RESEARCH PAPER

What controls liana success in Neotropical forests?

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ABSTRACT

Aim We seek to determine the factors which control the success of lianas across macroecological gradients. Lianas have a strong impact on the growth, mortality and biomass of tropical trees, and are reported to be increasing in dominance, so understanding their behaviour is important from the perspectives of both ecological and global change.

Location Lowland and montane Neotropical forests.

Methods Using 65 standardized samples of lianas ($\geq$ 2.5 cm diameter) from across the Neotropics, we attempted to account for characteristics of both the environment and the forest in explaining macroecological variation in liana success in Neotropical forests, using regression analyses and structural equation modelling.

Results We found that both liana density and basal area were unrelated to mean annual precipitation, dry season length or soil variables, except for a weak effect of mean annual precipitation on liana basal area. Structural characteristics of the forest explained more of the variation in liana density and basal area than the physical environment. More disturbed forests generally tended to have a higher liana density. Liana basal area, however, was highest in undisturbed forests.

Main conclusions The availability of host trees and their characteristics may be more important than the direct effects of the physical environment in controlling the success of lianas in Neotropical forests. Changes to the tropical climate in the coming century may not strongly affect lianas directly, but could have very substantial indirect effects via changes in tree community structure and dynamics.

Keywords

Disturbance, forest characteristics, lianas, Neotropical forests, rainfall, seasonality, soil, structural equation modelling, temperature.

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INTRODUCTION

Lianas (woody climbers) are an important and characteristic structural component of tropical forests, where they comprise between 10% and 45% of woody stems (Schnitzer, 2005). Lianas rely mainly on trees to support their biomass and this, in combination with efficient vascular systems (e.g. Ewers *et al.*, 1991), allows them to contribute up to 40% of the leaf area of tropical forests (Hegarty & Caballé, 1991) with only *c.* 5% of total above-ground biomass (Putz, 1983; DeWalt & Chave, 2004). Infestation with lianas may increase host tree mortality (Putz, 1984b; Phillips *et al.*, 2002, 2005) and reduce tree growth (Putz, 1984b; Clark & Clark, 1990) and fecundity (Stevens, 1987; Kainer *et al.*, 2006). Additionally, lianas affect tree composition by

affecting their gap-phase regeneration (Schnitzer *et al.*, 2000) and by infesting some host taxa more than others (Putz, 1984a).

Recent work suggests that lianas are increasing in dominance in mature Neotropical forests (Phillips *et al.*, 2002; Wright *et al.*, 2004; Wright & Calderón, 2006), and there is some evidence suggesting that the same may be occurring in temperate forests (Allen *et al.*, 2007; but see Londré & Schnitzer, 2006). Several factors could be driving this, including a direct response to the increased atmospheric CO_2 levels, which may have a disproportionately strong effect on lianas (Granados & Körner, 2002; Hättenschwiller & Körner, 2003; Mohan *et al.*, 2006; Zotz *et al.*, 2006), the increased turnover of trees (Phillips & Gentry, 1994; Phillips *et al.*, 2004), the recent warming of the tropics (Malhi & Wright, 2004) or even increases in hunting intensity which could

benefit predominantly wind-dispersed lianas at the expense of predominantly animal-dispersed trees (Wright *et al.*, 2007). Because of their role in many forest dynamic processes, increased dominance of lianas may in turn lead to changes in the tree floristic composition (biodiversity impact) and reduce the carbon sequestration capacity of tropical forests (carbon cycle and climate impact) (Schnitzer *et al.*, 2000; Phillips *et al.*, 2002). Determining which factors control liana success may therefore be a necessary prerequisite for accurate prediction of the impacts of climate change on tropical forests.

Some attempts have been made to document patterns between liana community attributes and environmental variables. For example, researchers have suggested that areas with a pronounced dry season and low annual rainfall generally have high liana densities (Gentry, 1991; Parthasarathy *et al.*, 2004), perhaps because lianas, due to their deep root systems and efficient vascular systems, have a competitive advantage over other life-forms in seasonally dry areas (Schnitzer, 2005). The vascular systems of lianas are also very prone to freezing-induced embolism (Ewers *et al.*, 1991), which may explain the observed decrease in liana density with altitude (e.g. Putz & Chai, 1987; Parthasarathy *et al.*, 2004) and latitude (Molina-Freaner *et al.*, 2004; Schnitzer, 2005). Liana density and basal area may also be greater on fertile soils (Gentry, 1991); however, a clear relationship with soil fertility remains elusive (Putz & Chai, 1987; Balfour & Bond, 1993; Laurance *et al.*, 2001; DeWalt & Chave, 2004).

