

Luciana F. Alves · Marco A. Assis · Juliano van Melis
Ana L. S. Barros · Simone A. Vieira
Fernando R. Martins · Luiz A. Martinelli
Carlos A. Joly

Variation in liana abundance and biomass along an elevational gradient in the tropical Atlantic Forest (Brazil)

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Abstract Lianas play a key role in forest structure, species diversity, as well as functional aspects of tropical forests. Although the study of lianas in the tropics has increased dramatically in recent years, basic information on liana communities for the Brazilian Atlantic Forest is still scarce. To understand general patterns of liana abundance and biomass along an elevational gradient (0–1,100 m asl) of coastal Atlantic Forest, we carried out a standard census for lianas ≥ 1 cm in five 1-ha plots distributed across different forest sites. On average, we found a twofold variation in liana abundance and biomass between lowland and other forest types. Large lianas (≥ 10 cm) accounted for 26–35% of total liana biomass at lower elevations, but they were not recorded

in montane forests. Although the abundance of lianas displayed strong spatial structure at short distances, the present local forest structure played a minor role structuring liana communities at the scale of 0.01 ha. Compared to similar moist and wet Neotropical forests, lianas are slightly less abundant in the Atlantic Forest, but the total biomass is similar. Our study highlights two important points: (1) despite some studies have shown the importance of small-scale canopy disturbance and support availability, the spatial scale of the relationships between lianas and forest structure can vary greatly among tropical forests; (2) our results add to the evidence that past canopy disturbance levels and minimum temperature variation exert influence on the structure of liana communities in tropical moist forests, particularly along short and steep elevational gradients.

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L. F. Alves (✉)
INSTAAR, University of Colorado,
Campus Box 450, Boulder, CO 80309, USA
E-mail: lu.falves@gmail.com
Tel.: +1-303-4927379
Fax: +1-303-4926388

L. F. Alves
University of Arizona, Tucson, AZ, USA

L. F. Alves
Instituto de Botânica, São Paulo, Brazil

M. A. Assis · A. L. S. Barros
Depto. de Botânica, Universidade Estadual Paulista,
CP 199, Rio Claro, SP 13506-900, Brazil

J. van Melis · F. R. Martins · C. A. Joly
Depto de Biologia Vegetal, Universidade Estadual de
Campinas, CP 6109, Campinas, SP 13083-970, Brazil

S. A. Vieira
NEPAM, Universidade Estadual de Campinas,
CP 6109, Campinas, SP 13083-970, Brazil

L. A. Martinelli
CENA/Esalq, Universidade de São Paulo,
CP 96, Piracicaba, SP 13400-970, Brazil

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Abbreviation

AGB Aboveground biomass

Introduction

Lianas contribute significantly to the species diversity and structural complexity of tropical forests and play an important role in ecosystem-level processes (Gentry 1991; Putz and Mooney 1991; Laurance et al. 2001; Schnitzer and Bongers 2002). Lianas comprise 1–14% of the total live aboveground biomass in tropical lowland forests (Gerwing and Farias 2000; Phillips et al. 2005; DeWalt and Chave 2004; Sarmiento et al. 2005), also contributing considerably to whole-forest transpiration and carbon sequestration (see Meinzer et al. 1999; Wright et al. 2004; Cai et al. 2009).

Across macroecological gradients, the distribution and abundance of lianas may be driven by environmental factors, such as dry season length or soil water

availability (Gentry 1991; Parthasarathy et al. 2004; Schnitzer 2005; DeWalt et al. 2006, 2010; Swaine and Grace 2007; Hu et al. 2010) and soil fertility (Gentry 1991; Laurance et al. 2001; DeWalt and Chave 2004). However, at the local scale, lianas have been shown to increase in dominance in response to canopy disturbance and support availability (Hegarty and Caballé 1991; DeWalt et al. 2000; Nabe-Nielsen 2001; van der Heijden and Phillips 2008). Woody lianas tend to attain their maximum abundance in tropical secondary forests and at forest edges (Laurance et al. 2001; Schnitzer and Bongers 2002; Gehring et al. 2004; Letcher and Chazdon 2009; Madeira et al. 2009), but biomass tends to be less variable in different aged forests, and evenly distributed within old-growth forests (DeWalt et al. 2000; Letcher and Chazdon 2009). This pattern can be explained by the lianas' ability to respond quickly to forest gap openness, capturing more light per unit mass than trees (Selaya and Anten 2008; Cai et al. 2009; Kazda et al. 2009) and suppressing the growth and recruitment of small trees and saplings in canopy gaps (Schnitzer et al. 2005; Toledo-Aceves and Swaine 2008; Schnitzer and Carson 2010), and even the growth of mature trees (Clark and Clark 1990; Ingwell et al. 2010). Old and large gaps are associated with aggregated spatial pattern of lianas in some tropical forests (Ibarra-Manríquez and Martínez-Ramos 2002; Malizia and Grau 2006; Foster et al. 2008). As local canopy height determines light availability, liana abundance tends to decrease with increasing canopy height (Hegarty and Caballé 1991; Balfour and Bond 1993; Gerwing and Farias 2000; Schnitzer and Bongers 2002; Parthasarathy et al. 2004) and canopy stature is also an important factor controlling the number of liana species (Molina-Freaner et al. 2004). Availability of support structures (host trees) also limits liana abundance and biomass, mainly for large lianas (Clark and Clark 1990; Phillips et al. 2002; Madeira et al. 2009). The climbing mechanism of lianas (tendrils, stem, or branch twiners) determines in great part the maximum diameter support a liana can use (DeWalt et al. 2000; Campanello et al. 2007).

Despite some attempts to disentangle the environmental variables controlling the distribution and abundance of lianas (Ibarra-Manríquez and Martínez-Ramos 2002; Molina-Freaner et al. 2004; van der Heijden and Phillips 2008), the effects of short, steep elevational gradients (< 2,000 m asl) on the structure and dynamics of liana communities are not well known (Balfour and Bound 1993; Parthasarathy et al. 2004; van der Heijden and Phillips 2008; Homeier et al. 2010). Minimum temperature and water availability may be important environmental factors constraining the distribution of lianas along short elevational gradients in the tropics (Gentry 1991; Parthasarathy et al. 2004) because lianas are vulnerable to cold- or drought-induced embolism due to characteristic wide and long vessel elements.

Our goal here was to evaluate general patterns of liana abundance and biomass along an elevational gradient (0–1,100 m asl) of coastal Atlantic Forest located

in southeastern Brazil. We investigated whether liana abundance and biomass are responsive to local forest structure rather than to abiotic factors that co-vary as function of elevation, such as temperature and solar radiation (see Korner 2007).

