Soil phosphorus and disturbance influence liana communities in a subtropical montane forest

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Abstract

Questions: What are the effects of soil, topography, treefall gaps, tree species composition, and tree density on liana species composition and total liana abundance?

Location: A 6-ha permanent plot in a subtropical montane forest in northwest Argentina.

Methods: Multiple regressions were used to quantify associations of liana species composition and total liana abundance with edaphic, disturbance and tree community variables. Gradients in liana and tree species composition were quantified using principal components analysis (PCA).

Results: Liana species composition was correlated most strongly with soil phosphorus concentration ($R^2 = 0.55$). Total liana abundance increased with phosphorus and the density of recent treefall gaps ($R^2 = 0.60$).

Conclusions: In our study area, liana composition and abundance are most strongly correlated with features of the physical environment, rather than host tree characteristics. Our results support the hypothesis that recent increases in liana abundance in mature tropical forests may be related to increased rates of gap formation.

Keywords: Climbers; Interstitial organisms; Soil nutrients; Treefall gaps; Woody vines; Yungas.

Nomenclature: Zuloaga & Morrone (1999)

Introduction

Lianas (woody climbing plants) are important elements of tropical and subtropical forests, where they constitute 10-20% of the stems and 10-44% of

the woody species diversity (Gentry 1991; Hegarty & Caballé 1991). Several studies have reported a recent increase in liana abundance in mature tropical forests (Phillips et al. 2002; Wright et al. 2004). This increase has been accompanied by a suite of changes in forest dynamics, structure and composition (Wright 2005; Lewis 2006), including increased tree recruitment and mortality (Baker et al. 2004; Lewis et al. 2004; Phillips et al. 2004; but see Clark et al. 2003; Clark 2004). Thus, there are multiple potential explanations for increased liana abundance, including increased abundance of favourable host trees, increased rates of canopy gap formation (Phillips et al. 2002; Schnitzer 2005) and shifts in abiotic conditions (Schnitzer 2005; Lewis 2006).

Understanding the causes of increased liana dominance will require a greater understanding of the factors controlling liana community structure. Because forest biomass is dominated by trees, lianas may behave as "interstitial organisms" (sensu Huston 1995), implying that they are more sensitive to the density and composition of the "structural organisms" (trees) than to the underlying environmental conditions (e.g. soil and topography). Some studies have found significant associations between lianas and particular tree species or guilds (Putz 1984; Schnitzer et al. 2000) or between lianas and tree properties (Talley et al. 1996a, b; Nabe-Nielsen 2001; Malizia 2003; van der Heijden et al. 2008). However, such associations may be weak (Carse et al. 2000; Pérez-Salicrup et al. 2001; Malizia & Grau 2006), suggesting an important role for nontree factors in structuring liana communities.

In contrast to the above interstitial viewpoint, liana community structure may depend primarily on the underlying physical environment. For example, liana abundance increases with soil nutrient availability (Putz & Chai 1987; Laurance et al. 2001; DeWalt et al. 2006) and decreases with soil moisture (Schnitzer 2005; but see Ibarra-Manríquez & Martínez-Ramos 2002; DeWalt et al. 2006).

Canopy disturbances, such as treefall gaps, are also likely to play an important role in controlling liana community structure. Liana abundance tends to increase with canopy disturbance (Putz 1984;

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Schnitzer et al. 2000; Laurance et al. 2001; Schnitzer & Carson 2001; Ibarra-Manríquez & Martínez-Ramos 2002; Malizia & Grau 2008), which may reflect changes in the host community (e.g. increased density of trellises; Putz 1984) and/or the physical environment (e.g. increased availability of light and belowground resources; Denslow et al. 1998; Scharenbroch & Bockheim 2007).

Numerous studies have explored associations between liana community structure and host trees, edaphic conditions, topography and disturbances (e.g. Putz 1984; Balfour & Bond 1993; Laurance et al. 2001; Pérez-Salicrup et al. 2001; Schnitzer & Carson 2001; Ibarra-Manríquez & Martínez-Ramos 2002; Schnitzer 2005; DeWalt et al. 2006; Malizia & Grau 2006, 2008). However, there is little consensus on the main factors controlling liana community structure, in part because most studies have focused on just one or a few factors.

