Liana–host tree associations in a subtropical montane forest of north-western Argentina

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Abstract: In a subtropical montane forest of north-western Argentina ($27°$S, 1000 m elevation), we analysed the effect of crown illumination, trunk diameter, foliar phenology and tree species identity as determinants of liana–host tree associations, as well as the spatial pattern of liana abundance in a 6-ha permanent plot. We recorded 2346 liana individuals ≥ 2 cm and 2320 trees ≥ 10 cm dbh. Sixty-five per cent of the trees hosted at least one liana stem. Large and well-lit trees were more likely to support lianas and supported more liana abundance than small and shaded trees. Yet, when trees were standardized by their size (liana basal area/tree basal area ratio), lianas were more abundant in smaller and less-exposed trees. Foliar phenology and tree species identity showed no association with the frequency of liana colonization and their abundance. Overall, tree features played a minor or even neutral role in structuring the liana community within this forest. Instead, lianas showed a positive autocorrelation at spatial scales up to 40 m. This suggests that lianas might be mostly structured by light- and dispersal-related factors such as those involving canopy access or canopy disturbances, with a negligible effect of host species identity and foliar phenology.

Key Words: climbers, lianas, liana-tree associations, montane forests, Yungas

INTRODUCTION

Lianas are woody climbing plants typical of tropical and subtropical forests that rely on trees for support in order to reach the illuminated canopy (Balfour & Bond 1993, Bongers *et al.* 2002, Gentry 1991). They represent up to 25% of woody species in diverse forests (Bongers *et al.* 2002) and contribute significantly to forest ecosystem functioning. Much of their influence on forests is likely due to their interactions with trees, for example by affecting tree demography (Pérez-Salicrup & Barker 2000, Putz 1984a, Stevens 1987) and ecophysiology (Meinzer *et al.* 1999, Pérez-Salicrup & Barker 2000).

Trees may represent a variety of niches to lianas, and the differences in their morphological and physiological features could lead to associations between lianas and trees, either at species or life-form levels. Alternatively, trees may act as ecologically neutral support structures, colonized by the lianas that happen to occur close to them, and liana communities may be mostly structured by other

factors largely unrelated to tree composition. The relative contribution of tree-related niches to the assemblage of lianas may be important in understanding the ecology of lianas in tropical and subtropical forests.

Differences between tree species in susceptibility to liana colonization due to morphological features have been demonstrated by several studies (Clark & Clark 1990, Putz 1984a, Schnitzer *et al.* 2000). Some studies found that the number of liana individuals per host tree tend to increase with tree bark roughness (Talley *et al.* 1996a,b), diameter (Chittibabu & Parthasarathy 2001, Clark & Clark 1990, Malizia 2003, Nabe-Nielsen 2001), and tree or bole height (Malizia 2003, Muthuramkumar & Parthasarathy 2001; but see Balfour & Bond 1993, Campbell & Newbery 1993). Other tree features such as fast growth rates, stem flexibility, branch shedding or evergreen foliage may help reduce lianas abundance (Malizia 2003, Putz 1984b). Yet, some of these tree features may be correlated with each other (e.g. tree diameter and tree height) potentially leading to spurious conclusions. Therefore, the relative effects of these variables need to be discriminated.

On the other hand, several studies have failed to find associations between liana and trees (Campbell &

Newbery 1993, Carse *et al.* 2000, Perez-Salicrup *et al.* 2001). This lack of association might be due to the fact that lianas hanging from a particular canopy tree (e.g. a large tree) may have reached the canopy by climbing successive small supports, leading to misleading hypotheses or incorrect conclusions; or because tree species do not differ in their capacity to act as support structures. As a result, trees may carry whatever lianas happen to be locally present in that given portion of the forest due to dispersal, clonal growth, local disturbances such as treefall gaps or micro-environment conditions which may exert a much stronger influence on liana establishment and proliferation (Nabe-Nielsen 2001, Perez-Salicrup *et al.* 2001).

Light availability is probably the most important micro-environmental factor related to forest architecture and canopy disturbances. Lianas are apparently very light-demanding and occur conspicuously in the most illuminated areas of the forest such as treefall gaps (Schnitzer & Carson 2001, Schnitzer *et al.* 2000) or at canopy level (Gentry 1991). Thus, tree features affecting light conditions such as crown illumination or foliar phenology may influence the associations between lianas and trees. These features, however, have seldom been analysed in liana studies.

Lianas are a prominent component of the montane forests of subtropical Argentina. Compared with tropical forests, these forests have low tree species richness (23 species ha^{-1}) and a high number of individuals per species (Grau 2002, Grau & Brown 1998). This allows a well-replicated sampling on lianas per life form and species in a relatively uniform environment, a major limitation in highly diverse forests. We took advantage of this situation to analyse the associations between liana and host trees considering the following tree features: crown illumination, tree diameter, foliar phenology and tree species identity. We attempted to evaluate the association of each of these tree features with lianas separately. In addition, we evaluated the spatial distribution of lianas. The study is framed as a set of questions, aiming to discriminate these different factors.

As crown illumination and tree diameter might be correlated with each other (e.g. larger trees are usually taller reaching higher canopy layers) we tried to quantify the associations of these variables with lianas individually addressing the following questions: (1) Do crown illumination and tree diameter contribute separately to explaining liana abundance? (2) Is the proportion of trees colonized by lianas and their liana abundance related to the illumination of the crown? (3) Is the proportion of trees colonized by lianas and their liana abundance related to tree diameter?

