crown. Species and morphospecies were assigned to one of four functional groups based on existing literature (Jardim *et al.* 2003, Justiniano *et al.* 2003, Mostacedo *et al.* 2003, Poorter *et al.* 2006) and field observations: 1 = shade-tolerant species; 2 = partial shade-tolerant species; 3 = long-lived pioneer species; and, 4 = pioneer species; about 1.5 percent and 1.8 percent of trees in the moist and dry forest, respectively, could not be assigned to a functional group. The functional groups indicate the ability of a species to tolerate closed canopy shade within a certain forest type. The dry forest canopy casts a lighter shade than the moist forest canopy, as the canopy is relatively more open, the leaf area index is lower, and the leaflets are smaller compared with the moist forest. As a result, a shade tolerant species in the dry forest might be more light-demanding compared with a shade tolerant species in the moist forest.

Soil samples were collected in 2005, two to five years after logging depending on forest site. Soil samples were, however, collected in areas not affected by logging, *i.e.*, away from logging gaps and skid trails. Soil parameters are, therefore, good indicators of pre-logging soil conditions. Samples were collected from the first 15 cm of topsoil below the litter layer (*i.e.*, layer with identifiable plant material was excluded) at 12 fixed locations in each of the 32 plots in the dry forest and in 47 of the 48 plots in the moist forest. Samples were air-dried in the field and pooled for each plot. Physical and chemical characteristics were determined at the Soil Laboratory of the Centro de Investigación Agricola Tropical (CIAT), Santa Cruz, Bolivia. The analyses included particle size (percentage of

clay, silt and sand content) using the Bouyoucos hydrometer; pH (on 10-g soil samples, using 50 mL of distilled water and equilibrating for 90 min); electrical conductivity (on the solution prepared for measuring pH); exchangeable Ca, Mg, Na, K (in 1 M ammonium acetate at pH 7); total exchangeable bases (TEB; sum of exchangeable cations); cation exchange capacity (CEC; TEB plus acidity); acidity (in 1 M KCl); base saturation (percent of CEC on the total exchangeable capacity of the soil); plant available P (Olsen method); organic matter (Walkley-Black method); and, total N (micro-Kjeldahl method).

DATA ANALYSES.—The 14 soil parameters were condensed into three variables using Principal Component Analyses (PCA). For the two forests combined one PCA was run with the physical soil properties as indicators of soil water holding capacity (*cf.* Swaine 1996), while another PCA was run with the chemical soil properties as indicators of soil fertility. Separate PCAs for chemical and physical characteristics were done not only to reduce the dimensionality of the data but also two have three axes that conceptually represent soil features related to soil fertility and soil water holding capacity. Additional advantages of this approach are that the soil axes represent the same environmental variables, and are expressed in the same units for both forest types. The first axis of the soil physical PCA and the first two axes of the soil chemical PCA were then used to determine the effect of soil on forest structure and diversity. They are referred to as 'texture axis,' 'nutrient axis 1' and 'nutrient axis 2,' respectively. These axes were chosen because they summarized patterns observed in the data and explained most of data variation.

Forest structure was described using the following variables: total tree density (number of individuals ≥ 10 cm dbh/ha); subcanopy and canopy tree densities (the moist forest has a taller stature than the dry forest, and subcanopy trees were, therefore, defined as individuals < 30 cm dbh in the moist forest, and as individuals < 20 cm dbh in the dry forest); basal area (m^2/ha); proportion of liana-free trees (liana infestation classes 1 and 2); average degree of liana infestation across all trees in the plot; and, the proportion of trees with exposed crowns (crown positions 4 and 5). The size structure of the forest was described as the slope of the size-class frequency distribution using diameter class bins of 10 cm (both axes ln-transformed). The slope varies from zero if it is a uniform size distribution, to negative if it is a negative exponential size distribution.

The following variables related to species diversity were also obtained for each forest sample: species richness; Shannon diversity index ($H' = -\Sigma p_i [\ln p_i]$, where p_i is the proportion of individuals found for species); dominance of the most common species (number of trees of the most common species [*Pseudolmedia laevis* for the moist forest and *Acosmium cardenasii* for the dry forest] divided by the total number of trees, multiplied by 100); and a successional index. The successional index was calculated as follows: first, the density of each species found in a given plot was multiplied by the functional group category to which each species belongs. These values were then summed up for each plot and divided by the total tree density in that particular plot. Consequently, the successional index varies between 1 (only shade-tolerant species) and 4 (only pioneer species), depending on the density of the various functional groups.