Here, we assess the effects of soil, topography, disturbance and host trees on liana community structure within a 6-ha plot in a subtropical montane forest. Compared to some tropical forests, our system has low tree and liana richness (23 species ha^{-1} of trees > 10 cm in diameter, and 11 species ha⁻¹ of lianas $\geq 2 \,\mathrm{cm}$ in diameter) and a high number of individuals per species (Grau & Brown 1998; Grau 2002; Malizia 2007). These features allow for wellreplicated species-level sampling, which facilitates tests for association between tree and liana species composition. Furthermore, the varied topography within our study site allows us to assess the role of numerous environmental factors while controlling for potentially confounding factors at broader spatial scales (e.g. landscape-scale disturbance regime; regional abundance of different liana species).

Methods

Study area

The study was conducted in a 6-ha $(200 \times 300 \text{ m})$ permanent plot at 1000 m elevation in Parque Sierra de San Javier, Tucumán, Argentina $(26^{\circ}76'\text{S}, 65^{\circ}33'\text{W})$. Annual rainfall is 1300–1500 mm, which is distributed in a monsoonal regime with dry winters and rainy summers (Hunzinger 1997). Mean annual temperature is 18°C, with frosts from June to August. Topography, which is highly variable within the plot (Fig. 1), influences soil moisture and tree species composition (Grau et al. 1997).

Vegetation is characteristic of the lower montane zone of the Argentine "Yungas," the



Fig. 1. Topographic map (contour interval = 5 m) of the 6-ha plot showing the 13 sampling units. Quadrats $(20 \times 20 \text{ m})$ were grouped into sampling units based on slope and aspect. The 990-m and 1000-m contours are labelled.

southernmost extension of neotropical Andean montane forest (Brown et al. 2001). The plot is located in mature forest with an average of 23 tree species ha⁻¹ \geq 10 cm diameter, including deciduous and evergreen species. The tree canopy (15-30-m high) is dominated by *Blepharocalyx salicifolius* (Myrtaceae), Cinnamomum porphyrium (Lauraceae) and Pisonia zapallo (Nyctaginaceae). The tree subcanopy (5-12-m height) is dominated by Eugenia uniflora (Myrtaceae), Piper tucumanum (Piperaceae) and Allophylus edulis (Sapindaceae). Light selective logging occurred ~ 50 years ago, probably for Cedrela lilloi (Meliaceae) and Juglans australis (Juglandaceae), with two cut stumps found in the plot. The disturbance regime is dominated by treefall gaps (Grau & Brown 1998; Grau 2002).

Data collection

A 6-ha permanent plot consisting of $150 \ 20 \times 20 \text{ m}$ quadrats was established in 1992. All living

trees $\geq 10 \text{ cm}$ in diameter at breast height (dbh) were tagged, measured for dbh, identified to species and mapped (App. 1). Trees were remeasured every 5 years. For the present study, we used the 2002 remeasurement data.

In 2003, we identified to species and permanently marked all liana individuals $\geq 2 \text{ cm}$ diameter (1.3 m from the ground surface) on all standing and living trees $\geq 10 \text{ cm}$ dbh. We defined a liana individual as a stem that was clearly rooted in the soil with no aboveground connections to other rooted individuals. We also recorded the diameter of additional stems $\geq 2 \text{ cm}$ diameter (at 1.3 m) that branched from an individual <1.3 m from its base. Thus, we quantified both the number of liana individuals and stems (Table 1) attached to living trees, which constituted the vast majority of lianas in the plot.

We grouped the 150 quadrats into 13 topographically uniform sampling units (Fig. 1). Because nearby quadrats are not expected to be statistically independent (Legendre 1993), grouping minimized the effect of pseudoreplication on our analyses. We recorded 13 microenvironmental variables for each sampling unit, nine soil variables (% sand, silt and clay; pH; concentrations of organic matter, phosphorus, total nitrogen and potassium; and soil moisture), two topographic variables (slope and aspect) and two disturbance variables (density of recent and old treefall gaps) (App. 2).