Methods

Study site

The elevational gradient encompasses a network of 1-ha permanent plots established in 2005–2006 (see Alves et al. 2010) to study forest diversity and dynamics, and ecosystem functioning of the coastal Brazilian Atlantic Forest, one of the global centers of vascular plant diversity and endemism in South America (Myers et al. 2000; Murray-Smith et al. 2009). The network of plots is located within the *Serra do Mar* State Park (PESM) (23°34'S–23°17'S and 45°02'W–45°11'W; 0–1,200 m asl), SE Brazil (Fig. 1). The vegetation is classified as tropical moist evergreen forest or lowland and upland rainforest (as in Oliveira-Filho and Fontes 2000), with dominant trees > 25 m and abundant epiphytes, ferns, bromeliads, and lianas (Morellato and Haddad 2000).

Geologically, this region is largely composed by crystalline basement with predominance of metamorphic (gneisses and migmatite) and granitic rocks; banks of sedimentary rocks are also observed at the coastal plain (IPT 2000). There is a clear dominance of sand texture in soils throughout the altitudinal gradient (Martins 2010). Soils are predominantly *Inceptisols* above 100 m asl without significant variance in soil texture and chemical attributes with elevation, still poor soils in terms of nutrients, but relatively more fertile than the *Quartzipsamment* soils at sea level (Martins 2010).

The regional climate is humid subtropical with hot summers, average annual precipitation of 2,500 mm, and monthly average temperature ranging from 19.1 to 25.5°C (Sentelhas et al. 1999). There is a decrease in precipitation during the winter, typically with 1 month per year with less than 50 mm rainfall, and up to 3 months with less than 100 mm (Sentelhas et al. 1999). As long-term climatic sequences are not available for different sites along the elevational gradient (except for the lowlands), we used a time-series of climate data derived from nearest weather stations (BIOCLIM database, Hijmans et al. 2005) to obtain interpolated bioclimatic values for three elevations (lowland: 100 m; submontane: 580 m; montane: 1,050 m) and characterize the microclimatic variation. Clearly, mean annual precipitation and temperature decrease with elevation (Table 1a).

Sampling

In 2007 and 2008, we carried out a liana census in five selected plots of the permanent network to cover a range of elevation (0–1,100 m asl). These plots represent four

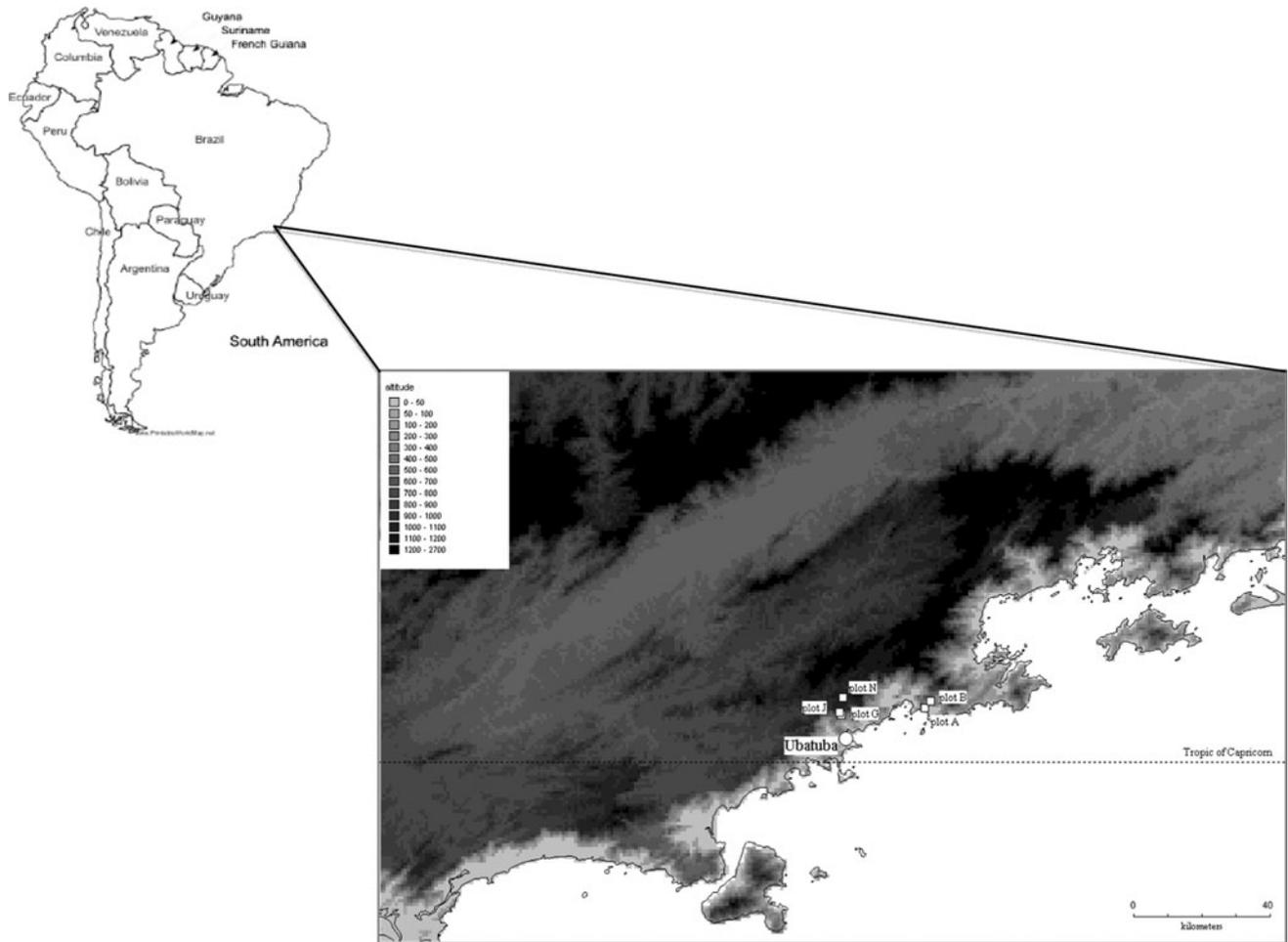


Fig. 1 Map of the study area showing the location of the forest plots in SE Atlantic Forest, Brazil

different forest types distinguished by their underlying floristic composition (Sanchez 2001) and topography (Joly et al. 2008): seasonally flooded forest (*restinga*), lowland, submontane, and montane forest (see Table 1b). The elevational gradient also represents a forest structure gradient (Alves et al. 2010; Table 1b) with higher forest biomass and abundance of large trees with increasing the elevation. Stem turnover rate and average gap area (Table 1b) tend to be higher in lowland sites, particularly at plot B, suggesting more intense past canopy disturbance in those sites.