Liana community attributes may be influenced by characteristics of the forest itself as well as by the physical environment. At least on a local scale, liana density and basal area may be positively related to forest disturbance (Putz, 1984b; Schnitzer & Carson, 2000), often indicated by low tree basal area, biomass and wood density (e.g. Laurance *et al.*, 2001; Baker *et al.*, 2004b). However, on a broader scale this relationship with forest disturbance may be weak (Schnitzer, 2005). Liana density has also been found to correlate positively with the density of trees of between 1 and 10 cm in diameter, probably because of their suitability as trellises (Nabe-Nielsen, 2001).

To date, many studies have focused on landscape-scale variation in liana community attributes (e.g. Laurance *et al.*, 2001; Ibarra-Manríquez & Martínez-Ramos, 2002), in which climatic variation can be controlled for, or at a broader geographical scale, but principally evaluating one variable at a time (e.g. Gentry, 1991; Schnitzer, 2005). However, the relationships amongst environmental variables and structural tropical forest variables are known to be complex and often confounded. For example, tree populations on fertile soils are known to turn over faster than on poorer soils (Phillips *et al.*, 2004). And, because of leaching of soil nutrients, soil fertility itself tends to correlate negatively with annual rainfall (e.g. Jordan & Herrera, 1981), which in turn affects forest structure and dynamics (e.g. Malhi *et al.*, 2002, 2004). To better understand how liana density and basal area are controlled across broad geographical scales requires unravelling of the direct and indirect effects of climate, soil and structural forest variables on lianas.

Here we report findings of the first study taking characteristics of both the environment (i.e. soil nutrition and climate) and the

forest into account to test whether climate, soil and/or structural forest variables influence liana density and basal area on a geographical scale. To this end, we use a data set collected with a consistent methodology across the Neotropics, and employ structural equation modelling to disentangle the direct and indirect effects of these variables on liana community attributes.

METHODS

Study sites

We use a subset of data collected by the late A. H. Gentry using a standardized sampling methodology (Phillips and Miller 2002; data available from http://www.mobot.org/MOBOT/Research/gentry/transect.shtml). Gentry measured all trees, lianas, hemi-epiphytes and shrubs with stems ≥ 2.5 cm diameter in 0.1-ha samples (each comprising ten 2 m × 50 m transects, distributed semi-randomly in zig-zag fashion across an area of several hectares) from mature forest plots worldwide. Site homogeneity was maximized by constraining the sample within a narrow elevational range and one soil type, and by avoiding anthropogenic edges and successional habitats. By using 10 different lines that traverse a wide area, Gentry's samples were intended to be representative of the whole forest community under study, and not unduly influenced by small-scale patchiness in forest structure and composition. Gentry deliberately targeted his sampling across the full global gradient of forest climate and soil conditions. Thus, the data set was specifically designed to address questions of forest community assembly, diversity, function and structure on a macroecological scale, and has been widely used for continental and global-scale analyses (e.g. Gentry, 1982, 1988, 1991; Clinebell *et al.*, 1995; Enquist & Niklas, 2001; Phillips *et al.*, 2002; Schnitzer, 2005).

From this data set we selected all Neotropical sites for which accurate and standardized data for both climatic conditions and soil nutrients were available (Fig. 1). This comprises 65 samples from 57 different sites, spanning a precipitation gradient from 400 to 9000 mm year^{-1}. In the three sites with more than one sample, transects were located on contrasting soil types and were therefore assumed to represent independent sampling points.

Liana and structural forest variables

Nomenclature was updated using the TROPICOS data base, with family-level taxonomy following the Angiosperm Phylogeny Group (APG, 2002). When individuals were represented by more than one voucher, we only updated nomenclature when all vouchers for a record had the same species determination. We followed Gentry's habit category concepts (trees and shrubs, lianas, hemi-epiphytes) and in cases where habit codes for lianas and hemi-epiphytes were ambiguous we referred to local floras and field guides (e.g. Gentry, 1993) to confirm their habit. Following Gerwing *et al.* (2006), we excluded (hemi-)epiphytic climbers, climbing palms and Poaceae before calculating liana density and basal area (Appendix S1 in Supplementary Material).

Figure 1 Location of the 65 Neotropical transects used in this study. Sites with multiple transects are indicated with a single black dot.