Soil chemistry and texture analyses were based on a single compound sample collected from each sampling unit during the 2005 dry season. Samples (20 cm depth) were extracted with a soil borer from five evenly spaced locations across the sampling

Table 1. Liana species recorded in the study plot, numbers of individuals and stems and loadings on the first PCA axis (PC1). *This species was confused with *Cissus tweediana* in Malizia & Grau (2006, 2008).

| Liana species | Family | Individuals | Stems | PC1 |
|-------------------------------|---------------|-------------|-------|-------|
| Cissus striata* | Vitaceae | 586 | 722 | -0.10 |
| Chamissoa altissima | Amaranthaceae | 445 | 515 | -0.12 |
| Celtis iguanaea | Celtidaceae | 352 | 424 | -0.38 |
| Vernonia fulta | Asteraceae | 247 | 371 | -0.41 |
| Macfadyena unguis- | Bignoniaceae | 211 | 230 | 0.30 |
| Serjania meridionalis | Sapindaceae | 148 | 188 | -0.55 |
| Malpighiaceae sp. | Malpighiaceae | 134 | 138 | 0.41 |
| Acacia tucumanensis | Fabaceae | 108 | 130 | -0.80 |
| Hebanthe occidentalis | Amaranthaceae | 65 | 67 | -1.04 |
| Pisoniella arborescens | Nyctaginaceae | 35 | 35 | -0.93 |
| Muehlenbeckia sagittifolia | Polygonaceae | 3 | 3 | |
| Baccharis trinervis | Asteraceae | 1 | 1 | |
| Unidentified | | 17 | 20 | |
| Total | | 2352 | 2844 | |

unit; the five samples were then thoroughly mixed to form the compound sample. Compound samples were analysed using a commercial laboratory (Tecnosuelo, San Miguel de Tucumán, Argentina) for all soil variables except moisture (SAMLA 2004).

Soil moisture was quantified from the 2005 compound samples and from a second set of compound samples collected in 2006. All soil samples were collected during the dry season after a rain-free period of at least 7 days, so our soil moisture analysis reflects conditions of relatively high water stress. We calculated dry season soil moisture content by comparing fresh and oven-dried weight. Soil moisture was measured separately for each of three subsamples extracted from each compound sample; these three values were averaged to yield a single value per sampling unit. We used the average of the 2005 and 2006 soil moisture values in our analysis (App. 2).

Topography of each sampling unit was quantified in terms of slope and aspect, which affect both soil moisture and light availability. These topographic variables complement our direct measurements of dry season soil moisture. Slope was calculated from the topographic map (Fig. 1) using the lowest and highest points in the sampling unit and the horizontal distance between the two points. Slope ranged from 3° to 46° (App. 2). Aspect was assigned an ordinal value indicating increasing water availability: northeast and southwest = 1, east = 2, southeast and south = 3. None of the sampling units had north or northwest aspects (Fig. 1).

To describe the disturbance history of each sampling unit, we estimated the density of recent and old treefall gaps (number of gaps per quadrat; App. 2). We define a gap as a fallen tree (dead or alive) or branch with a minimum diameter of 50 cm and a minimum length of 5 m. Gaps ranged between 5 and 40 m in length. By defining gaps according to fallen trees/branches (rather than direct observation of canopy openings) allowed us to quantify the disturbance history of each sampling unit using dendroecological methods (Grau et al. 2003). "Recent gaps" were formed between 1997 and 2002 (i.e. up to 6 years old at the time of the 2003 liana census) and were mapped in the field in 2002 by systematically searching the entire plot for trees and branches that had fallen since the previous gap census in 1997. "Old gaps" occurred between 1975 and 1996 (i.e. 7-28 years old at the time of the 2003 liana census), and were mapped and dated by Grau (2002) using dendroecological methods or direct observation. In our study site, these methods can be used to date treefalls using the following types of information (see Grau 2002 for details): (1) establishment dates of Solanum riparium (determined from annual growth rings), an abundant pioneer that typically germinates during the first year post-disturbance; (2) the age of resprouts of C. porphyrium, an abundant multi-stemmed species that produces annual rings and resprouts prolifically; treefalls of this species, or of other species that impacted C. porphyrium individuals, can be aged by aging the C. porphyrium resprouts; (3) establishment or release dates of individuals of C. lilloi, J. australis and Duranta serratifolia, all light-demanding species with annual rings; and (4) the size of individuals of Bohemeria caudata and Urera baccifera (both pioneer species), which were assumed to have established soon after the treefall; these species do not produce annual rings, but their ages can be estimated from observed growth rates.