Liana stem measurement

We followed the standard census protocol for lianas recommended by Gerwing et al. (2006) and Schnitzer et al. (2008) to allow comparison with similar studies (as in Schnitzer et al. 2006). Our estimates of liana abundance and biomass were based on census of all ramets (i.e., clonally derived stems) with stems ≥ 1 cm in diameter. We marked all liana stems ≥ 1 cm diameter with numbered

plastic tags in each of the five 1-ha plots, but we excluded epiphytes, hemi-epiphytes, and climbing bamboos. We located the point of measurement (POM) at 130 cm along the stem from the main rooting point (as in Gerwing et al. 2006). Although some liana stems are non-cylindrical or very irregular, we measured all liana stems as nearly cylindrical forms using a circumference tape to simplify the measurement protocol (see Gerwing et al. 2006). In some cases (as in one of the plots), we measured the diameter directly with a caliper. Circumference was converted into diameter to calculate the biomass. For lianas with two or more stems, the final diameter was obtained through the summed basal area. We estimated liana biomass (AGB, aboveground dry weight expressed as kg) from diameter (D) following the allometric equation developed from destructive measurements of lianas ≥ 1 –23 cm by Schnitzer et al. (2006): $AGB = \exp[-1.484 + 2.657 \ln(D)]$. This allometric equation was developed using data on diameter and biomass of 424 liana individuals ≥ 1 –23 cm in diameter from five independent studies collected in tropical forests of Brazil, Venezuela, French Guiana, and Cambodia. For multi-stemmed lianas, we summed the

Table 1 Microclimatic characterization and forest structure variation across the elevational gradient of tropical Atlantic Forest, Brazil

| (a) | Climate ^a | | | |
|--|-----------------------------|------------|------------|---------|
| | <i>Restinga</i> and lowland | Submontane | Submontane | Montane |
| Mean annual temperature (°C) | 22.6 | 19.3 | | 16.3 |
| Max temperature of warmest month (°C) | 30.5 | 27.0 | | 24.1 |
| Min temperature of coldest month (°C) | 13.7 | 9.8 | | 6.1 |
| Mean annual precipitation (mm year ⁻¹) | 2,406 | 2,159 | | 1,724 |
| Precipitation of driest month (mm year ⁻¹) | 95 | 68 | | 40 |

| (b) | Plot characteristics | | | | |
|--|----------------------|------------|------------|------------|------------|
| | <i>Restinga</i> | Lowland | Submontane | Submontane | Montane |
| Plot code | A | B | G | J | N |
| Elevation (m asl) | 11 | 45 | 188 | 375 | 1,025 |
| Forest structure ^b | | | | | |
| Stem density ≥4.8 cm (ind ha ⁻¹) | 1,626 | 1,154 | 1,506 | 1,833 | 1,454 |
| Stem density ≥10 cm (ind ha ⁻¹) | 770 | 597 | 688 | 870 | 791 |
| Stem biomass ≥4.8 cm (Mg ha ⁻¹) | 166.7 | 218.1 | 242.7 | 270.7 | 252.4 |
| Canopy height (m) 95th % distribution | 17.7 | 25.3 | 24.2 | 23.2 | 23.2 |
| Canopy disturbance ^c | | | | | |
| Stem turnover rate | 2.03 | 2.28 | 1.14 | 1.05 | 1.86 |
| Gaps ha ⁻¹ | 24 | 39 | 24 | 24 | 31 |
| Total gap area (m ²) | 1,244.6 | 2,934.0 | 1,178.0 | 1,152.9 | 1,543.3 |
| Average gap area (m ²) ± SE | 51.9 ± 3.2 | 61.4 ± 4.1 | 49.1 ± 3.0 | 48.0 ± 3.9 | 49.8 ± 2.7 |

^aData interpolation using BIOCLIM (Hijmans et al. 2005)

^bForest structure and biomass data from Alves et al. (2010)

^cStem turnover rate calculated after a 2-year interval census (Scaranello 2010; Alves et al. unpublished data). Gap size per plot was estimated following Runkle's (1982) extended gap definition (Alves et al. unpublished data)

AGB of each individual stem to obtain the individual-level AGB estimate.

Forest structure

For each plot, we used the initial census data (2006–2007; Alves et al. 2010) of all tree and palm stems ≥ 4.8 cm diameter at breast height (dbh) to estimate the following forest structure variables: total stem density (≥4.8 cm dbh) and stem density by size class (4.8–9.9, 10–29.9, ≥30 cm dbh), total live stem biomass (AGB), and average canopy height per 0.01-ha subplot. Data on forest structure and biomass were collected using standardized protocols (Phillips and Baker 2001; Joly et al. 2008). Alves et al. (2010) estimated individual tree biomass (live aboveground dry weight—AGB) by applying a pan-tropical allometric model developed by Chave et al. (2005) for tropical moist forests that expresses AGB as a function of dbh, total tree height, and average wood density. For palms, dbh data were converted to AGB using the equation developed by Hughes (1997) apud Nascimento and Laurance 2002; Alves et al. 2010).

Statistical analysis

We related differences in liana abundance and biomass to the forest structure attributes with the aim to assess potential local-scale effects driving the distribution of abundance and biomass of lianas. We chose variables that potentially describe complementary aspects of forest

structure components related to support availability: total stem density (≥4.8 cm dbh) and stem density of different size class (4.8–9.9, 10–29.9, ≥30 cm dbh), total stem biomass (stems ≥4.8 cm); and canopy disturbance (Balfour and Bond 1993; Gerwing and Farias 2000); average canopy height (m), at subplot scale (0.01 ha; $n = 100$ per plot). As the presence of spatial patterning within the data violates the assumption of many standard statistical tests (Legendre and Fortin 1989; Legendre and Legendre 1998), we first tested statistically whether there was any significant spatial autocorrelation for liana abundance and biomass, as well for each forest structure variable at subplot scale (0.01 ha). We used the function “sp.correlogram” for aerial data (which provides basic functions for building grid neighbor lists and spatial weights; see Bivand et al. 2008) in the R package “spdep” to test for spatial autocorrelation among different-order neighbors in a grid (that is, directly adjacent subplots are first-order neighbors, subplots separated by one degree of distance are second-order neighbors, etc.). As most of the forest structure variables were spatially autocorrelated at short distances (see Table S1, Electronic Supplementary Material), we applied the partial Mantel test to assess correlations between liana abundance and AGB on forest structure variables, controlling for the distance effect (Legendre and Legendre 1998). Probabilities of partial Mantel r values were obtained after 999 permutations in Passage 1.1 package (Rosenberg 2001). We also run the same analyses (spatial autocorrelation and partial Mantel test) using 20 × 20 m subplots (0.04 ha scale; $n = 25$ per plot). The results for the spatial auto-

correlation were not significant for liana abundance and biomass (not shown), which means there is no spatial autocorrelation at this scale. Also, increasing subplot size to 20 × 20 m (0.04-ha scale) did not change greatly the outcome of the partial Mantel test when compared to the 0.01 ha as liana variables were weakly related to structural variables at 0.04-ha scale (see Table S2, Electronic Supplementary Material).

