

# 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 non-tree 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.

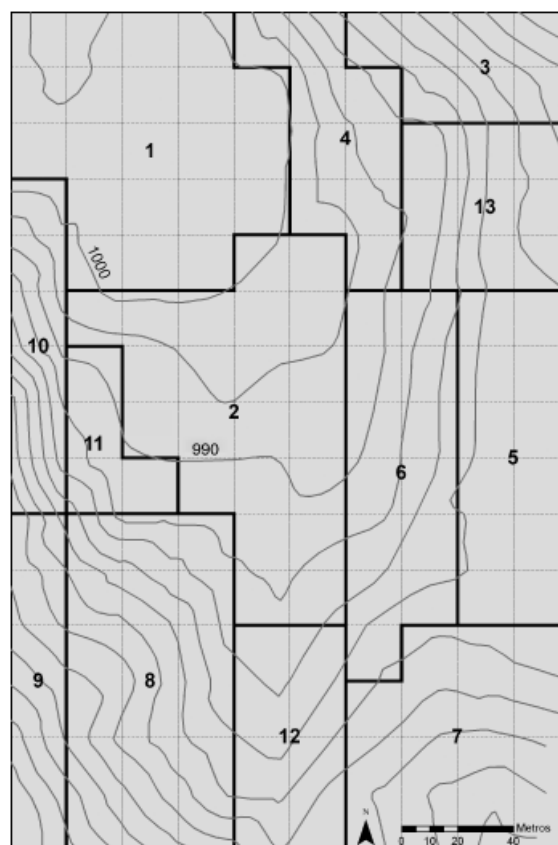
Here, we assess the effects of soil, topography, disturbance and host trees on liana community structure within a 6-ha plot in a subtropical montane forest. Compared to some tropical forests, our system has low tree and liana richness (23 species  $\text{ha}^{-1}$  of trees  $\geq 10$  cm in diameter, and 11 species  $\text{ha}^{-1}$  of lianas  $\geq 2$  cm in diameter) and a high number of individuals per species (Grau & Brown 1998; Grau 2002; Malizia 2007). These features allow for well-replicated 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 (200×300 m) permanent plot at 1000 m elevation in Parque Sierra de San Javier, Tucumán, Argentina (26°76'S, 65°33'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 (20×20 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  $\text{ha}^{-1}$   $\geq 10$  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 sub-canopy (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 20×20 m quadrats was established in 1992. All living

trees  $\geq 10$  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 re-measurement data.

In 2003, we identified to species and permanently marked all liana individuals  $\geq 2$  cm diameter (1.3 m from the ground surface) on all standing and living trees  $\geq 10$  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  $\geq 2$  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

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 (SAMPLA 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  $3^\circ$  to  $46^\circ$  (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 informa-

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

tion (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 ( $<1$  for 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  $\geq 10$  cm dbh) revealed no clear non-linear 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 (mean = 392 individuals  $\text{ha}^{-1}$ ) and 2844 liana stems, belonging to 12 species and 10 families (Table 1). We recorded a total of 2429 tree individuals  $\geq 10$  cm dbh (mean = 405 individuals  $\text{ha}^{-1}$ ) 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 me  $100 \text{ g}^{-1}$  (range 0.42–0.87 me  $100 \text{ g}^{-1}$ ). 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  $R^2 = 0.60$ ,  $F_{2,10} = 10.1$ ,  $P < 0.004$ ).

**Table 2.** Pearson correlation matrix for explanatory variables (soil, topography, trees and disturbance). Bold numbers indicate significant correlations. \* $P < 0.05$ , \*\* $P < 0.001$

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

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-Salícup 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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## References

- Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Natalino, J., Silva, M. & Vásquez Martínez, R. 2004. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London. B* 359: 353–365.
- Balfour, D.A. & Bond, W.J. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81: 93–99.
- Brown, A.D., Grau, H.R., Malizia, L.R. & Grau, A. 2001. Argentina. In: Kappelle, M. & Brown, A.D. (eds.). *Bosques nublados del neotrópico*. pp. 623–659. Inbio, San José, CR.
- Carse, L.E., Fredericksen, T.S. & Licona, J.C. 2000. Liana–tree species associations in a Bolivian dry forest. *Tropical Ecology* 41: 1–10.
- Clark, D.A. 2004. Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition. *Philosophical Transactions of the Royal Society of London. B* 359: 477–491.
- Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences* 100: 5852–5857.