To evaluate how soils affect vegetation characteristics, one should take the effect of spatial pattern into account, as both forest characteristics and environmental characteristics might be spatially structured (Borcard *et al.* 1992). To separate the spatial from environmental effects on forest structure and diversity, we used a two-step approach. First, for each site separately, we conducted a forward multiple regression of each forest characteristic on the *x* and *y* coordinates of the plot. To better describe the spatial pattern we included also the quadratic and cubic terms of the coordinates and their interactions to obtain a cubic trend surface regression (Borcard *et al.* 1992). The R^2 of this regression indicates the amount of variation explained by local spatial variation (which includes as well spatially structured environmental variation). In a second step, we used either the forest variables directly (when space did not have an effect) or the residuals of the forest variables (when space had an effect), to determine what soil characteristics best predict forest structure, and species diversity in each forest type. In the latter case we do a conservative test how environment shapes forest variables, as only the role of non-spatial environmental variation is evaluated (Borcard *et al.* 1992). For each site separately, we performed forward stepwise multiple regressions for each forest characteristics against PCA texture axis 1, nutrient axis 1, and nutrient axis 2. All statistical analyses were conducted with SPSS 17 (SPPS Inc.). Successional index was ln-transformed and variables given in percentage (trees free of lianas, trees in high light, dominance by single species) were arcsine-transformed before data analyses to approximate normality. Residuals of regressions met the assumptions of normality. Additionally, we tested whether response variables showed a non-linear relationship with environmental factors. We did so by repeating the forward multiple regression analysis of our second step, by including this time the quadratic terms of each of the environmental variables. The quadratic term of the environmental variables were either not included in the final models or they explained very little of the additional variation in the data (range between 0.2 percent and 3 percent). Consequently, we have not included the quadratic terms into the models, as we think that linear relationships are more parsimonious and straightforward.

RESULTS

ASSOCIATION AMONG SOIL CHARACTERISTICS.—The moist and dry forest studied differed significantly in all soil characteristics with the exception of total N (see Table S1). The moist forest was, in general, more fertile than the dry forest (Table S1). For both forest types combined, the first axis of the soil physical characteristics PCA accounted for 62 percent of the variation and was strongly negatively correlated with clay and positively correlated with sand percentage (Table 1). The PCA of the soil chemical characteristics revealed two main gradients. The first axis explained 48 percent of the variation and was strongly positively related to CEC, Ca, and pH (Table 1). The second axis explained 20 percent of the variation and was strongly positively related to organic matter content and K (Table 1).

DIFFERENCES IN FOREST STRUCTURE AND DIVERSITY.—The moist and dry forest studied differed significantly in all structural and diversity characteristics measured, with the exception of basal area (see Table

TABLE 1. *Loading of the soil parameters on the first two axes of a soil texture PCA and a soil nutrient PCA. Analyses were done for both forest types combined (N = 79 plots). Significance levels are based on a Spearman's correlation between soil properties and PCA axes):* *P ≤ 0.05, **P ≤ 0.01, ***P ≤ 0.001, ns = non significant.*

	Both forests	
Soil characteristics	Axis 1	Axis 2
Soil texture characteristics		
Sand (%)	0.68***	− 0.73***
Silt (%)	0.63***	0.78***
Clay (%)	− 0.99***	− 0.01[ns]
Variation explained by PCA (%)	62.1	37.9
Soil chemical characteristics		
pH (water ph)	0.86***	− 0.36***
Electrical conductivity (μS/cm)	0.76***	− 0.06[ns]
Ca (cmol/kg)	0.95***	− 0.09[ns]
Mg (cmol/kg)	0.42***	0.22*
Na (cmol/kg)	0.65***	− 0.12[ns]
K (cmol/kg)	0.16[ns]	0.86***
CEC (cmol/kg)	0.96***	− 0.01[ns]
Base saturation (%)	0.75***	− 0.11**
P (mg/kg)	0.72***	− 0.22*
Organic matter (%)	0.16[ns]	0.92***
Total N (%)	0.63**	0.62***
Variation explained by PCA (%)	47.8	20.2