We estimated the dominance of lianas relative to tree and palm stems as a ratio between liana and stem number per subplot, and liana and stem live AGB per subplot. Values above 1.0 indicate liana dominance over stems at 0.01-ha scale.

Results

Liana abundance and biomass along the gradient

We recorded a total of 2,865 lianas ≥1 cm diameter in five 1-ha plots (Table 2). Across plots, lianas contributed between 1.7 and 5.6% to the total forest live AGB (Table 2). At the scale of the 0.01-ha subplots, we obtained an average density (\pm SE) of 5.7 ± 2.5 lianas ≥1 cm. On average, we found a twofold variation in abundance and biomass between lowland forests (B) and other forest types (Table 2). The abundance and live AGB of lianas were greater in lowland forests than in other forest types. Additionally, large (> 5 cm) and very large (> 10 cm) lianas were more abundant in the lowland forest (Table 2). Very large lianas (> 10 cm) accounted for 26–35% of total liana biomass at low elevation (< 375 m asl), but they were not recorded in montane forests (Table 2).

Spatial structure at plot scale

Lianas were significantly spatially structured along the elevational gradient, with clumps concentrated at short

(up to the second-order neighbor) and large distances (fifth and sixth neighbors); the correlograms for liana density were globally significant for all forest types (Monte Carlo permutation bootstrap test of Moran's I; $p < 0.01$), except for one submontane forest plot (G; Fig. 2a). Liana AGB showed less spatial autocorrelation, suggesting randomness at 1-ha scale (Fig. 2b); the biomass of lianas was aggregated only at short distances in the lowland forest.

Lianas and forest structure

The positive spatial autocorrelation component of liana abundance at short distances was not clearly explained by forest structure variables (Table 3). After controlling for the distance effect (Partial Mantel test) we found that both liana abundance and biomass were poorly related to site structural characteristics, such as availability for support (tree and palm density) or average canopy height, or were not correlated at all (Table 3). Liana abundance was mostly correlated with liana AGB in lowland (B), submontane (J), and montane (N) forest plots. Availability of support was only correlated with liana abundance for one submontane forest plot (J; stems 10–30 cm) and for the montane forest (N; stems ≥4.8 cm). Liana AGB was correlated with one structural variable (number of stems ≥4.8 cm) in the montane forest (N). The liana community in the *restinga* forest (A), as well as in one submontane forest plot (G) did not show correlations with local forest structure. Canopy disturbance, described as the average canopy height, was not correlated with liana community structure in any forest type.

The dominance structure also differed greatly among forest types, with high liana dominance over stems in the lowland forest (B). We found that lianas outnumbered tree and palm stems with dbh ≥4.8 cm in ca. 50% of the subplots in the lowland forest, whereas only 10% of the subplots were dominated by lianas in other forest types

Table 2 Size-class structure (N : ind. ha⁻¹ and AGB: Mg ha⁻¹) of lianas and its contribution to total live aboveground biomass (AGB) along the elevational gradient of tropical Atlantic Forest, Brazil

| Diameter class (cm) | Restinga | | Lowland | | Submontane | | | | Montane | |
|---------------------|----------|------|---------|-------|------------|------|--------|------|---------|------|
| | Plot A | | Plot B | | Plot G | | Plot J | | Plot N | |
| | N | AGB | N | AGB | N | AGB | N | AGB | N | AGB |
| 1 | 222 | 0.14 | 187 | 0.15 | 129 | 0.10 | 255 | 0.16 | 81 | 0.07 |
| 2 | 87 | 0.22 | 256 | 0.66 | 160 | 0.40 | 102 | 0.24 | 117 | 0.31 |
| 3 | 56 | 0.33 | 198 | 1.24 | 103 | 0.62 | 65 | 0.40 | 93 | 0.58 |
| 4 | 24 | 0.29 | 114 | 1.36 | 52 | 0.59 | 36 | 0.43 | 52 | 0.62 |
| 5 | 19 | 0.35 | 65 | 1.31 | 32 | 0.63 | 27 | 0.53 | 36 | 0.77 |
| 6 | 15 | 0.47 | 45 | 1.39 | 17 | 0.53 | 16 | 0.54 | 22 | 0.68 |
| 7 | 10 | 0.46 | 27 | 1.23 | 21 | 0.93 | 9 | 0.41 | 11 | 0.50 |
| 8 | 12 | 0.84 | 13 | 0.88 | 6 | 0.38 | 4 | 0.23 | 8 | 0.52 |
| 9 | 1 | 0.10 | 12 | 1.11 | 2 | 0.13 | 6 | 0.51 | 2 | 0.19 |
| > 10 | 9 | 1.69 | 16 | 3.36 | 7 | 1.69 | 6 | 1.54 | 0 | 0.00 |
| Total | 455 | 4.90 | 933 | 12.68 | 529 | 6.01 | 526 | 4.99 | 422 | 4.25 |
| % Total AGB | | 2.9 | | 5.8 | | 2.5 | | 1.8 | | 1.7 |

(Fig. 3a). The relative dominance of lianas in terms of live AGB was not observed as no subplots showed dominance ratio values above 1.0 (Fig. 3b).