- Denslow, J.S., Ellison, A.M. & Sanford, R.E. 1998. Treefall gap size effects on above- and below- ground processes in a tropical wet forest. *Journal of Ecology* 86: 597–609.
- DeWalt, S.J., Ickes, K., Nilus, R., Harms, K.E. & Burslem, D.F.R.P. 2006. Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecology* 186: 203–216.
- Gentry, A.H. 1991. Distribution and evolution of climbing plants. In: Putz, F.E. & Mooney, H.A. (eds.) *The biology of vines*. pp. 3–49. Cambridge University Press, Cambridge, UK.
- Grau, H.R. 2002. Scale-dependent relationships between treefalls and species diversity in a Neotropical montane forest. *Ecology* 83: 2591–2601.
- Grau, H.R. & Brown, A.D. 1998. Structure, composition and inferred dynamics of a subtropical montane forest of northwest Argentina. In: Dallmeier, F. & Camiskey, J.A. (eds.) *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*. pp. 715–726. UNESCO and the Parthenon Publishing Group, Paris, FR and Carnforth, UK.
- Grau, H.R., Arturi, M.F., Brown, A.D. & Aceñolaza, P.G. 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. *Forest Ecology and Management* 95: 161–171.
- Grau, H.R., Easdale, T.A. & Paolini, L. 2003. Subtropical dendroecology-dating disturbances and forest dynamics in northwestern Argentina montane ecosystems. *Forest Ecology and Management* 177: 131–143.
- Hegarty, E.E. & Caballé, G. 1991. Distribution and abundance of vines in forest communities. In: Putz, F.E. & Mooney, H.A. (eds.) *The biology of vines*. pp. 313–335. Cambridge University Press, Cambridge, UK.
- Hunzinger, H. 1997. Hydrology of montane forest in the Sierra de San Javier, Tucumán, Argentina. *Mountain Research and Development* 17: 299–308.
- Huston, M. 1995. *Biological diversity: The coexistence of species in changing landscapes*. 1st ed. Cambridge University Press, Cambridge, UK.
- Ibarra-Manríquez, G. & Martínez-Ramos, M. 2002. Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology* 160: 91–112.
- Laurance, W.F., Pérez-Salicrup, D., Delamônica, M., Fearnside, P.M., D'Angelo, S., Jerozolinski, A., Pohl, L. & Lovejoy, T.E. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 81: 105–116.
- Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673.
- Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. 1st ed. Cambridge University Press, Cambridge, UK.
- Lewis, S.L. 2006. Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society of London. B* 361: 195–210.
- Lewis, S.L., Phillips, O.L., Baker, T.R., Lloyd, J., Malhi, Y., Almeida, S., Higuchi, N., Laurance, W.F., Neill, D.A., Silva, J.N.M., Terborgh, J., Torres Lezama, A., Vásquez Martínez, R., Brown, S., Chave, J., Kuebler, C., Núñez Vargas, P. & Vinceti, B. 2004. Concerted changes in tropical forest structure and dynamics: evidence from 50 South American long-term plots. *Philosophical Transactions of the Royal Society of London. B* 359: 421–436.
- Macía, M.J., Ruokolainen, K., Tuomisto, H., Quisbert, J. & Victoria, C. 2007. Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. *Ecography* 30: 561–577.
- Malizia, A. 2003. Host tree preference of vascular epiphytes and climbers in a subtropical montane cloud forest of northwest Argentina. *Selbyana* 24: 196–205.
- Malizia, A. 2007. *Interacciones entre lianas y árboles en una selva montana madura de las Yungas argentinas*. Tesis doctoral, Universidad Nacional de Tucumán, Tucumán, AR.
- Malizia, A. & Grau, H.R. 2006. Liana–host tree associations in a subtropical montane forest of northwestern Argentina. *Journal of Tropical Ecology* 22: 331–339.
- Malizia, A. & Grau, H.R. 2008. Landscape context and microenvironment influences on liana communities within treefall gaps. *Journal of Vegetation Science* 19: 591–604.
- McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.
- Nabe-Nielsen, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. *Journal of Tropical Ecology* 17: 1–19.
- Paoli, G.D., Curran, L.M. & Zak, D.R. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology* 94: 157–170.
- Peñalosa, J. 1984. Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica* 16: 1–9.
- Peres-Neto, P.R., Jackson, D.A. & Somers, K.M. 2005. How many principal components? Stopping rules for determining the number of non-trivial axes revisited. *Computational Statistics and Data Analysis* 49: 974–997.
- Pérez-Salicrup, D.R., Sork, V.L. & Putz, F.E. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33: 34–47.
- Phillips, O.L., Vásquez Martínez, R., Arroyo, L., Baker, T.R., Killeen, T.J., Lewis, S.L., Malhi, Y., Monteagudo Mendoza, A., Neill, D., Núñez Vargas, P., Alexiades, M., Cerón, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. 2002. Increasing dominance of large lianas in Amazonian forests. *Nature* 418: 770–774.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, W.F., Lewis, S.L., Lloyd, J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez

- Vargas, P., Silva, J.N.M., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N.C.A., Quesada, C.A., Saldias, M., Torres Lezama, A. & Vinceti, B. 2004. Pattern and process in Amazon tree turnover 1976–2001. *Philosophical Transactions of the Royal Society of London. B* 359: 381–407.
- Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713–1724.
- Putz, F.E. & Chai, P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75: 523–531.
- SAMLA. 2004. *Recopilación de técnicas de laboratorio*. 1st ed. Dirección de agricultura, Buenos Aires, AR, CD-ROM.
- Scharenbroch, B.C. & Bockheim, J.G. 2007. Impacts of forest gaps on soil properties and processes in old growth northern hardwood–hemlock forests. *Plant and Soil* 294: 219–233.
- Schnitzer, S.A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist* 166: 262–276.
- Schnitzer, S.A. & Carson, W.P. 2001. Treefall gaps and the maintenance of species diversity in a tropical rain forest. *Ecology* 82: 913–919.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88: 655–666.
- Sollins, P. 1998. Factors influencing species composition in tropical lowland rain forest: does soil matter? *Ecology* 79: 23–30.
- Talley, S.M., Setzer, W.N. & Jackes, B.R. 1996b. Host associations of two adventitious root climbing vines in a north Queensland tropical rain forest. *Biotropica* 28: 356–366.
- Talley, S.M., Lawton, R.O. & Setzer, W.N. 1996a. Host preferences of *Rhus radicans* (Anacardiaceae) in a southern deciduous hardwood forest. *Ecology* 77: 1271–1276.
- van der Heijden, G.M.F. & Phillips, O.L. 2008. What controls liana success in Neotropical forests? *Global Ecology and Biogeography* 17: 372–383.
- van der Heijden, G.M.F., Healey, J.R. & Phillips, O.L. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. *Journal of Vegetation Science* 19: 747–756.
- Vitousek, P.M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285–298.
- Vitousek, P.M. & Stanford, R.L. 1986. Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* 17: 137–167.
- Wright, S.J. 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution* 20: 553–560.
- Wright, S.J., Calderón, O., Hernández, A. & Paton, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panamá. *Ecology* 85: 484–489.
- Zuloaga, F.O. & Morrone, O. 1999. *Catálogo de las plantas vasculares de la República Argentina, Vols. 1 and 2*. Missouri Botanical Garden Press, MO, US.

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**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  $n \geq 5$ . The tree census included all living individuals  $\geq 10$ -cm dbh.

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

**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).

Variable	U1	U2	U3	U4	U5	U6	U7	U8	U9	U10	U11	U12	U13	Mean (CV)
Area (m <sup>2</sup> )	8400	8800	2800	3600	4800	5200	5600	7200	2400	2400	1600	3200	3600	
Quadrats (#)	21	22	7	9	12	13	14	18	6	6	4	8	9	
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 <sup>-1</sup> )	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 (°)	3	8	24	14	2	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)