Data analysis

We considered both detrended correspondence analysis (DCA) and principal components analysis (PCA) to quantify gradients in liana and tree species composition (number of liana stems or tree individuals per species) across the 13 sampling units. We omitted species with fewer than five total liana stems or five tree individuals, and log(x+1) transformed the species densities (McCune & Grace 2002). Gradient lengths from DCA were short (<1for both lianas and trees), suggesting that PCA was more appropriate (Lepš & Šmilauer 2003). We only present the PCA results, which was performed on the correlation matrix of species densities. According to the Rnd-Lambda randomization test in PCORD (McCune & Grace 2002), only the first axes in both the liana and tree PCAs had eigenvalues significantly greater than expected under the null hypothesis of random species distributions (Peres-Neto et al. 2005). Therefore, subsequent analyses included only the first PCA axes, which explained 34% and 26% of the variation in liana and tree composition, respectively. Hereafter, we refer to these axes as "liana composition" and "tree composition."

Pair-wise scatter plots among all response (liana composition and total liana density) and explanatory variables (13 microenvironmental variables described above, plus tree composition and total density of trees $\geq 10 \text{ cm dbh}$) revealed no clear nonlinear relationships. Therefore, we used Pearson correlations and multiple linear regressions to quantify relationships among the variables. Due to the small number of sampling units (13) and the large number of explanatory variables, we had insufficient degrees of freedom to examine all variables simultaneously in multiple regressions. Therefore, we adopted the following protocol: to identify candidate variables for inclusion in multiple regressions, we first calculated Pearson correlations between the two dependent variables in each sampling unit and each of the 15 explanatory variables. Variables with significant univariate correlations were then used as candidates for inclusion in multiple regression models. For each dependent variable, we ran both forward and backward selection algorithms to identify the model with the highest R^2 that only included significant (P < 0.05) effects. Pair-wise correlations between the explanatory variables are shown in Table 2.

Results

We recorded a total of 2352 liana individuals $(\text{mean} = 392 \text{ individuals ha}^{-1})$ and 2844 liana stems, belonging to 12 species and 10 families (Table 1). We recorded a total of 2429 tree individuals > 10 cm dbh (mean = 405 individuals ha⁻¹) belonging to 33 species and 22 families (App. 1). Soils had loam and sandy-loam textures, and were moderately acidic (mean pH 5.57, range 5.03-6.36). All sampling units had high organic matter (mean 5.50%; range 3.34-6.08%). The mean value for phosphorus was 18.5 ppm (range 8.0–27.0 ppm), for nitrogen was 0.29% (range = 0.18-0.32%) and for potassium $0.72 \text{ me } 100 \text{ g}^{-1}$ (range 0.42-0.87 me $100 \,\mathrm{g}^{-1}$). The variables with the highest coefficients of variation were phosphorus, recent gap density and slope (App. 2).

Liana composition was correlated with phosphorus (r = -0.76, P = 0.002) and tree composition (r = 0.67, P = 0.01). However, only phosphorus was significant when both explanatory variables were considered together in multiple regressions. Thus, the final regression model for liana composition only included phosphorus (adjusted $R^2 = 0.55$, $F_{1,11} = 15.5$, P < 0.002). Because most species had negative loadings on the liana composition axis (Table 1), the negative association between liana composition and phosphorus implies that most liana species increased in abundance with increasing phosphorus.