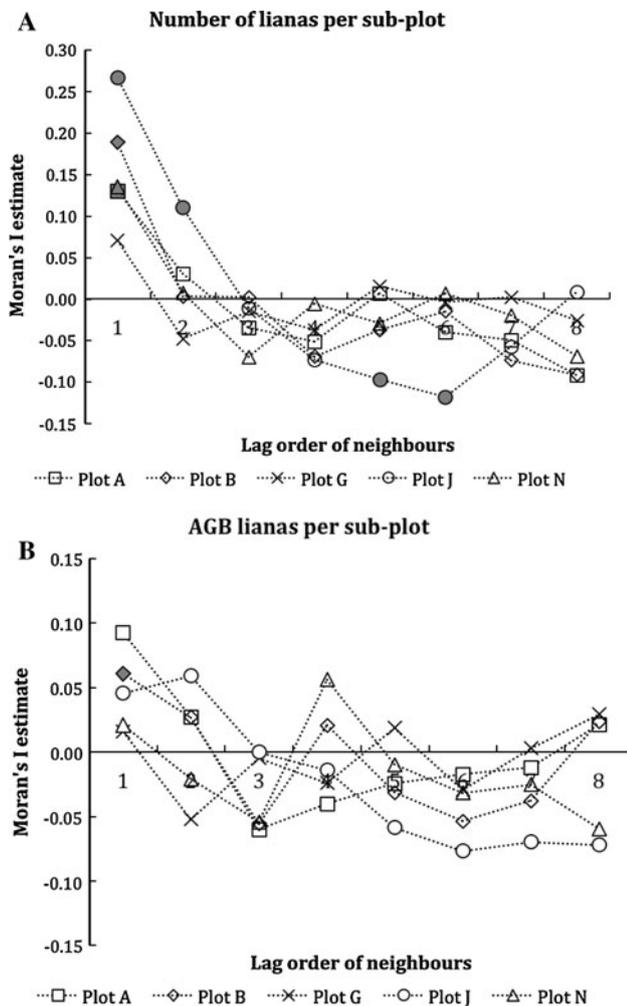


Fig. 2 Spatial correlograms (Moran's I) of liana abundance (a) and AGB (b) for eight successive radial lag orders of neighbors. Closed symbols represent significant Moran's I estimate at $p < 0.05$ (for globally significant correlograms after a Monte Carlo permutation bootstrap test of Moran's I; $n = 999$ permutations)

Table 3 Partial Mantel tests for correlation (r_{partial}) between abundance (#) and aboveground biomass (AGB) of liana community and forest structural variables, controlling for the distance effect

| Forest type | Plot | Matrix 1 | Matrix 2 | r_{partial} |
|-------------------|------|------------|----------------------|----------------------|
| Lowland forest | B | # lianas | AGB stems ≥ 4.8 | 0.19** |
| Lowland forest | B | # lianas | AGB lianas | 0.27*** |
| Submontane forest | J | # lianas | # stems 10–30 cm | 0.12* |
| Submontane forest | J | # lianas | AGB lianas | 0.33*** |
| Montane forest | N | # lianas | AGB lianas | 0.45*** |
| Montane forest | N | # lianas | AGB stems ≥ 4.8 | 0.12* |
| Montane forest | N | AGB lianas | # stems ≥ 4.8 | 0.16* |
| Montane forest | N | AGB lianas | AGB stems ≥ 4.8 | 0.15** |

Only significant correlations are shown

Probabilities of Mantel r values (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$) were obtained after 999 permutations

Discussion

The lowland forest supports more lianas with higher biomass than any other forest type along the elevational range, and the high liana dominance indicates that trees are overloaded with lianas in at least half of the plot area. Although the overall abundance of lianas displayed strong spatial autocorrelation at short distances, the present local forest structure played a minor role structuring liana communities within the Atlantic Forest sites at the scale of 0.01 or 0.04 ha. This implies that liana communities along the elevational gradient seem to be mostly structured by other factors unrelated to small-scale forest structure. We presented here two potential and complementary hypothesis to explain this pattern: (1) minimum temperature variation along this short elevational gradient; (2) high rates of past canopy disturbance in the lowland forests.

Minimum temperature is one important environmental factor that seems to constrain the distribution of lianas along short elevational gradients in the tropics (Gentry 1991; Parthasarathy et al. 2004). In spite of their efficient vascular system, low temperatures at high elevations can affect the distribution of lianas by promoting embolisms in xylem vessels (Ewers 1985), preventing water conductance and thus limiting large lianas to low elevation, warmer sites (Gentry 1991; Hu et al. 2010). As water rarely is a limiting factor for the non-seasonal coastal Atlantic Forest in Brazil (see Oliveira-Filho and Fontes 2000), low minimum temperatures may be one important factor suppressing total liana abundance and the abundance and biomass of large lianas at the montane forests, thus explaining their absence or rarity. Changes in temperature are far more distinctive than precipitation among sites (Table 1), and Sousa-Neto et al. (2011) found the lowest soil and air temperature for montane forest sites (1,000 m). However, climatic factors co-varying with elevation cannot completely explain the patterns of abundance and biomass found for the Atlantic Forest.

The present clumps of lianas at short distances found for all forest types can be explained primarily by liana clonal growth and dispersal (Morellato and Leita-Filho 1996; Schnitzer and Bongers 2002). However, a high rate

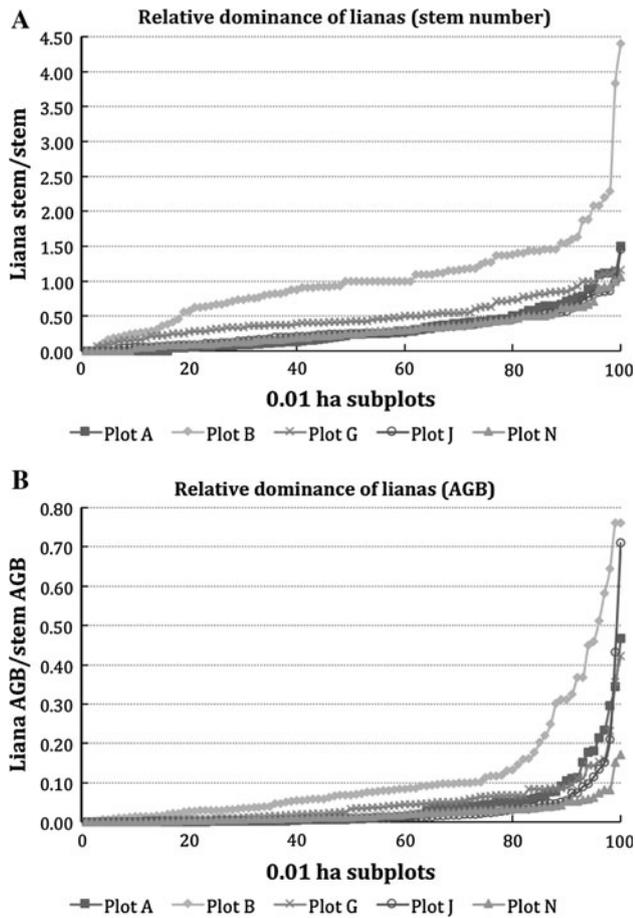


Fig. 3 Relative dominance of lianas (≥ 1 cm diameter) as a function of tree and palm stem number (a) and live AGB (b) along the elevational gradient of tropical moist forest (Atlantic Forest, Brazil). Each point represents data from 0.01-ha subplots