As the effects of tree foliar phenology and species identity on lianas may be easily masked by the effect of crown illumination and tree size we controlled for these two variables when addressing two more questions: (4) Is the proportion of colonized trees and their liana abundance related to tree foliar phenology? (5) Does the proportion of colonized trees and their liana abundance translate into specific liana–tree associations?

If tree features play a minor (neutral) role in structuring the liana community and no clear or weak associations emerge between lianas and host trees, we were interested in exploring the spatial distribution of lianas by addressing the last question: (6) Does liana abundance show a spatial pattern unrelated to tree features?

STUDY SITE AND METHODS

Plot location and characteristics

The study was conducted in a 6-ha (200×300 m) permanent plot located at 1000 m elevation in the sub-tropical montane forest of Parque Sierra de San Javier, Tucumán, Argentina ($27°30'$ S, $65°40'$ W). Annual rainfall is 1300–1500 mm and is distributed in a monsoonal regime (Hunzinger 1997). Mean annual temperature is *c.* 18 °C. Frosts occur between June and August. The plot includes a wide range of topographic conditions and slope inclination (Grau 2002).

Forest vegetation is characteristic of the lower montane zone of the Argentine *yungas*, which is the southernmost extension of neotropical Andean montane forests (Brown *et al.* 2001). The plot is located in mature forests with an average of 23 species ha^{-1}, including deciduous and evergreen species. Canopy height varies between 15 and 30 m. Canopy tree composition (> 20 m) is dominated by *Blepharocalyx salicifolius* (Myrtaceae), *Cinnamomum porphyrium* (Lauraceae) and *Pisonia ambigua* (Nyctaginaceae); and subcanopy tree composition (5–12 m) is dominated by *Eugenia uniflora* (Myrtaceae), *Piper tucumanum* (Piperaceae) and *Allophylus edulis* (Sapindaceae). The forest experienced a very light selective logging *c.* 50 y ago, probably for the species *Cedrela lilloi* (Meliaceae) and *Juglans australis* (Juglandaceae), of which only two cut stumps were found in the plot (Grau 2002, Grau & Brown 1998).

The permanent plot was established in 1992 when all living trees ≥ 10 cm diameter at breast height (dbh) were tagged, measured for stem diameter, identified to species level and mapped into an X-Y coordinate system. For the present study we used the 2002 re-measurement data, considering as replicate units only individuals that were living and standing.

Data collection

In 2003 we measured and permanently marked all liana individuals ≥ 2 cm diameter on every standing and

living tree ≥ 10 cm dbh. We considered a separate liana individual when a stem was clearly rooted into the forest floor and no above-ground connections with other stems were evident. After focusing on each tree, each liana stem was followed to where it rooted, measured at 1.30 m from its base, and identified to species level. Liana diameter was measured with a caliper unless it was thicker than 10 cm, in which case a diameter tape was used. When stems differed clearly from a round section we averaged the maximum and minimum diameter.

For each individual tree we visually estimated an index of crown illumination based on Clark & Clark (1992) which ranges from 1–5, where 1 = individuals completely overshadowed; 1.5 = exposed only to minor lateral light; 2 = exposed to medium lateral light; 2.5 = exposed to much lateral light, 3 = 10–50% crown exposed to overhead light; 3.5 = 50–90% of the crown exposed to overhead light; 4 = 90–99% overhead light; and 5 = 100% crown overhead light (e.g. emergent trees). Based on Brown (1995), Digilio & Legname (1966) and local experts' opinions, tree species were classified according to foliar phenology as deciduous if their tree individuals shed their leaves for at least 1 mo, or evergreen otherwise. Botanical nomenclature follows Zuloaga & Morrone (1999).

Data analysis

Effects of crown illumination and tree diameter. To test if crown illumination and tree size contributed separately to liana abundance (question 1), tree diameters were grouped into classes of 10 cm and we performed a multiple regression using crown illumination index and tree diameter as the predictor variables and mean liana abundance as the dependent variable.

To test if the proportion of trees colonized by lianas and their liana abundance were related to the illumination of the crown (question 2), we performed Kendall's non-parametric correlation analysis that assessed the trends in the relationship between the proportion of those colonized trees and the illumination of the crown. To assess differences in liana abundance between crown illumination index classes we performed Kruskal–Wallis analysis. To analyse the relationships between mean liana abundance and tree crown illumination we used Kendall's non-parametric correlation coefficients.

To test if the proportion of trees colonized by lianas and their liana abundance were related to tree diameter (question 3), tree diameters were grouped into classes of 10 cm, and we performed Kendall's non-parametric correlation analysis to assess trends in the relationship among the proportion of trees colonized by lianas and tree diameter. To assess trends between mean liana abundance and tree size categories, and for descriptive

purposes we fitted non-linear regressions as suggested by the scatterplots.

When performing the analysis of liana abundance in relation to crown illumination and tree diameter we considered tree individuals in two ways: independently of their size and standardized by them (liana basal area/tree basal area ratio).