Highly disturbed or dynamic forests usually have high tree stem densities, low tree basal area, low tree basal area to stem ratio and low wood density (Laurance *et al.*, 2001; Debski *et al.*, 2002; Baker *et al.*, 2004b). We therefore developed a suite of variables based upon these parameters as indicators of disturbance history (Appendix S1). Shrubs and trees may react differently to disturbance, therefore we also calculated tree density and basal area for stems ≥ 10 cm diameter to exclude shrubs. As lianas depend on other plants for support to reach the canopy, but are limited by the diameter they can surround (e.g. Putz, 1984b), we used tree and shrub density and basal area of stems of diameter 2.5–10 cm to represent trellis availability for lianas (cf. Nabe-Nielsen, 2001). Wood density data were derived from Chave *et al.* (2006) and Baker *et al.* (2004b). When species-specific wood density values were not available, a genus-level (for 56% of the species), family-level (for 15% of the species) or Neotropical mean (0.63 g cm^{-3} for 2.3% of the species) was used. All Cyatheaceae were allocated the Arecaceae family mean of 0.41 g cm^{-3} (1% of the species). Average wood densities per sample were weighted by basal area (cf. Baker *et al.*, 2004b) and calculated for stems ≥ 10 cm diameter only to exclude shrub species for which no data were available.

Environmental variables

Mean annual precipitation (MAP) was interpolated from rainfall maps by Gentry; dry season length (DSL) – the number of consecutive months of rainfall averaging < 100 mm month^{-1} – was derived from atlases (Clinebell *et al.*, 1995). Both were supplemented by data from local weather stations where possible. Mean annual temperature (MAT) for each site was derived from the Climatic Resource Unit (CRU) observed climatology data base, which includes mean monthly climatology data measured and interpolated over a 10′ latitude by longitude grid of global land areas for the period 1961–90 (New *et al.*, 2002). Where the elevation between the site and the CRU estimate differed, MAT was adjusted using a lapse rate of 0.006 °C m^{-1} (Barry 1992).

Soil data were obtained from Clinebell *et al.* (1995). For each 0.1-ha sample, topsoil (0–10 cm) was collected at three random points located within the transect area. The composite of the three samples was analysed for concentrations of exchangeable Al, Ca, Cu, Fe, Mg, K, Na, P, Si and total N. We calculated the effective cation exchange capacity (ECEC) (the sum of the concentration of Al, Ca, Mg, K and Na in cmol kg^{-1}) and the aluminium saturation [(Al/ECEC) × 100]. Soil and climate data are reported in Appendix S2.

Data analysis

We employed three different statistical techniques (correlation, multiple regression analysis and structural equation modelling) to investigate whether soil, climate and structural characteristics of the forest could predict liana density and basal area. All three analyses were carried out on the full data set of 65 samples as well as a subset of 58 samples which only included lowland forests (≤ 1000 m a.s.l.).

Simple correlations were used to explore the association between liana density and basal area and each of the environmental and structural forest variables. As this encompassed a large number of tests, we applied the sequential Bonferroni adjustment of Hochberg (1988) to adjust *P*-values to reduce the likelihood of spurious correlations (i.e. Type 1 errors). Soil variables were transformed to improve normality and reduce skewedness prior to the analyses (Appendix S3).

Multiple-regression analyses were used to combine soil, climate and forest variables in a single analysis. To reduce the number of soil variables in the regression analysis, we applied principal components analysis (PCA) (PC-ORD, McCune & Mefford, 1995) to the transformed soil data to describe the major gradients. These axes were statistically independent and fewer than the soil variables, so using PCA axes in regression analyses ensured that multiple regressions did not suffer from multi-colinearity and minimized the chance of spurious associations (Legendre & Legendre, 1998).

To assess the relative importance of soil, regression models were constructed in three stages, starting by including only the soil axes and sequentially adding the climate and structural forest variables. To accommodate the unimodal relationship between MAP and liana basal area we included the second-order term

MAP^2, centred around the mean, as an extra variable in the analyses. Since the structural forest variables were partially derived from one another, they could not be included in a single analysis. Therefore, the regression analyses were repeated three times using: (1) tree stem density and basal area; (2) tree stem density and basal area of the size classes 2.5–10 cm and ≥ 10 cm; (3) tree basal area: stem ratio. Wood density was included in all three analyses.

The efficacy of the different variables was assessed using best-subsets regression, a model-building technique used to find subsets of variables that best predict responses of a dependent variable (Draper & Smith, 1998). For each candidate model, each variable was evaluated in terms of R^2 (cf. Crawley, 1993) and variance inflation (Belsey *et al.*, 1980). The final regression model was assessed by comparing the standardized residuals to the fitted values and to each significant variable (cf. Crawley, 1993).