of past canopy disturbance probably explains the high abundance, biomass, and dominance of lianas in the lowland forest in comparison with other forest types. It is well documented that liana abundance is influenced by gap size and frequency. Canopy disturbance by an increase in treefall rate usually leads to the proliferation of lianas, as they require the high light levels of a gap or larger-scale disturbance for colonization (Schnitzer and Bongers 2002) and a trellis, increasing stem accessibility for other lianas (Putz and Chai 1987). After establishment, clumps of lianas probably were able to proliferate rapidly through the canopy and even to persist in the forest understory by capturing more light per unit mass than long-lived pioneer trees (Selaya and Anten 2008), remerging in new forest gaps (Schnitzer et al. 2000; DeWalt et al. 2000) and establishing a dominance in most of the plot area through time. In our study, liana abundance and biomass were highest in the most disturbed site, the lowland plot B, which had the maximum percentage of gap area and turnover rate (Table 1). Therefore, the high light availability provided by old gaps in the past would be one of the strongest drivers of this pattern (Schnitzer 2005).

Despite the fact that liana AGB had a strong correlation with liana abundance at subplot scale in most of the forest types, the biomass of lianas did not show a strong positive autocorrelation at large spatial scales (except for the lowland forest), suggesting that liana AGB is not structured by factors related to local canopy access. This pattern may be attributed to the low availability of hosts to load large lianas at the scale of 0.01 ha (Putz 1984) and different climbing mechanism of liana species (DeWalt et al. 2000; Nabe-Nielsen 2001). Thus, the patch size for liana growth and biomass increase would be larger than 0.01 ha in these Atlantic Forest sites due to low frequency of large gaps (i.e., > 400 m²; see Tabarelli and Mantovani 2000; Lima and Moura 2008) and very large trees (Alves et al. 2010).

The total biomass of lianas found along the elevational gradient of Atlantic Forest (Table 1) is within the range of values estimated in Central Amazon forests (lianas ≥ 2 cm: 4.6–13.7 Mg ha⁻¹; Nascimento and Laurance 2002; lianas ≥ 2 m tall: 43 Mg ha⁻¹; Gerwing and Farias 2000), Panamanian, Costa Rican, and Peruvian forests (lianas ≥ 0.5 cm; 8.0–17.2 Mg ha⁻¹; DeWalt and Chave 2004) and Venezuelan forests (lianas ≥ 2 m tall: 15.7 Mg ha⁻¹; Putz 1983) across different soil types, but the contribution of large lianas ≥ 10 cm to the total live AGB (stems ≥ 10 cm) was higher for the Atlantic Forest plots (0.6–1.6%) in comparison to Costa Rican forests (0.4–0.8%; Clark and Clark 2000). On the other hand, the number of large lianas ≥ 10 cm per hectare (7.6 ± 5.7) was smaller than for Amazonian (13.98 ± 5.95 ; Phillips et al. 2005) and Costa Rican forests (Mascaro et al. 2004). Compared to similar moist and wet Neotropical forests (DeWalt and Chave 2004; Mascaro et al. 2004), lianas are slightly less abundant in the Atlantic Forest (573 ± 181 stems ≥ 1 cm per ha), but the reason is unknown. A possible explanation would be the high abundance of palms and tree ferns in the Brazilian Atlantic Forest (Henderson et al. 1995; Negrelle 2002), which have architecture believed to inhibit liana establishment (Nesheim and Økland 2007).

Although local forest structure does not seem to have a strong influence on liana distribution, certainly lianas have an important influence on tree growth and AGB of these Atlantic Forest sites, as liana infestation is associated with high risk of tree mortality and growth suppression (Clark and Clark 1990; Phillips et al. 2002; Schnitzer and Carson 2010; Ingwell et al. 2010). The lowland forest plot (B) probably has undergone substantial change in canopy dynamics in the last years (Scaranello 2010; Table 1b) and the increase in liana density and dominance over trees may be the first evidence for a shift in forest dynamics. The biomass allocation strategy of lianas is efficient in high light environments like gaps and above tree canopy, as they are able to produce much more leaf mass per cross-sectional area than trees (Cai et al. 2009) with faster elongation growth rates, ascending successfully by specific climbing mechanisms. In this scenario of high dominance in the lowland forest, lianas could significantly reduce

tree sapling growth (Schnitzer et al. 2005; Schnitzer and Carson 2010) and tree survivorship (Schnitzer et al. 2000; Ingwell et al. 2010) and, consequently the potential capacity of this forest stand to sequester CO₂.

In conclusion, our study calls attention to two important points. One related to the local present structure and other related to disturbance history. Whereas some studies have shown the importance of local, small-scale canopy disturbance and support availability (Hegarty and Caballé 1991; DeWalt et al. 2000; Nabe-Nielsen 2001; Malizia and Grau 2006; van der Heijden and Phillips 2008), average canopy height at the 0.01-ha scale did not explain the distribution of liana abundance or biomass in any forest type, and support availability did not strongly influence liana abundance and biomass in our study. The present local forest structure was not a good predictor of liana community structure for the Atlantic moist forest, suggesting that the spatial scale of the relationship between lianas and forest structure can vary among different tropical forests. Our study adds to the evidence that past canopy disturbance levels (Schnitzer 2005) and the rates of gap formation (Malizia et al. 2010), as well minimum temperature variation (Gentry 1991) may exert some influence on the structure of liana communities in tropical moist forests, particularly along short and steep elevational gradients.