Effects of foliar phenology and tree species identity. To control for crown illumination and tree size when evaluating for foliar phenology and tree species identity, we analysed only trees with crown index ≥ 4 and diameter ≥ 60 cm. To test if the proportion of tree individuals colonized by lianas and their liana abundance were related to foliar phenology (question 4), we performed Chi-square tests for independence to evaluate the differences between the observed and expected colonized trees within the two analysed foliar phenology categories (evergreen and deciduous); and a Mann–Whitney U-test to assess for differences between categories, respectively.

To test if the proportion of colonized trees and liana abundance translated into specific liana–tree associations (question 5), we used the Multi Response Permutation Program (MRPP, McCune & Mefford 1999) to assess the differences among tree species based on their liana composition, and an Indicator Species Analysis (ISA, Dufrêne & Legendre 1997) to assess which tree and liana species were producing these differences. MRPP is a non-parametric procedure that tests the hypothesis of no difference between two or more groups of entities defined a priori (e.g. tree species). MRPP computes two distance measures within groups: the 'observed delta' which is the average within-group distance and the 'expected delta' calculated to represent the mean delta for all possible partitions of the data. The observed delta is compared with the expected delta, and as a result the test statistic describes the separation between the groups. The output includes a probability value (P), and the statistic A which is a descriptor of within-group homogeneity compared with the random expectation. When all items are identical, delta = 0 and A = 1; if heterogeneity within groups equals expectation by chance, A = 0.

ISA is a method that produces Indicator Values (IV) which are the product of the relative abundance and relative frequency of each liana species for every tree species:

$$IV_{ij} = A_{ij} \times B_{ij} \times 100,$$

where

$$A_{ij} = \text{liana abundance}_{ij}/\text{liana abundance}_i$$
$$B_{ij} = \text{Ntress}_{ij}/\text{Ntress}_j$$

Liana abundance$_{ij}$ is the mean abundance of liana species i across tree species j, liana abundance$_i$ is the sum of the mean abundance of liana species i over all tree species, Ntrees$_{ij}$ is the number of trees species j where liana species i is present and Ntrees$_j$ is the total number of trees of that species (Dufrêne & Legendre 1997). IV ranges from 0% (no indication) to 100% (perfect indication). Perfect indication occurs when a given liana species has the highest abundance in a particular tree species and is present in all the individuals of that tree species. We used a Monte Carlo test (1000 permutations) to evaluate the statistical significance of the observed maximum IV for each liana species.

For both MRPP and ISA we used an input matrix of 98 rows by 10 columns where the rows represented individuals of each tree species (we only considered tree species with ≥ 5 individuals, thus we only considered the five tree species that met this restriction) and the columns were liana species with ≥ 5 individuals (Table 1).

Spatial pattern of lianas. To test whether liana abundance showed a spatial pattern unrelated to tree features (question 6) we estimated liana abundance per 20×20-m quadrat within the plot and calculated the Moran's I spatial autocorrelation coefficient. This analysis used an input matrix of liana abundance per quadrat (n = 150) and its corresponding X-Y coordinates. The output includes the distance classes (d) for which values of Moran's I coefficient were calculated, the value of Moran's I coefficient (I(d)) for each distance class, the statistic z of Moran's I coefficient for each distance class and a probability value (P).

As a measure of liana abundance we considered both liana basal area (cm^2) and number of liana stems. As these variables were highly correlated (n = 1502, tau = 0.62, P < 0.0001) and results were similar, we only report the results for liana basal area to avoid repetition. In the crown illumination index, foliar phenology and tree species analyses the percentages of the total variance explained by ANOVA are also reported for descriptive purposes. Multivariate analyses were performed with PC-ORD 4.0 (McCune & Mefford 1999), univariate analyses with STATISTICA software (STATISTICA v.6.0, Statsoft, Inc., Tulsa, Oklahoma, USA) and the spatial analysis was performed with SPATIAL software (SPATIAL analysis program, v. 2000, Canterbury, New Zealand).

RESULTS

We recorded a total of 2346 liana individuals ≥ 2 cm dbh (391 individuals ha^{-1}) belonging to 12 species. The three most abundant liana species were *Cissus tweediana*, *Chamissoa altissima* and *Celtis iguanaea* which altogether

Table 1. Liana species recorded in a 6-ha plot in Parque Sierra de San Javier, Tucumán, Argentina; listed by botanical family and total number of individuals. Indicator values (IV) for liana species are shown. Bold numbers indicate maximum IV for each liana species on each tree species and are accompanied by significant levels from Monte Carlo test. Tree abundances used for Indicator Species Analysis are reported in parentheses by each tree species.

Liana species	Family	Abundance	Parapiptadenia excelsa (20)	Cinnamomum porphyrium (49)	Terminalia triflora (7)	Terminalia triflora (16)	Tipuana tipu (6)
Cissus tweediana	Vitaceae	584	18	9	34*	8	8
Chamissoa altissima	Amaranthaceae	444	8	12	8	1	0
Celtis iguanaea	Celtidaceae	351	10	7	4	0	0
Vernonia fulta	Asteraceae	246	3	1	5	2	2
Macfadyena unguis-cati	Bignoniaceae	211	2	4	2	18	9
Serjania meridionalis	Sapindaceae	147	5	6	12	4	1
Malpighiacea 1	Malpighiaceae	133	5	4	15	3	1
Acacia praecox	Fabaceae	109	9	4	2	0	0
Hebanthe occidentalis	Amaranthaceae	64	5	0	9	0	1
Pisoniella arborescens	Nyctaginaceae	35	0	0	14	0	0
Indets		18					
Muehlenbeckia sagittifolia	Polygonaceae	3					
Baccharis trinervis	Asteraceae	1					
Total		2346					

Note: * P < 0.01. Indets, *Muehlenbeckia sagittifolia* and *Baccharis trinervis* were not used for this analysis.

represented *c.* 60% of the individuals (Table 1). Of the 2320 standing and living trees ≥ 10 cm dbh recorded, 1502 (65%) hosted at least one liana stem. Most tree species ranged from 50–80% of tree individuals colonized by lianas (Appendix).