Structural equation modelling (SEM) is a modelling technique that is designed to provide insight into systems with a network of interactions (e.g. Shipley, 2000). A hypothesized model, usually based upon previous knowledge, is constructed using linear equations. SEM evaluates the degree of fit of the model by comparing the model-implied covariance matrix to the covariance matrix obtained from the data. It has an advantage over multiple regression analysis in that it can be used to disentangle direct (from one variable to another) and indirect (via one or more mediating variables) relationships between variables and, unlike path analysis, it takes measurement error into account. Although this technique is widely practised in other research areas, its application in ecology is still rather limited.

Prior to SEM analyses, we developed a priori hypotheses (Appendix S4), expressed as path diagrams, based on previous studies and discussions with soil experts (J. Lloyd and C. Quesada, pers. comm.). The relevant literature is not extensive and therefore we have included paths from all soil variables to the liana variables. The results of the best-subsets regression analysis were used to narrow down the wide array of possible structural forest variables which could be used in the model. This led us to include only wood density and tree density or basal area data for stems ≥ 10 cm. All relationships within the model were examined for linearity. We built the variable MAP^2 into the models to accommodate the unimodal relationship of MAP with DSL, the cation axis and liana basal area.

Amos 5.0.1 (Arbuckle, 2003) was used to fit the data to the hypothesized path models and to determine path coefficients and their standard errors using the maximum likelihood (ML) method. We assessed model fit using the chi-square (χ^2) statistic, with good-fitting models having an associated *P*-value > 0.05. We used the comparative fit index (CFI) and the root mean square error of approximation (RMSEA) to assess the closeness of fit, because they perform better than other fit indices when sample sizes are small (Fan *et al.*, 1999). Models with a CFI > 0.95, and a RMSEA < 0.05 are generally considered to be good-fitting (Browne & Cudeck, 1989; Hu & Bentler, 1995). As our data were non-normal and the ML method assumes multivariate normality, the Bollen–Stine bootstrap method (Bollen & Stine, 1993) and the ML bootstrap method (West *et al.*, 1995) were

used with 2000 iterations to correct the χ^2 statistic and the confidence intervals of the parameter estimates, respectively.

Since we used SEM in a 'model-generating' context, the original models have been subject to evaluation and modification. We removed insignificant paths one by one to test whether including those paths in the model significantly increased the χ^2 value. After deleting a path we examined model fit again using the criteria described above. Different models were also compared using the Akaike information criterion (AIC), which penalizes model complexity and therefore selects the simplest most likely model.

As the results for both the full and the lowland data set were similar in general, we focus here on results from lowland forests. Results of analyses that include the seven montane forest samples are reported in Appendices S5 and S6.

RESULTS

Variation in liana density and basal area

Density and basal area of lianas varied greatly among the samples. Liana density averaged 59 (± 25 SD) individuals per 0.1 ha, but spanned a 20-fold range from 5 to 105 individuals per 0.1 ha. Liana basal area averaged 0.11 (± 0.07 SD) m^2 per 0.1 ha, but ranged 50-fold from 0.005 to 0.26 m^2 per 0.1 ha (Appendix S1).

Simple correlations

After application of the sequential Bonferroni adjustment, no variable correlated significantly with liana density or basal area. Without applying the Bonferroni adjustment, liana density in lowland forests correlated with soil phosphorus ($r = 0.286$, $P = 0.017$) (Fig. 2). Liana basal area, on the other hand, correlated with soil copper concentrations ($r = -0.255$, $P = 0.049$), total tree and shrub basal area ($r = 0.291$, $P = 0.027$) and tree basal area of stems ≥ 10 cm diameter ($r = 0.290$, $P = 0.027$). Also, MAP seemed to be unimodally related to liana basal area (Fig. 3). However, this relationship was driven by the two sites with MAP > 7000 mm year^{-1} and when excluded there was no apparent association between MAP and liana basal area (Fig. 3). MAT was only positively correlated with both liana density ($r = 0.292$, $P = 0.018$) and basal area ($r = 0.298$, $P = 0.016$) when montane sites were incorporated (Figs 2 and 3).

PCA of soil nutrients

Ordination of soil data revealed four main linear combinations of soil properties with eigenvalues > 1, which together accounted for almost 82% of the variation. These major axes indicated gradients in: (1) cations; (2) Fe and total N; (3) Si, Na and total N; and (4) Cu, Si and Na (Appendix S7).