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References

- Alves LF, Vieira S, Scaranello MA, Camargo PB, Santos FA, Joly CA, Martinelli LA (2010) Forest structure and live above-ground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). *For Ecol Manag* 260:679–691. doi:10.1016/j.foreco.2010.05.023
- Balfour DA, Bond WJ (1993) Factors limiting climber distribution and abundance in a southern African forest. *J Ecol* 81:93–99
- Bivand RS, Pebesma EJ, Gómez-Rubio V (2008) *Applied spatial data analysis with R*. Springer, New York
- Cai Z, Schnitzer SA, Bongers F (2009) Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161:25–33. doi:10.1007/s00442-009-1355-4
- Campanello PI, Gatti MG, Ares A, Montti L, Goldstein G (2007) Tree regeneration and microclimate in a liana and bamboo-dominated semideciduous Atlantic Forest. *For Ecol Manag* 252:108–117. doi:10.1016/j.foreco.2007.06.032
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, Lescure JP, Nelson BW, Ogawa H, Puig H, Riéra B, Yamakura T (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99. doi:10.1007/s00442-005-0100-x
- Clark DB, Clark DA (1990) Distribution and effects on tree growth of lianas and hemiepiphytes in a Costa Rican tropical wet forest. *J Trop Ecol* 6:321–331
- Clark DB, Clark DA (2000) Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For Ecol Manag* 137:185–198
- DeWalt SJ, Chave J (2004) Structure and biomass of four lowland Neotropical forests. *Biotropica* 36:7–19
- DeWalt SJ, Ickeset K, Nilus R, Harms KE, Burslem DFRP (2006) Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecol* 186:203–216. doi:10.1007/s11258-006-9123-6
- DeWalt SJ, Schnitzer SA, Chave J, Bongers F et al (2010) Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica* 42:309–317. doi:10.1111/j.1744-7429.2009.00589.x
- DeWalt SJ, Schnitzer SA, Denslow JS (2000) Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *J Trop Ecol* 16:1–20
- Ewers FW (1985) Xylem structure and water conduction in conifer trees, dicot trees, and lianas. *IAWA Bull* 6:309–317
- Foster JR, Townsend PA, Zganjar CE (2008) Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. *Remote Sens Environ* 112:2104–2117. doi:10.1016/j.rse.2007.07.027
- Gehring C, Park S, Denich M (2004) Liana allometric biomass equations for Amazonian primary and secondary forest. *For Ecol Manag* 195:69–83
- Gentry AH (1991) Distribution and evolution of climbing plants. In: Putz FE, Mooney HA (eds) *Biology of vines*. Cambridge University Press, Cambridge, pp 3–49
- Gerwing JJ, Farias DL (2000) Integrating liana abundance and forest stature into an estimate of aboveground biomass for an eastern Amazonian forest. *J Trop Ecol* 16:327–336
- Gerwing JJ, Schnitzer SA, Burnham RJ, Bongers F, Chave J, DeWalt SJ, Ewango CEN, Foster R, Kenflack D, Martínez-Ramos M, Parren M, Parthasarathy N, Pérez-Salicipur DR, Putz FE, Thomas DW (2006) A standard protocol for lianas censuses. *Biotropica* 38:256–261. doi:10.1111/j.1744-7429.2006.00134.x
- Hegarty EE, Caballé G (1991) Distribution and abundance of vines in forest communities. In: Putz FE, Mooney HA (eds) *Biology of vines*. Cambridge University Press, Cambridge, pp 263–282
- Henderson A, Galeano G, Bernal B (1995) *Field guide to the palms of the Americas*. Princeton University Press, New Jersey
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi:10.1002/joc.1276
- Homeier J, Englert F, Leuschner C, Weigelt P, Unger M (2010) Factors controlling the abundance of lianas along an altitudinal transect of tropical forests in Ecuador. *For Ecol Manag* 259:1399–1405. doi:10.1016/j.foreco.2010.01.008
- Hu L, Li M, Li Z (2010) Geographical and environmental gradients of lianas and vines in China. *Glob Ecol Biogeogr* 19:554–561. doi:10.1111/j.1466-8238.2010.00527.x
- Ibarra-Manríquez G, Martínez-Ramos M (2002) Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecol* 160:91–112
- Ingwell LL, Wright SJ, Becklund KK, Hubbell SP, Schnitzer SA (2010) The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *J Ecol* 98:879–887. doi:10.1111/j.1365-2745.2010.01676.x
- IPT—Instituto de Pesquisas Tecnológicas (2000) Diagnóstico da situação atual dos recursos hídricos da Unidade de Gerenciamento dos Recursos Hídricos do Litoral Norte—UGRHI-3: Relatório 46172 Governo do Estado de São Paulo