S2). On average, the dry forest had a higher tree density than the moist forest (437 vs. 368 trees/ha) but the two forests did not differ in total basal area (19.7 m²/ha). The moist forest had higher species richness than the dry forest (59 vs. 34 species per ha). The most dominant species in the moist forest (*Pseudolmedia laevis* [Ruiz & Pav.] J.F. Macbr.) represented, on average, 25 percent of the sampled individuals in each 1-ha plot, while the most dominant species in the dry forest (*Acosmium cardenasii* H.S. Irwin & Arroyo) represented, on average, 36 percent of the sampled individuals in each 1-ha plot. The successional index in the moist forest was higher than in the dry forest, which indicates that the moist forest contains more trees that belong to light-demanding species.

SPATIAL AND ENVIRONMENTAL EFFECTS ON STRUCTURE AND DIVERSITY WITHIN FOREST TYPE.—The multiple regression analysis indicated that space had a significant effect on 50 percent of the forest characteristics evaluated at each site, and explained for those characteristics more of the variation in the dry forests (on average 34 percent) than in the moist forest (17 percent) (Table 2). Space had a significant effect on forest structure (*e.g.*, tree density, basal area) but not on species diversity. Liana infestation in the dry forest was highly spatially structured (R^2 = 0.68), whereas in the moist forest there was no spatial effect at all.

Once the significant spatial effect was removed, a multiple regression analysis was used to determine the effect of soil characteristics on forest structure and diversity in each forest type. Soil characteristics were significantly related to a larger number of forest variables (9 vs. 3) in the dry forest than in the moist forest (Table 2), and explained for those variables a larger proportion of the variation (average R^2 = 0.26 vs. 0.13). These results suggest that soil plays a more important role in determining the structure and diversity of the dry forest than of the moist forest. Of all 24 vegetation-environment relationships analyzed, seven forest characteristics were significantly affected by the texture axis, four by nutrient axis 1 and four by nutrient axis 2.

Soil characteristics tended to have different effects on structure and diversity in the dry and moist forest (Table 2). For example, the basal area increased significantly with the texture axis (*i.e.*, decreasing clay content) in the dry forest, but was not related to texture in the moist forest (Fig. 1A). Shannon diversity decreased significantly with nutrient axis 2 (*i.e.*, increasing organic matter and K) in the dry forest (Fig. 1B), while it decreased significantly with nutrient axis 1 (*i.e.*, increasing fertility) in the moist forest (Fig. 1C). A similar positive response was observed for the dominance by a single species in both forest types (Fig. 1D and E). Only one forest characteristics was affected by the same soil axis in both forests: the percentage trees in high light conditions decreased in both forests with the texture axis (*i.e.*, decreasing clay content, Table 2). For correlations between forest characteristics and individual soil variables see Table S3.

DISCUSSION

In this study, we asked how soil characteristics affect forest structure and diversity within each forest type, and whether their effect varied with forest type. After correcting for the spatial effect, soil conditions had a moderate effect on forest parameters, being stronger in the dry than in the moist forest (Table 2). Additionally, soil characteristics tended to have a different effect on structure and diversity in dry and moist forest (Table 2; Fig. 1). It should be mentioned, however, that soil not only affects vegetation but that vegetation may drive some of the soil variability that we measured (Wardle *et al.* 2004, Townsend *et al.* 2008).

SPATIAL EFFECTS.—Spatial effects were equally strong as environmental effects and when significant, they explained a higher amount of variation (Table 2). Often such spatial effects are interpreted as being caused by dispersal limitation as a limited dispersal capability should affect species distribution, composition, and diversity (*e.g.*, Condit *et al.* 2002, Tuomisto *et al.* 2003a, Macía *et al.* 2007). However, spatial effects were—surprisingly—not significant for any of our diversity measures but instead were driving forest structure. These results may be caused by spatial variation in topography and canopy gap disturbance (*e.g.*, Borcard *et al.* 1992, Poorter *et al.* 1994). For example, in the dry forest, liana infestation showed a strong spatial effect (Table 2), which may be due to the association of lianas with past canopy gap disturbances. This link is also supported by the fact that the successional index showed only a spatial effect in the dry forest (Table 2).