Effects of crown illumination and tree diameter

Crown illumination index and tree diameter combined showed a strong and statistically significant correlation with mean liana basal area (adjusted $R^2 = 0.77$; df = 2.5; $P < 0.01$; n = 8). The partial correlation coefficient was significant for crown illumination index (r = 0.84; P = 0.02) and marginally non-significant for tree diameter (r = −0.73; P = 0.06).

The proportion of trees with lianas increased with crown illumination index (Figure 1a). Liana basal area ranged from 0–230 cm^2 per tree and increased with crown illumination; trees with low illumination only had small liana abundance while trees with high crown illumination showed the complete range of lianas abundance (Figure 1b). Tree individuals with higher crown index values showed higher liana abundance (median for index 5 = 40.9 cm^2 of liana basal area) than tree individuals with lower crown indices (median for index 1 = 7.50 cm^2 of liana basal area). Although the increase of liana basal area showed with the illumination of the crown was statistically significant, the explained variance was only 6.4%. In turn, liana basal area/tree basal area ratio showed a decrease with crown illumination (explained variance = 10.6%), as trees with crown index ≥ 4 showed significantly lower values than tree individuals with crown index ≤ 3.5 (Figure 1c).

The proportion of trees colonized by lianas increased with tree diameter (Figure 2a) and larger tree diameter classes carried significantly more liana basal area per tree (Figure 2b). A quadratic equation explained 78% of this relationship as lianas basal area showed an increasing trend with tree diameter up to trees of 70–80 cm diameter and a decreasing trend as tree diameter increased over 80 cm diameter (Figure 2b). In turn, smaller tree diameter classes showed greater liana abundance per liana basal area/tree basal area ratio and an exponential decay equation explained 93% of this relationship (Figure 2c).

Effects of foliar phenology and tree species

The proportion of individual trees with crown index ≥ 4 and diameter ≥ 60 cm colonized by lianas did not significantly differ between deciduous (97%) and evergreen (88%) trees ($\chi^2 = 2.82$; n = 107; P > 0.05).
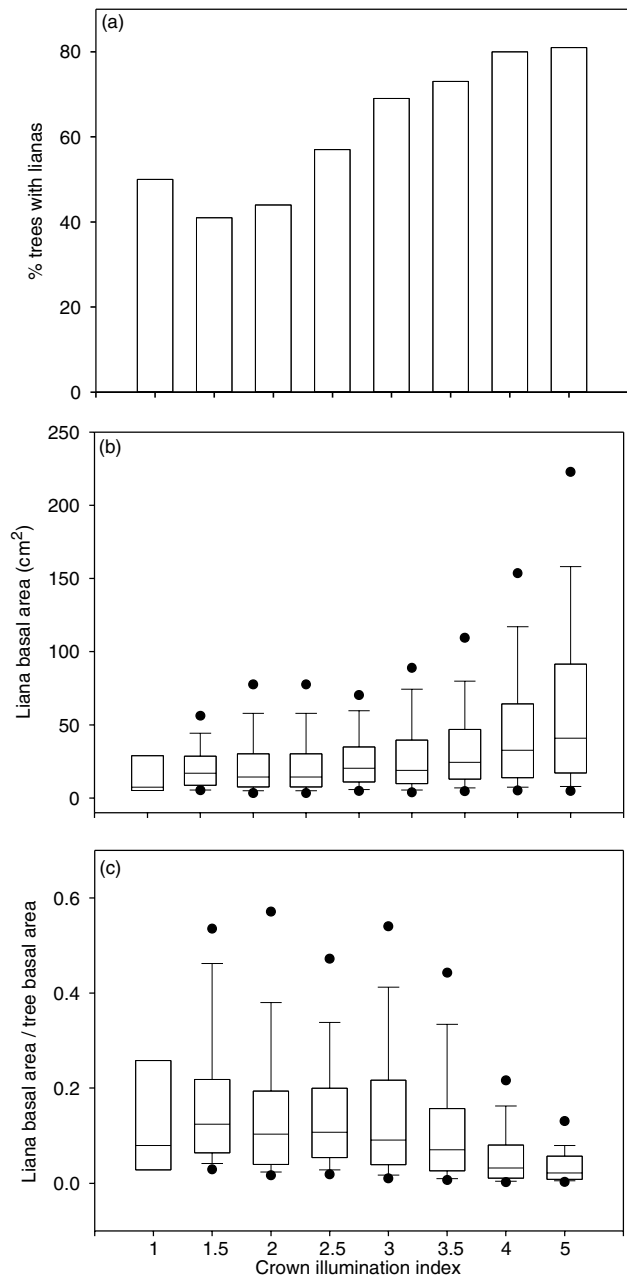

Figure 1. Relationship with crown illumination index of (a) percentage of tree individuals colonized by lianas (tau = 0.86; n = 8; P < 0.01), (b) liana basal area (H = 82.7; n = 1480; P < 0.001) (tau = 0.1; n = 8; P < 0.001), and (c) ratio of liana basal area/tree basal area (H = 197; n = 1480; P < 0.0001) (tau = −0.64; n = 8; P < 0.05) . Medians and 5th–95th percentiles range are shown for parts b and c.