Total liana density was correlated with phosphorus (r = 0.60, P = 0.03) and the density of recent treefall gaps (r = 0.60, P = 0.03), and both of these variables remained significant in multiple regressions (adjusted $R^2 = 0.60$, $F_{2.10} = 10.1$, P < 0.004).

| | Tree density | Ηd | Total nitrogen (%) | Phosphorus (ppm) | Potassium (me 100 g ⁻¹) | Soil moisture availability (%) | Density of recent gaps | Density of old gaps | Sand (%) | Silt (%) | Clay (%) | Organic matter (%) | Aspect | Slope (°) |
|--------------------|-----------------|-------|-----------------------|---------------------|--|-----------------------------------|------------------------|------------------------|-------------|--------------|--------------|-----------------------|-------------|--------------|
| Tree composition | 0.20 | -0.40 | -0.03 | -0.68^{*} | 0.11 | 0.58^{*} | -0.14 | -0.30 | 0.16 | -0.13 | -0.21 | -0.04 | 0.52 | -0.34 |
| Tree density | | -0.32 | -0.44 | -0.08 | -0.06 | -0.53 | 0.18 | -0.44 | 0.19 | -0.16 | -0.23 | -0.44 | -0.59^{*} | 0.23 |
| Hd | | | 0.37 | 0.03 | 0.56^{*} | -0.06 | -0.23 | 0.28 | -0.49 | 0.47 | 0.52 | 0.37 | 0.04 | 0.21 |
| Total nitrogen (%) | | | | 0.17 | -0.18 | 0.39 | 0.37 | 0.56^{*} | -0.59^{*} | 0.58^{*} | 0.59^{*} | 1.00^{**} | 0.45 | -0.27 |
| Phosphorus (ppm) | | | | | -0.43 | -0.44 | 0.07 | 0.42 | -0.01 | -0.03 | 0.06 | 0.17 | -0.28 | 0.07 |
| Potassium | | | | | | 0.18 | -0.60^{*} | -0.36 | -0.05 | 0.06 | 0.04 | -0.18 | -0.01 | 0.12 |
| $(me100 g^{-1})$ | | | | | | | | | | | | | | |
| Soil moisture | | | | | | | -0.12 | 0.20 | -0.02 | 0.02 | 0.01 | 0.39 | 0.66^{*} | -0.37 |
| availability (%) | | | | | | | | | | | | | | |
| Density of recent | | | | | | | | 0.29 | -0.25 | 0.29 | 0.20 | 0.37 | -0.33 | 0.20 |
| gaps | | | | | | | | | | | | | | |
| Density of old | | | | | | | | | -0.23 | 0.21 | 0.27 | 0.56^{*} | 0.12 | 0.17 |
| gaps | | | | | | | | | | | | | | |
| Sand (%) | | | | | | | | | | -0.99^{**} | -0.99^{**} | -0.59^{*} | -0.15 | 0.25 |
| Silt (%) | | | | | | | | | | | 0.98^{**} | 0.59^{*} | 0.14 | -0.25 |
| Clay (%) | | | | | | | | | | | | 0.59^{*} | 0.16 | -0.24 |
| Organic matter | | | | | | | | | | | | | 0.45 | -0.27 |
| (%) | | | | | | | | | | | | | | |
| Aspect | | | | | | | | | | | | | | -0.61^{*} |

Both partial correlation coefficients were positive (phosphorus: r = 0.70, P = 0.01; gaps: r = 0.70, P = 0.01). Thus, total liana density increased with both factors, which is consistent with the above results for liana composition. The congruence of these results follows from the fact that the liana composition axis was strongly correlated with liana density (r = -0.88).

Discussion

In our subtropical study area, soil phosphorus concentration and the density of recent treefall gaps (i.e. up to 6 years old) appear to be the most important factors structuring liana communities. Total liana density increased with both of these factors, and both associations were significant in multiple regressions. Liana composition was correlated with soil phosphorus and tree species composition, but only phosphorus was significant in multiple regressions. Neither liana composition nor abundance was correlated with the density of trees \geq 10-cm dbh.