TABLE 2. *Spatial and environmental effects on forest structure and diversity of a Bolivian moist- (N = 48 plots) and dry forest (N = 32 plots). The effect of space is analyzed with a forward multiple regression of forest variables on the x and y coordinates of each plot. Simple, quadratic, and cubic x and y terms and their interactions were included to allow for a cubic trend surface regression. The effect of environment is analyzed with a forward multiple regression of the forest variables (when space had no significant effect) or the residuals of the forest variables (when space had a significant effect) on the environmental variable. Environmental variables are soil texture axis, and two soil nutrient axes. Regression coefficient (of environmental variables), coefficient of determination (R^2) and significance (p) of the model are provided.* *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$, ns = non significant.

| | Moist forest | | | | | | | | Dry forest | | | | | | | |
| | Space | | Environment | | | | | | Space | | Environment | | | | | |
Variable	R^2	p	Text axis	Nut axis 1	Nut axis 2	R^2	F	p	R^2	p	Text axis	Nut axis 1	Nut axis 2	R^2	F	p
Structure																
Density	0.12	*						ns	0.18	*	20.1		18.7	0.29	5.9	**
Density subcanopy trees	0.21	***						ns	0.25	**						ns
Density canopy trees	0.19	**						ns	0.20	*	11.6	8.9		0.32	6.9	**
Basal area	0.13	*						ns		ns	1.8		1.0	0.39	9.2	***
Slope population structure	0.14	**						ns		ns	− 0.06			0.15	5.3	*
Trees free of lianas		ns						ns	0.58	***						ns
Degree liana infestation		ns						ns	0.68	***						ns
Trees in high light	0.23	***	− 5.04			0.15	8.0	**		ns	− 2.3			0.19	7.1	*
Diversity																
Species richness		ns						ns		ns	2.4			0.18	6.8	*
Shannon diversity index		ns		− 0.23		0.16	8.6	**		ns			− 0.15	0.33	14.9	***
Dominance single species		ns	4.1			0.09	4.6	*		ns			4.2	0.29	12.3	***
Successional index		ns						ns	0.17	*		− 0.04		0.20	7.4	*

ARE SOIL-VEGETATION RELATIONSHIPS THE SAME IN MOIST AND DRY FOREST?—We hypothesized that soil-vegetation relationships would be similar in both forest types. This was the case only for one of the 12 variables studied (Table 2). Soil axes that were significantly related to a certain forest characteristic in the dry forest were not significantly related to that forest characteristic in the moist forest, and vice versa (Table 2; Fig. 1). One explanation for these results could be that the range of soil conditions differs between the forest types. The range for texture axis and the nutrient axis 2 is larger in the dry forest compared with the moist forest (texture: 3.4 vs. 1.6, nutrient axis 2: 4.2 vs. 2.8), and this might explain why more forests characteristics were significantly related to these axes in the dry forest than in the moist forest (Table 2). The nutrient axis 1 had a similar length in both forests (2.8 vs. 3.0), and affected a similar number of forest variables in both forests.

ARE NUTRIENTS A MORE IMPORTANT SOIL RESOURCE IN MOIST FOREST THAN IN DRY FOREST?—We hypothesized that soil nutrients would play a more important role in the moist forest because vegetation in the moist forest is less constrained by water availability and thus can show its full potential response to soil fertility. Contrary to our expectation, however, we found that soil fertility affected a larger number of forest variables in the dry forest (50 percent) than in moist forest (17 percent) and explained more of the variation in the data (30 percent vs. 12 percent, Table 2).

One explanation for these counterintuitive results could be that nutrients were less limiting in the moist forest than in the dry forest. Soils in the dry forest had a relatively low pH (5.3 compared with 7.0 in the moist forest) and were poor in nutrients (average CEC in dry forest is 5.5 cmol/kg compared with 9.3 cmol/kg in the moist forest). Therefore, species in the dry forests may be particularly responsive to small increases in fertility. In contrast, about 20 percent of the moist forest area is underlain by very fertile, anthropogenic black soil (Paz-Rivera & Putz 2009). Because of these generally richer soils, the moist forest plants may have shown less response to within-site differences in soil fertility.