Liana basal area did not show statistically significant differences among categories (Z = 1.73; n = 107; P > 0.05) (explained variance = 2.9%).

Individuals of tree species with crown index ≥ 4 and diameter ≥ 60 cm differed in their liana composition (observed delta = 65.6, expected delta = 66.6, A = 0.001, P < 0.05) (explained variance = 10.1%) but

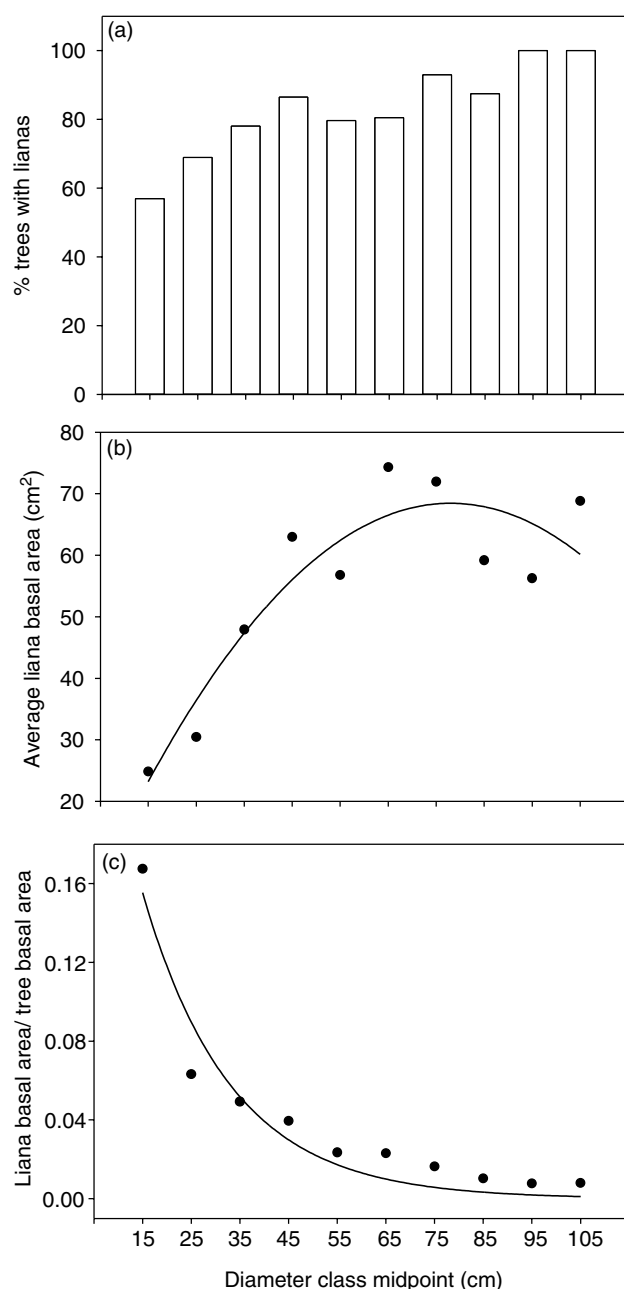**Figure 3.** Spatial correlogram of liana basal area for radial distance classes (d) of 20 m; Z = normalized values of Moran´s I coefficient for each distance class.

Spatial distribution of lianas

Liana basal area showed a positive spatial autocorrelation, which was statistically significant up to 40 m of radial distance (Figure 3).

DISCUSSION

Percentage of tree colonization in our study (65%) is comparable with and even higher than various tropical forests where the range of total tree occupancy by lianas (considering trees ≥ 10 cm dbh) ranges between 40 and 63% (Boom & Mori 1982, Clark & Clark 1990, Pérez-Salicrup & de Meijere 2005, Putz 1983, Talley *et al.* 1996b, but see Perez-Salicrup *et al.* 2001). Our record of *c.* 400 liana individuals ≥ 2 cm per hectare is also comparable to a tropical forest of Malaysia where Putz & Chai (1987) found 348 lianas ha^{-1} in the valley region; although liana density in our forest is relatively low compared with other tropical forests (Campbell & Newbery 1993, Laurance *et al.* 2001, Perez-Salicrup *et al.* 2001).

Both crown illumination and tree size were related to liana abundance. However, the effect of crown illumination appears to be more influential than tree size in controlling the liana loads carried by trees, as it showed a higher partial correlation coefficient, and tree size (diameter) showed a negative partial correlation value when controlled for crown illumination. Well-illuminated trees may represent appropriate micro-environments for liana establishment and proliferation while larger trees may just imply a longer time of exposure to liana colonization.