We explored a wide range of factors (tree composition and abundance, canopy disturbance and edaphic/topographic variables) that have been hypothesized to structure liana communities. However, given the inter-relatedness among these factors, our limited sample size (6-ha plot partitioned into 13 sampling units) and the observational nature of our study, it is not possible to draw strong inferences from our analysis as to the causal factors structuring liana communities. For example, the fact that liana species composition was more strongly correlated with soil phosphorus than with tree species composition does not necessarily reflect the causal relationships among these variables, which may all affect each other. Thus, we caution that our results should be interpreted in light of other observations from the literature, which we now discuss.

In our study, lianas do not appear to behave as interstitial organisms that respond primarily to tree density and/or tree species composition after accounting for other factors, such as soil phosphorus. This result is consistent with other local-scale studies (e.g. Nabe-Nielsen 2001; Pérez-Salicrup et al. 2001). However, host tree characteristics may exert a stronger influence on liana communities at broad geographic scales (van der Heijden & Phillips 2008). Nonetheless, our results do suggest an important indirect role for trees in structuring liana communities via the formation of canopy gaps. This result is consistent with other studies that have found lianas respond favourably to canopy disturbance (Putz 1984; Schnitzer et al. 2000; Laurance et al. 2001; Schnitzer & Carson 2001; Ibarra-Manríquez & Martínez-Ramos 2002; Malizia & Grau 2008). A variety of mechanisms may contribute to this pattern, including high density of trellises in gaps (Putz 1984); lateral proliferation of lianas into gaps from adjacent forest (Peñalosa 1984); proliferation within gaps of lianas that survive treefalls (Putz 1984; Schnitzer et al. 2000); and competitive advantage of lianas over trees in disturbed environments (Schnitzer 2005).

Among the edaphic variables considered, phosphorus appears to have the strongest influence on the liana community in our study area (but we note that it is possible that lianas affect, rather than respond to, soil phosphorus). Soil phosphorus is widely believed to have a strong impact on floristic patterns in the tropics (Vitousek 1984; Vitousek & Stanford 1986; Sollins 1998; Paoli et al. 2006, but see Macía et al. 2007), and Laurance et al. (2001) found liana biomass was positively correlated with soil phosphorus and fertility. Other studies (e.g. Putz & Chai 1987; DeWalt et al. 2006) have also found positive correlations between liana abundance and fertility. Thus, the results from our subtropical site are consistent with evidence from some tropical sites for a positive association between liana abundance and soil fertility. This pattern is not universal, however, as nutrient-poor soils may also harbour high liana abundance (Pérez-Salicrup et al. 2001).

Water availability is another edaphic factor that may play an important role in structuring liana communities, as liana abundance tends to decrease across tropical forest sites as precipitation increases (Schnitzer 2005). However, neither liana composition nor abundance was correlated with soil moisture in our study area. Furthermore, some studies have found an increase in liana abundance with increasing soil moisture (Ibarra-Manríquez & Martínez-Ramos 2002; DeWalt et al. 2006). Thus, like soil fertility, water availability does not appear to provide a universal explanation for liana abundance.

Liana communities appear to be more influenced by edaphic conditions and canopy disturbance, rather than by the abundance or species composition of canopy trees. At present, there does not appear to be a simple, general rule that explains liana abundance along edaphic gradients. Liana abundance often increases with soil fertility and decreases with water availability, but exceptions to both patterns exist. In contrast, the association of lianas with canopy disturbance appears consistent across studies. Two of the proposed hypotheses for the recent increase in liana abundance in mature tropical forests are increasing drought-prone climatic conditions and increasing rates of gap formation (Phillips et al. 2002; Schnitzer 2005). Our study, in which liana abundance increased with gap density but was not correlated with soil moisture, supports the latter hypothesis.