- Joly CA, Martinelli LA, Alves LF, Vieira SA, Tamashiro JY, Aidar MPM, Camargo PBC, Assis MA, Bernacci LC (2008) As Parcelas Permanentes do Projeto Temático Biota Gradiente Funcional: Composição Florística, Estrutura e Funcionamento da Floresta Ombrófila Densa dos Núcleos Picinguaba e Santa Virgínia do Parque Estadual da Serra do Mar, Estado de São Paulo, Brasil. In: Sanquetta CR (ed) Experiências de monitoramento no bioma Mata Atlântica com uso de parcelas permanentes. RedeMAP and Funpar, Curitiba, pp 109–148
- Kazda M, Miladera EJC, Salzer J (2009) Optimisation of spatial allocation patterns in lianas compared to trees used for support. *Trees* 23:295–304. doi:10.1007/s00468-008-0277-9
- Korner C (2007) The use of “altitude” in ecological research. *Trends Ecol Evol* 22:569–574
- Laurance WF, Perez-Salicipur D, Delamonica P, Fearnside PM, D’Angelo S, Jerozolinski A, Pohl L, Lovejoy TE (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* 82:105–116
- Legendre P, Legendre L (1998) Numerical ecology. Elsevier, Amsterdam
- Legendre P, Fortin MJ (1989) Spatial pattern and ecological analysis. *Vegetatio* 80:107–138
- Letcher SG, Chazdon RL (2009) Lianas and self-supporting plants during forest succession. *For Ecol Manag* 257:2150–2156. doi:10.1016/j.foreco.2009.02.028
- Lima RAF, Moura LC (2008) Gap disturbance regime and composition in the Atlantic Montane Rain Forest: the influence of topography. *Plant Ecol* 197:239–253. doi:10.1007/s11258-007-9374-x
- Madeira BG, Espírito-Santo MM, D’Angelo Neto S, Nunes YRF, Sanchez-Azofeifa GA, Fernandes GW, Quesada M (2009) Changes in tree and liana communities along a successional gradient in a tropical dry forest in south-eastern Brazil. *Plant Ecol* 201:291–304. doi:10.1007/s11258-009-9580-9
- Malizia A, Grau HR (2006) Liana-host tree associations in a subtropical montane forest of north-western Argentina. *J Trop Ecol* 22:331–339
- Malizia A, Grau HR, Lichstein JW (2010) Soil phosphorus and disturbance influence liana communities in a subtropical montane forest. *J Veg Sci* 21:551–560. doi:10.1111/j.1654-1103.2009.01162.x
- Martins SC (2010) Caracterização dos solos e serapilheira ao longo do gradiente altitudinal da Mata Atlântica, Estado de São Paulo. Dissertation, Universidade de São Paulo
- Mascaro J, Schnitzer SA, Carson WP (2004) Liana diversity, abundance, and mortality in a tropical wet forest in Costa Rica Forest. *Ecol Manag* 190:3–14
- Meinzer FC, Andrade JL, Goldstein G, Holbrook NM, Cavelier J, Wright SJ (1999) Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301
- Molina-Freaner F, Gamez R, Tinoco-Ojaguren C, Castellanos AE (2004) Vine species diversity across environmental gradients in northwestern Mexico. *Biodivers Conserv* 13:1853–1874
- Morellato LPC, Leitao-Filho HF (1996) Reproductive phenology of climbers in a southeastern Brazilian Forest. *Biotropica* 28:180–191
- Morellato LPC, Haddad CFB (2000) Introduction: the Brazilian Atlantic Forest. *Biotropica* 32:786–792
- Murray-Smith C, Brummitt NA, Oliveira-Filho AT, Bachman S, Moat J, Lughadha EMN, Lucas EJ (2009) Plant diversity hotspots in the Atlantic coastal forests of Brazil. *Conserv Biol* 23:151–163. doi:10.1111/j.1523-1739.2008.01075.x
- Myers N, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Nabe-Nielsen J (2001) Diversity and distribution of lianas in a Neotropical rain forest, Yasuni National Park, Ecuador. *J Trop Ecol* 17:1–19
- Nascimento HEM, Laurance WF (2002) Total aboveground biomass in central Amazonian rainforests: a landscape-scale study. *For Ecol Manag* 168:311–321
- Negrelle RRB (2002) The Atlantic Forest in the Volta Velha Reserve: a tropical rain forest site outside the tropics. *Biodivers Conserv* 11:887–917
- Nesheim I, Økland RH (2007) Do vine species in Neotropical forest see the forest or the trees? *J Veg Sci* 18:395–404
- Oliveira-Filho AT, Fontes MAL (2000) Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica* 32:793–810
- Parthasarathy N, Muthuramkumar S, Reddy MS (2004) Patterns of liana diversity in tropical evergreen forests of peninsular India. *For Ecol Manag* 190:15–31
- Phillips OL, Baker TR (2001) Field manual for plot establishment and remeasurement RAINFOR (Amazon Forest Inventory Network). <http://www.geog.leeds.ac.uk/projects/rainfor>. Accessed June 2009
- Phillips OL, Martínez RV, Mendoza AM, Baker TR, Vargas PN (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology* 86:1250–1258
- Phillips OL, Martínez RV, Arroyo L, Baker TR et al (2002) Increasing dominance of large lianas in Amazonian forests. *Nature* 418:770–774
- Putz FE (1983) Liana biomass and leaf area of a tierra firme forest in the Rio Negro basin, Venezuela. *Biotropica* 15:185–189
- Putz FE (1984) How trees avoid and shed lianas. *Biotropica* 16:19–23
- Putz FE, Mooney HE (1991) The biology of vines. Cambridge University Press, Cambridge
- Putz FE, Chai P (1987) Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J Ecol* 75:523–531
- Rosenberg MS (2001) PASSAGE pattern analysis, spatial statistics, and geographic exegesis version 11 (Release 34). Department of Biology, Arizona State University, AZ. <http://www.passagesoftware.net>. Accessed 15 June 2009
- Runkle JR (1982) Patterns of disturbance in some old-growth mesic forests of North America. *Ecology* 63:1533–1556
- Sanchez M (2001) Composição florística e estrutura da comunidade arbórea num gradiente altitudinal da Mata Atlântica. Dissertation, Universidade Estadual de Campinas
- Sarmiento G, Pinillos M, Garay I (2005) Biomass variability in tropical American lowland rainforests. *Ecotropicos* 18:1–20
- Scaranello MAS (2010) Dinâmica da comunidade arbórea de Floresta Ombrófila Densa de Terras Baixas e de Restinga no Parque Estadual da Serra do Mar, SP. Thesis, Universidade de São Paulo
- Schnitzer SA (2005) A mechanistic explanation for the global patterns of liana abundance and distribution. *Am Nat* 166:262–276
- Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. *Trends Ecol Evol* 17:223–230
- Schnitzer SA, Carson WP (2010) Lianas suppress tree regeneration and diversity in treefall gaps. *Ecol Lett* 13:849–857. doi:10.1111/j.1461-0248.2010.01480.x
- Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J Ecol* 88:655–666
- Schnitzer SA, Kuzee ME, Bongers F (2005) Disentangling above- and below-ground competition between lianas and trees in a tropical forest. *J Ecol* 93:1115–1125
- Schnitzer SA, Dewalt SJ, Chave J (2006) Censusing and measuring lianas: a quantitative comparison of the common methods. *Biotropica* 38:581–591. doi:10.1111/j.1744-7429.2006.00187.x
- Schnitzer SA, Rutishauser S, Aguilar S (2008) Supplemental protocol for liana censuses. *For Ecol Manag* 255:1044–1049. doi:10.1016/j.foreco.2007.10.012
- Selaya NG, Anten NPR (2008) Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forest. *Funct Ecol* 22:30–39. doi:10.1111/j.1365-2435.2007.01350.x
- Sentelhas PC, Pereira AR, Marin FR, Angelocci LR, Alfonsi RR, Caramori PF, Swart S (1999) Balanços Hídricos Climatológicos do Brasil—500 balanços hídricos de localidades brasileiras. ESALQ, Piracicaba. <http://www.bdclima.cnpem.embrapa.br/index.php>. Accessed June 2009

- Sousa-Neto E, Carmo JB, Keller M, Martins SC, Alves LF, Vieira SA, Piccolo MC, Camargo P, Couto HTZ, Joly CA, Martinelli LA (2011) Soil-atmosphere exchange of nitrous oxide, methane and carbon dioxide in a gradient of elevation in the coastal Brazilian Atlantic forest. *Biogeosciences* 8:733–742. doi: [10.5194/bg-8-733-2011](https://doi.org/10.5194/bg-8-733-2011)
- Swaine MD, Grace J (2007) Lianas may be favored by low rainfall: evidence from Ghana. *Plant Ecol* 192:271–276
- Tabarelli M, Mantovani W (2000) Gap-phase regeneration in a tropical montane forest: the effects of gap structure and bamboo species. *Plant Ecol* 148:149–155
- Toledo-Aceves T, Swaine MD (2008) Effects of lianas on tree regeneration in gaps and forest understorey in a tropical forest in Ghana. *J Veg Sci* 19:717–728. doi: [10.3170/2008-8-18444](https://doi.org/10.3170/2008-8-18444)
- van der Heijden GMF, Phillips OL (2008) What controls liana success in Neotropical forests? *Glob Ecol Biogeogr* 17:372–383. doi: [10.1111/j.1466-8238.2007.00376.x](https://doi.org/10.1111/j.1466-8238.2007.00376.x)
- Wright SJ, Calderón O, Hernández AS, Paton S (2004) Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85:484–489