The proportion of trees colonized by lianas gradually increased with tree crown illumination and

Figure 2. Diameter class midpoint plotted against (a) the percentage of tree individuals colonized by lianas (tau = 0.85; n = 8; P < 0.001), (b) average of liana of basal area ($F_{(2,7)} = 17.18$; $R^2_{adj} = 0.78$; P = 0.002) (Average liana basal area = 7.68 + 16.6x − 1.14x^2), and (c) ratio of liana basal area/tree basal area ($F_{(1,8)} = 112$; $R^2_{adj} = 0.93$; P < 0.0001) (Average liana basal area/tree basal area ratio = 0.27 exp (−0.55x)).

the differences in tree heterogeneity were minor as the A value was very small. Indicator species analysis showed only one significant association: between the liana *Cissus tweediana* and the host tree *Terminalia triflora* (Table 1).
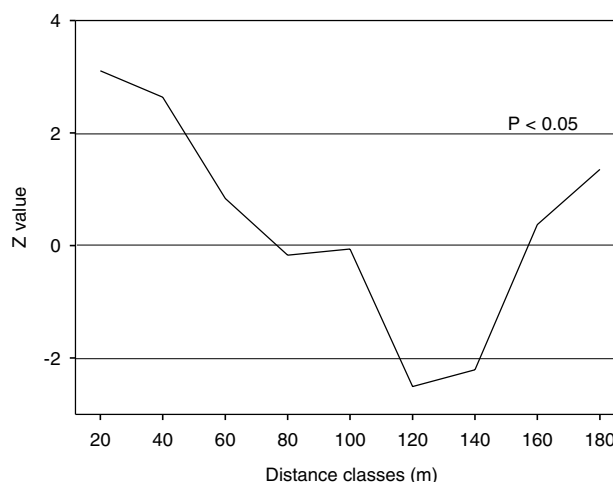
well-illuminated crowns supported significantly larger liana loads over their crowns. This is consistent with the idea that lianas are a light-demanding life form (Gentry 1991). However, per liana basal area/tree basal area ratio tree individuals at canopy level (with crown index 4 and 5) carried fewer liana loads than those that were less light exposed; which may imply that despite having less total liana loads, trees growing under shade conditions may be more affected by liana competition, with probably stronger effects on tree growth and mortality.

Also, as trees became larger they showed more liana colonization frequency and loads, probably due to more area and time exposure to liana colonization. This is consistent with several studies which found that liana abundance and frequency increased with tree size (Chittibabu & Parthasarathy 2001, Clark & Clark 1990, Malizia 2003, Nabe-Nielsen 2001, Pérez-Salicrup & de Meijere 2005). Nevertheless, in this study, liana loads per tree individual peaked at 70 and 80 cm diameter decreasing at larger diameters. Probably most trees with 70 and 80 cm diameter had already reached into the canopy exposing their entire crowns to direct overhead light encouraging lianas to proliferate into their whole crowns. Once the entire crown has been colonized, larger trees did not necessarily imply new liana-free crown area. Why liana loads decrease on trees over 80 cm diameter remains to be answered. However, on per liana basal area/tree basal area ratio smaller tree individuals had more liana loads than larger trees. Thus, these small-sized trees could be more affected in their fitness compared with larger trees until they get away or balance liana loads with their own size. When controlling for light exposure and size, foliar phenology seemed to have no significant influence on liana colonization.

When the effects of crown index and tree size were controlled, tree species identity showed very weak effects on the liana community. A clear liana–tree association was only detected for one of the five species analysed, *Terminalia triflora* which was particularly suitable for hosting the liana *Cissus tweediana*. However, most of the Indicator Values obtained suggest that no particular liana species were either too frequent or too abundant on particular tree species. This is consistent with other studies where little evidence was found for significant associations between liana and tree species (Carse *et al.* 2000, Perez-Salicrup *et al.* 2001).

These results suggest that, among the tree features studied, illumination of the crown and tree size may have some influence on the association patterns between lianas and host trees, but may not have a very strong effect in structuring the liana community as they explained less than 10% of the total variance of liana loads and showed wide ranges of variation. Foliar phenology and tree species identity showed little or no effect over liana–tree associations. Thus, trees seem to act mostly as ecologically neutral supports which have higher liana colonization levels and proliferation under suitable light conditions associated to intermediate or large size.

In contrast to the relatively weak effect of tree features in structuring the liana community, lianas showed a strong spatial structure. This could be attributed to different factors such as dispersal, clonal growth and micro-environmental factors such as tree-fall gaps or edaphic conditions (Gentry 1991, Putz & Chai 1987, Schnitzer & Bongers 2002). The scale of spatial autocorrelation in liana abundance is consistent with the scale of spatial autocorrelation found for time-since-gap formation in the same plot (Grau 2002), suggesting that recruitment in gaps may play a key role in allowing liana recruitment. Consistently, Schnitzer (2005) reported that at a local scale lianas are particularly abundant within gaps. Once lianas are able to colonize a canopy opening, they may be prone to infest whatever tree individuals are growing in the surroundings or inside the gap and may also be favoured by high light availability.

Overall, the liana community in this subtropical montane forest of north-west Argentina seems mostly structured by light- and dispersal-related factors such as those involved in access to canopy or canopy disturbances, with only a very minor effect of species identity and phenology.

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LITERATURE CITED

BALFOUR, D. A. & BOND, W. J. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81:93–99.