VEGETATION RESPONSES TO NUTRIENTS ARE MEDIATED BY THE DOMINANT SPECIES.—PCA soil nutrient axes mainly affected diversity-related parameters (Table 2). In the dry forests, Shannon diversity declined with increasing organic matter and K (dry forest, Fig. 1B) and in the moist forest, it declined with increasing soil fertility (Fig. 1C). This is in line with Huston's hypothesis (1979) that with increase nutrient availability a few competitive species should exclude the other species. Indeed, in both forest types the abundance of the shade tolerant dominant species (*Pseudolmedia laevis* in the moist forest, *Acosmium cardenasii* in the dry forest) increased with soil fertility (Table 2; Fig. 1D and E). The abundance of the dominant species determined, in turn, the patterns of the Shannon diversity (in the moist forest) and the successional index (in the dry forest), as these variables are negatively correlated with dominance
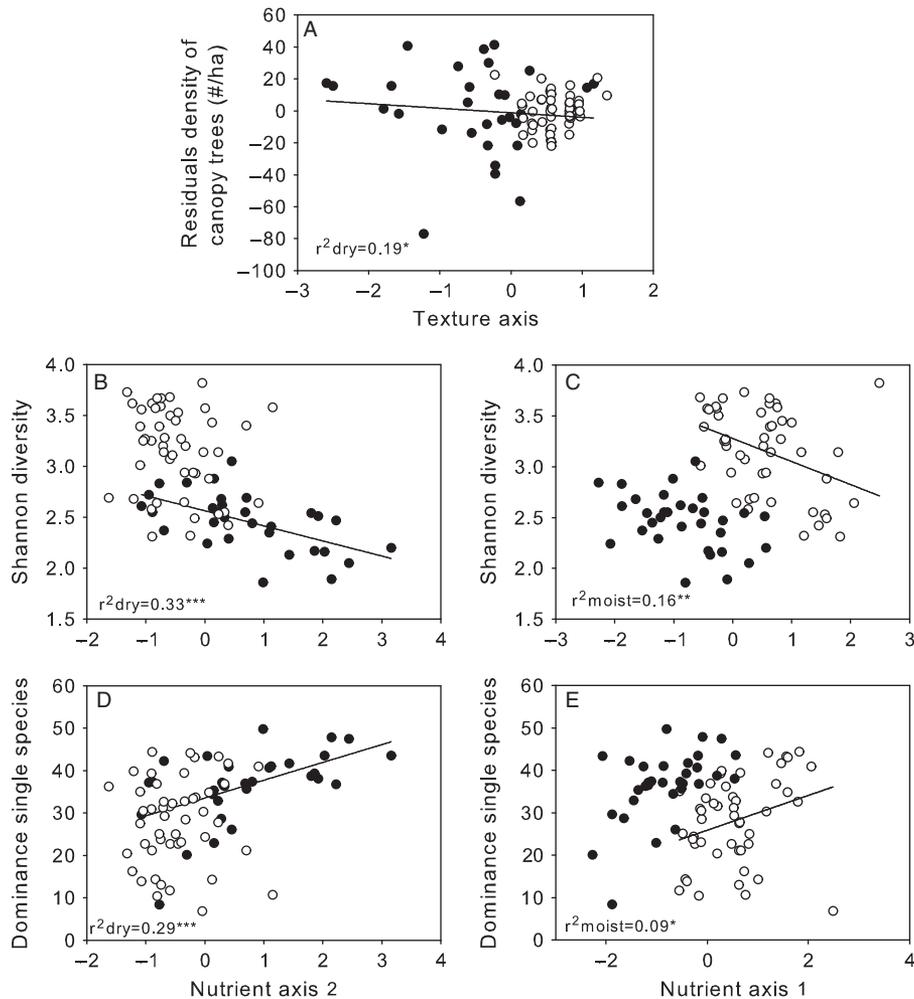
FIGURE 1. Relationships between forest characteristics and soil PCA axes for dry forest plots (*N* = 32, closed symbols) and moist forest plots (*N* = 47, open symbols). Density of canopy trees vs. the texture axis (A), Shannon diversity vs. nutrient axis 2 (B) or vs. nutrient axis 1 (C), Dominance single tree species vs. nutrient axis 2 (D) or vs. nutrient axis 1 (E). The spatial effect on forest characteristics has first been removed, and the residuals were then related to the environmental axes (when applicable). The texture axis represents a gradient from high to low percentage clay. The nutrient axis 1 represents a gradient from low to high soil fertility. The nutrient axis 2 represents a gradient from low to high levels of organic matter content and K. Regression lines, coefficients of determination (R^2), and significance levels are shown. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

(Pearson correlations, $R \geq -0.85$, $P < 0.001$ in all cases). An increase in the dominant species resulted in a decrease in species diversity and successional index (*i.e.*, fewer light-demanding trees).