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| Tree species | Family | п | PC1 |
|---|---------------|------|-------|
| Eugenia uniflora L. | Myrtaceae | 463 | 0.28 |
| Piper tucumanum C. DC. | Piperaceae | 304 | -0.32 |
| <i>Myrcianthes pungens</i> (O. Berg) D. Legrand | Myrtaceae | 191 | 0.03 |
| Pisonia zapallo Griseb.var. zapallo | Nyctaginaceae | 189 | 0.24 |
| Cinnamomum porphyrium (Griseb.) Kosterm. | Lauraceae | 175 | 0.00 |
| Allophylus edulis (A. StHil., Cambess. & A. Juss.) Radlk. | Sapindaceae | 164 | 0.07 |
| Urera baccifera (L.) Gaudich | Urticaceae | 152 | -0.09 |
| Terminalia triflora (Griseb.) Lillo | Combretaceae | 135 | 0.04 |
| Blepharocalyx salicifolius (Kunth) O. Berg | Myrtaceae | 130 | 0.34 |
| Solanum riparium Pers. | Solanaceae | 128 | -0.33 |
| Myrsine laetevirens (Mez) Arechav | Myrsinaceae | 81 | 0.12 |
| Ruprechtia laxiflora Meisn. | Polygonaceae | 74 | 0.15 |
| Parapiptadenia excelsa (Griseb.) Burkart | Fabaceae | 58 | -0.27 |
| Duranta serratifolia (Griseb.) Kuntze | Verbenaceae | 44 | 0.24 |
| Urera caracasana (Jacq.) Gaudich ex Griseb. | Urticaceae | 21 | -0.31 |
| Boehmeria caudata Sw. | Urticaceae | 19 | -0.24 |
| Cupania vernalis Cambess. | Sapindaceae | 19 | 0.11 |
| Vassobia breviflora (Sendtn.) Hunz. | Solanaceae | 14 | -0.22 |
| Chrysophyllum marginatum (Hook. & Arn.) Radlk. | Sapotaceae | 13 | 0.17 |
| Cedrela lilloi C. DC. | Meliaceae | 12 | 0.00 |
| Juglans australis Griseb. | Juglandaceae | 9 | 0.03 |
| Tipuana tipu (Benth.) Kuntze | Fabaceae | 8 | -0.32 |
| Xylosma pubescens Griseb. | Salicaceae | 7 | 0.06 |
| Citrus aurantium L. | Rutaceae | 4 | |
| Pentapanax angelicifolius Griseb. | Araliaceae | 3 | |
| Fagara naranjillo (Griseb.) Engl. | Rutaceae | 3 | |
| Anadenanthera colubrina (Vell) Brenan var. cebil (Griseb.) Altschul | Fabaceae | 2 | |
| Randia armata (Sw.) DC. | Rubiaceae | 2 | |
| Carica quercifolia (A.StHil.) Hieron. | Caricaceae | 1 | |
| Enterolobium contortisiliquum (Vell.) Morong | Fabaceae | 1 | |
| Heliocarpus popayanensis Kunth | Malvaceae | 1 | |
| Morus alba L. | Moraceae | 1 | |
| Ruprechtia apetala Wedd. | Polygonaceae | 1 | |
| Total | | 2429 | |

App. 1. Tree species recorded in the 6-ha study plot, number of individuals (*n*), and loadings on the first PCA axis (PC1) for species with $n \ge 5$. The tree census included all living individuals ≥ 10 -cm dbh.