BONGERS, F., SCHNITZER, S. A. & TRAORE, D. 2002. The importance of lianas and consequences for forest management in West Africa. *Bioterre* [Special issue]:59–70.

BOOM, B. M. & MORI S. A. 1982. Falsification of two hypotheses on liana exclusion from tropical trees possessing buttresses and smooth bark. *Bulletin of the Torrey Botanical Club* 109:447–450.

BROWN, A. D. 1995. Fenología y caída de hojarasca en las selvas montanas del Parque Nacional El Rey, Argentina. Pp. 93–102 in Brown, A. D. & Grau, H. R. (eds). *Investigación, conservación y desarrollo en selvas subtropicales de Montaña*. Laboratorio de Investigaciones Ecológicas de las Yungas, Tucumán.

BROWN, A. D., GRAU, H. R., MALIZIA, L. R. & GRAU, A. 2001. Argentina. Pp. 623–659 in Kappelle, M. & Brown, A. D. (eds). *Bosques Nublados del Neotrópico*. Inbio, San José.

CAMPBELL, E. J. F. & NEWBERY, D. M. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology* 9:469–490.

CARSE, L. E., FREDERICKSEN, T. S. & LICONA, J. C. 2000. Liana-tree species associations in a Bolivian dry forest. *Tropical Ecology* 41:1–10.

CHITTIBABU, C. V. & PARTHASARATHY, N. 2001. Liana diversity and host relationships in a tropical evergreen forest in the Indian Eastern Ghats. *Ecological Research* 16:519–529.

CLARK, D. A. & CLARK, D. B. 1992. Life history of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs* 62:315–344.

CLARK, D. B. & CLARK, D. A. 1990. Distribution and effects on tree growth of lianas and woody hemi-epiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6:321–331.

DIGILIO, A. P. & LEGNAME, P. R. 1966. *Los árboles indígenas de la provincia de Tucumán*. Universidad Nacional de Tucumán, Tucumán. 236 pp.

DUFRÊNE, M. & LEGENDRE, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345–366.

GENTRY, A. H. 1991. Distribution and evolution on climbing plants. Pp. 3–49 in Putz, F. E. & Mooney H. A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.

GRAU, H. R. 2002. Scale–dependant 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. Pp. 715–726 in Dallmeier, F. & Camiskey, J. A. (eds). *Forest biodiversity in North, Central and South America, and the Caribbean. Research and monitoring*. UNESCO, Paris & the Parthenon Publishing Group, Carnforth.

HUNZINGER, H. 1997. Hydrology of montane forest in the Sierra de San Javier, Tucumán, Argentina. *Mountain Research and Development* 17:299–308.

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.

MALIZIA, A. 2003. Host tree preference of vascular epiphytes and climbers in a subtropical montane cloud forest of northwest Argentina. *Selbyana* 24:196–205.

MCCUNE, B. & MEFFORD, M. J. 1999. *Multivariate analysis of ecological data version 4.01*. Mjm Software Design, Gleneden Beach, Oregon. 237 pp.

MEINZER, F. C., ANDRADE, J. L., GOLDSTEIN, G., HOLBROOK, N. M., CAVELIER, J. & WRIGHT, S. J. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301.

MUTHURAMKUMAR, S. & PARTHASARATHY, N. 2001. Tree-liana relationships in a tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. *Journal of Tropical Ecology* 17:395–409.

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.

PÉREZ-SALICRUP, D. R. & BARKER, M. G. 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124:469–475.

PÉREZ-SALICRUP, D. R. & DE MEIJERE, W. 2005. Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas, Mexico. *Biotropica* 37:153–156.

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.

PUTZ, F. E. 1983. Liana biomass and leaf area of a "tierra firme" forest in the Rio Negro basin, Venezuela. *Biotropica* 15:185–189.

PUTZ, F. E. 1984a. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.

PUTZ, F. E. 1984b. How trees avoid and shed lianas. *Biotropica* 16:19–23.

PUTZ, F. E. & CHAI, P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75:523–531.

SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist* 166:262–276.

SCHNITZER, S. A. & BONGERS, F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17:223–230.

SCHNITZER, S. A. & CARSON, W. P. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 84:913–919.

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.

STEVENS, G. C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecology* 68:77–81.

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.

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.

ZULOAGA, F. O. & MORRONE, O. 1999. *Catálogo de las plantas vasculares de la República Argentina*, Vols. 1 & 2. Missouri Botanical Garden Press, Missouri.

Appendix: Total number of trees per species and per diameter class recorded in a 6-ha plot in Parque Sierra de San Javier, Tucumán, Argentina; listed by botanical family and foliar phenology. Numbers in parentheses indicate tree individuals colonized by at least one liana. Diameter classes: 1 = 10–19.9 cm; 2 = 20–29.9 cm; 3 = 30–39.9 cm; 4 = 40–49.9 cm; 5 = 50–59.9 cm; 6 = 60–69.9 cm; 7 = 70–79.9 cm; 8 = 80–89.9 cm; 9 = 90–99.9 cm; 10 = > 100 cm.