Most studies that evaluated soil-vegetation relationships in the tropics have focused on wet forests, with an annual rainfall > 2000 mm. Compared with these forests, our sites are both relatively dry, less species-rich, and show stronger dominance. For example, in the moist forest, *Pseudolmedia laevis* comprised 25 percent of the stems in the forest (range 8–49 percent of individuals in the 1 ha plots), and in the dry forest, the Chiquitano forest endemic *Acosmium cardenasii* made up as much as 36 percent of the stems (range 2–58 percent of individuals in the 1 ha plots). In these drier systems, there is therefore more scope for canopy dominants to modify community-level responses. Interestingly, it has been suggested than in wet forests the dominant species (in terms of frequency of plots occupied) should be soil generalists (Paoli *et al.*

2006), whereas in our drier forests, the canopy dominants (in terms of abundance) show very clear responses to soil resources, especially so in the dry forest site (Table S3).

DIFFERENT VEGETATION RELATIONSHIPS WITH P AND N IN MOIST AND DRY FORESTS.—A greater proportion of vegetation variables were significantly related to P in the moist forest (6 out of 12) than in the dry forest (2 out of 12, Table S3). P has also been found to play a major role in the distributions of dipterocarp trees in Borneo (Paoli *et al.* 2006), on *Entandrophragma* species in Central Africa Republic (Hall *et al.* 2004), and to have a negative effect on species richness in Costa Rica (Huston 1980).

In the dry forest, more soil-vegetation relationships were related to Ca, organic matter, N, Mg, and CEC (Table S3). It is likely that organic matter is not the cause, but rather the result of, variation in vegetation structure and composition. Organic matter and

N are rarely included in studies looking at the effect of soil on species diversity or distribution. In the few studies in which organic matter and N were included, they were weakly or not linked to species diversity and distribution (Huston 1980, Clinebell *et al.* 1995, Swaine 1996, Costa *et al.* 2005, Paoli *et al.* 2006), reportedly because tropical rainforest soils tend to be P- rather than N limited (Sollins 1998).

Dry forest trees may have higher N requirements than moist forest trees because of higher leaf turnover rates and higher leaf nitrogen concentrations. As most dry forest trees shed their leaves in the dry season, they have a higher nutrient loss compared with species in wet forests. Moreover, the nitrogen concentration per unit leaf mass is generally higher for dry than wet forest species (Holbrook *et al.* 1995). For example, at our study sites, average leaf N concentration is 3.7 percent for dry forest species vs. 2.0 percent for moist forest species (L. Poorter *et al.* unpubl. data). Such high nitrogen concentrations may be part of a water saving strategy in dry forests as they allow for higher photosynthetic rates for the same stomatal aperture (Wright *et al.* 2001).

CONCLUSIONS.—Soil nutrient and soil texture have independent effects on forest structure and diversity. Vegetation responses to nutrients were mediated by the dominant, shade-tolerant species in each forest type. In contrast to what is reported for wetter forests (*cf.* Pitman *et al.* 2001), the dominant species in these drier forests are not soil generalists and they respond clearly to local variation in soil conditions. Soils had a different impact in dry and moist forest and explained more of the (variation in) vegetation responses in the dry forest than in the moist forest. Although this is a fairly large study, it only concerns two forest sites, and therefore, it is important to determine whether these results hold for other tropical forests at the lower end of the rainfall gradient.

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SUPPORTING INFORMATION

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

TABLE S1. *Soil characteristics of a moist forest and a dry forest in lowland Bolivia.*

TABLE S2. *Structure and diversity of a moist forest and a dry forest in Bolivia.*

TABLE S3. *Correlation coefficients between soil physical and chemical characteristics and structure and diversity of two Bolivian forests.*

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