| Variable | UI | U2 | U3 | U4 | US | D6 | U7 | U8 | 6N | U10 | UII | U12 | U13 | Mean (CV) |
|--------------------------------------|--------|-------|--------|--------|-------|-------|--------|--------|--------|--------|--------|-------|-------|---------------|
| Area (m ²) | 8400 | 8800 | 2800 | 3600 | 4800 | 5200 | 5600 | 7200 | 2400 | 2400 | 1600 | 3200 | 3600 | |
| Quadrats (#) | 21 | 22 | 7 | 6 | 12 | 13 | 14 | 18 | 9 | 9 | 4 | 8 | 6 | |
| Sand (%) | 39.0 | 41.8 | 35.3 | 44.6 | 47.8 | 42.9 | 45.0 | 47.4 | 52.6 | 46.2 | 52.0 | 51.3 | 52.5 | 46.03 (11.71) |
| Silt (%) | 37.4 | 35.5 | 38.9 | 34.2 | 32.5 | 35.2 | 33.6 | 32.8 | 29.6 | 33.5 | 30.1 | 30.4 | 29.4 | 33.32 (8.92) |
| Clay (%) | 23.3 | 22.6 | 25.7 | 21.1 | 19.6 | 21.8 | 21.3 | 19.7 | 17.7 | 20.2 | 17.8 | 18.2 | 18.0 | 20.54 (11.77) |
| PH | 5.34 | 5.56 | 6.36 | 5.03 | 5.69 | 5.48 | 6.10 | 5.47 | 5.35 | 5.93 | 5.35 | 5.51 | 5.18 | 5.57 (6.69) |
| Organic matter (%) | 5.93 | 5.72 | 6.01 | 5.93 | 5.88 | 5.91 | 6.08 | 5.05 | 4.77 | 5.80 | 3.34 | 5.91 | 5.17 | 5.50 (13.98) |
| Phosphorus (ppm) | 12.3 | 8.0 | 30.8 | 26.2 | 18.9 | 19.5 | 18.8 | 13.3 | 25.4 | 9.3 | 11.9 | 18.9 | 27.0 | 18.48 (39.38) |
| Total nitrogen (%) | 0.31 | 0.30 | 0.32 | 0.31 | 0.31 | 0.31 | 0.32 | 0.27 | 0.25 | 0.31 | 0.18 | 0.31 | 0.27 | 0.29 (14.00) |
| Potassium (me 100 g^{-1}) | 0.58 | 0.80 | 0.77 | 0.52 | 0.75 | 0.78 | 0.82 | 0.74 | 0.74 | 0.79 | 0.87 | 0.78 | 0.42 | 0.72 (18.14) |
| Water holding capacity (%) | 30.1 | 29.2 | 31.1 | 28.7 | 27.9 | 29.1 | 28.8 | 27.1 | 25.6 | 28.2 | 24.1 | 27.0 | 25.9 | 27.91 (6.93) |
| Aspect (arbitrary scale) | SE (3) | S (3) | NE (1) | NE (1) | E (2) | E (2) | SE (3) | SO (1) | SO (1) | SO (1) | SO (1) | S (3) | E (2) | 1.85 |
| Slope (°) | ŝ | 8 | 24 | 14 | 0 | 22 | 18 | 23 | 29 | 46 | 23 | 13 | 27 | 19.38 (61.13) |
| Tree density | 18.05 | 15.00 | 15.86 | 18.11 | 15.00 | 13.15 | 13.33 | 19.11 | 20.83 | 17.67 | 17.75 | 15.13 | 14.22 | 16.40 (14.36) |
| Tree composition | 3.04 | 1.56 | -5.93 | 0.76 | -1.88 | 0.14 | 1.36 | 0.98 | -2.18 | -0.12 | 1.46 | 3.24 | -2.43 | 0.00 |
| Density of recent gaps | 1.0 | 0.5 | 0.7 | 1.3 | 0.8 | 0.9 | 0.3 | 0.9 | 0.5 | 1.3 | 0.3 | 0.4 | 1.0 | 0.77 (48.15) |
| Density of old gaps | 1.0 | 0.9 | 1.3 | 1.2 | 1.1 | 1.4 | 1.7 | 1.3 | 1.0 | 1.2 | 0.5 | 0.9 | 1.6 | 1.16 (27.25) |
| | | | | | | | | | | | | | | |

App. 2. Values, mean and coefficient of variation (%) of the microenvironmental variables recorded for each sampling unit in the 6-ha plot (Fig. 1). The area and number of quadrats in each unit is reported in the first two rows. Coefficient of variation is not reported for aspect or tree composition (PCA axis 1) because these variables are measured on arbitrary units (aspect was assigned an ordinal value from 1 = driest to 3 = wettest).