Tree species	Family	Foliar phenology	1	2	3	4	5	6	7	8	9	10	Total
Pentapanax angelicifolius	Araliaceae	Deciduous	1	1 (1)	–	–	1 (1)	–	–	–	–	–	3 (2)
Carica quercifolia	Caricaceae	Deciduous	–	–	–	1 (1)	–	–	–	–	–	–	1 (1)
Terminalia triflora	Combretaceae	Deciduous	19 (14)	21 (17)	31 (27)	29 (28)	13 (10)	7 (7)	5 (5)	1 (1)	–	–	126 (109)
Anadenanthera colubrina	Fabaceae	Deciduous	–	–	–	2	–	–	–	–	–	–	2 (1)
Enterolobium contortisiliquum	Fabaceae	Deciduous	1	–	–	–	–	–	–	–	–	–	1
Parapiptadenia excelsa	Fabaceae	Deciduous	1	1	9 (8)	10 (9)	8 (7)	13 (13)	7 (6)	6 (6)	–	–	55 (49)
Tipuana tipu	Fabaceae	Deciduous	–	–	–	1 (1)	1 (1)	–	3 (3)	–	2 (2)	1 (1)	8 (8)
Xylosma pubescens	Flacourtiaceae	Deciduous	4 (2)	–	2 (1)	1 (1)	–	–	–	–	–	–	7 (4)
Juglans australis	Juglandaceae	Deciduous	2	2 (2)	3 (3)	2 (2)	–	–	–	–	–	–	9 (7)
Cinnamomum porphyrium	Lauraceae	Evergreen	27 (16)	8 (6)	15 (8)	11 (10)	20 (14)	12 (9)	15 (15)	18 (14)	12 (12)	31 (31)	169 (135)
Cedrela lilloi	Meliaceae	Evergreen	7 (5)	3 (2)	1	–	–	–	1 (1)	–	–	–	12 (8)
Morus alba	Moraceae	Evergreen	1 (1)	–	–	–	–	–	–	–	–	–	1 (1)
Myrsine laetevirens	Myrsinaceae	Evergreen	4 (21)	24 (15)	11 (9)	4 (3)	1 (1)	–	1	–	–	1 (1)	82 (50)
Blepharocalyx salicifolius	Myrtaceae	Evergreen	37 (18)	25 (15)	20 (20)	15 (13)	9 (8)	6 (3)	6 (6)	4 (4)	1 (1)	2 (2)	125 (90)
Eugenia uniflora	Myrtaceae	Evergreen	432 (216)	15 (9)	–	–	–	–	–	–	–	–	447 (225)
Myrcianthes pungens	Myrtaceae	Evergreen	64 (38)	64 (45)	35 (29)	14 (12)	1 (1)	–	1 (1)	–	–	–	179 (126)
Pisonia ambigua	Nyctaginaceae	Deciduous	81 (48)	50 (35)	18 (11)	14 (11)	8 (6)	2	3 (2)	2 (2)	–	–	178 (115)
Piper tucumanum	Piperaceae	Evergreen	281 (173)	14 (12)	–	–	–	–	–	–	–	–	290 (185)
Ruprechtia apetala	Polygonaceae	Evergreen	–	1	–	–	–	–	–	–	–	–	1
Ruprechtia laxiflora	Polygonaceae	Deciduous	32 (20)	16 (11)	12 (8)	5 (4)	2 (2)	1 (1)	1 (1)	1 (1)	–	1 (1)	71 (49)
Randia spinosa	Rubiaceae	Deciduous	2 (1)	–	–	–	–	–	–	–	–	–	2 (1)
Citrus aurantium	Rutaceae	Evergreen	2	2 (2)	–	–	–	–	–	–	–	–	4 (2)
Fagara sp.	Rutaceae	Deciduous	1 (1)	–	2 (1)	–	–	–	–	–	–	–	3 (2)
Allophylus edulis	Sapindaceae	Evergreen	112 (75)	41 (25)	4 (3)	1 (1)	–	–	–	–	–	–	158 (103)
Cupania vernalis	Sapindaceae	Evergreen	17 (8)	–	1 (1)	1 (1)	–	–	–	–	–	–	19 (10)
Chrysophyllum marginatum	Sapotaceae	Evergreen	9 (5)	1 (1)	1 (1)	–	–	–	–	–	–	–	11 (7)
Solanum riparium	Solanaceae	Deciduous	79 (43)	33 (24)	4 (2)	1	–	–	–	–	–	–	117 (69)
Vassobia breviflora	Solanaceae	Evergreen	14 (12)	1 (1)	–	–	–	–	–	–	–	–	15 (13)
Heliocarpus popayanensis	Tiliaceae	Deciduous	1 (1)	–	–	–	–	–	–	–	–	–	1 (1)
Boehmeria caudata	Urticaceae	Evergreen	14 (9)	–	–	–	–	–	–	–	–	–	14 (9)
Urera baccifera	Urticaceae	Deciduous	14 (78)	2 (1)	–	–	–	–	–	–	–	–	142 (79)
Urera caracasana	Urticaceae	Deciduous	16 (7)	5 (4)	–	–	–	–	–	–	–	–	21 (11)
Duranta serratifolia	Verbenaceae	Deciduous	36 (27)	5 (3)	–	–	–	–	–	–	–	–	41 (30)
Total			1473 (839)	335 (231)	169 (132)	111 (96)	64 (51)	41 (33)	43 (40)	32 (28)	15 (15)	36 (36)	2320 (1502)