Regression analyses

Best-subsets regression analyses for liana density indicated that only density of trees with stems ≥ 10 cm in diameter was related
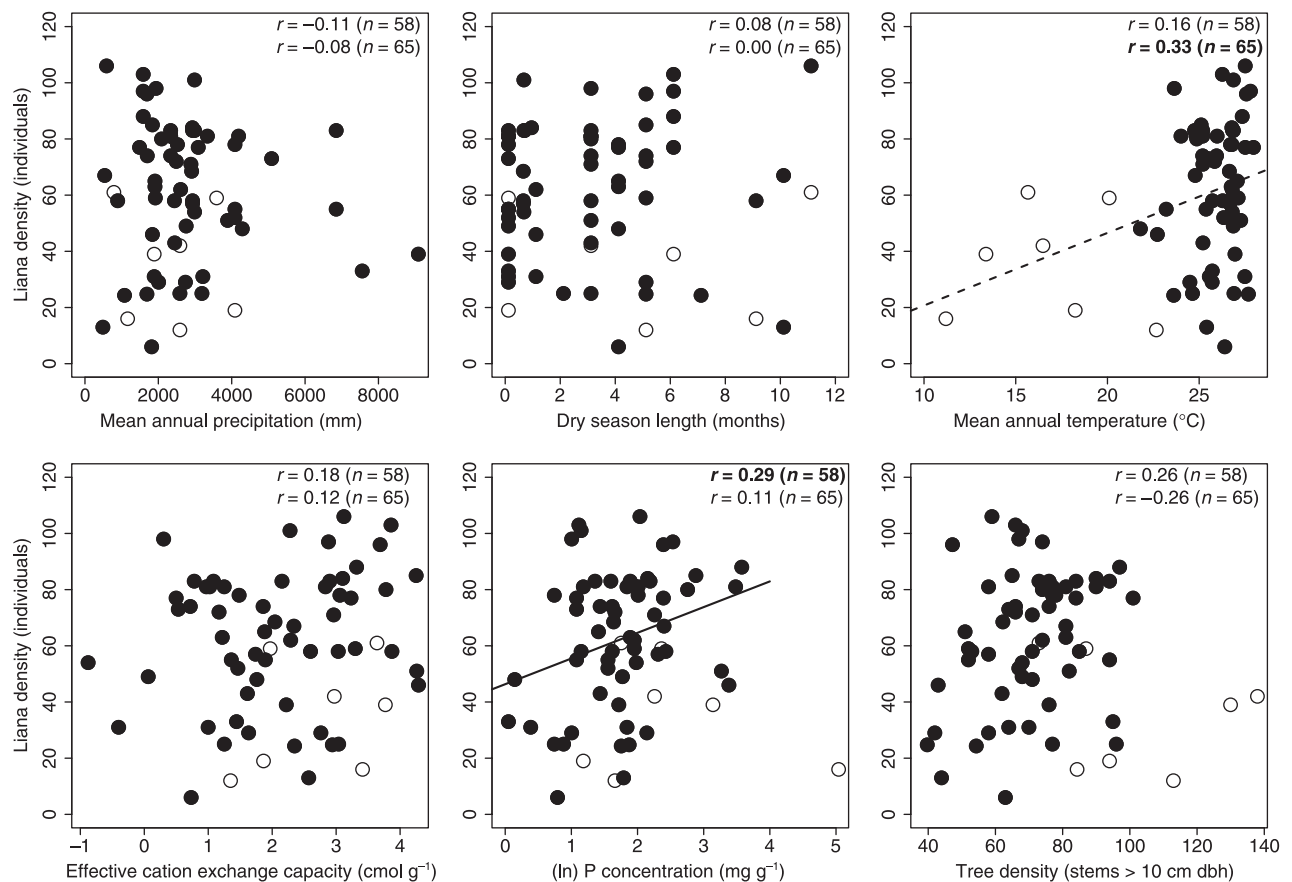
Figure 2 Bivariate relations between liana density and the climate variables, the effective cation exchange capacity (as indicator of soil fertility) and the most influential soil and structural forest variables. Closed circles indicate lowland sites (≤ 1000 m a.s.l.), open circles montane forests (> 1000 m a.s.l.). Lines of best fit are only indicated for associations which were significant before Bonferroni correction, with a continuous line for lowland forests and a dashed line for the data set including montane forests. Bold correlation coefficients are significant before sequential Bonferroni correction (none are significant after this correction).

to liana density in lowland forests, although the relationship was marginally insignificant statistically (Table 1). There was no evidence for a relationship between liana density and either MAP or DSL.

The optimal variable subset predicting liana basal area in lowland forests incorporated the Cu axis (indicating a negative effect of copper), the cation axis (indicating a negative effect of soil fertility), MAP^2, and, depending on which model, either tree and shrub basal area or tree basal area of stems ≥ 10 cm diameter (both positive) and MAP (Table 1). However, after excluding the two outlier samples with rainfall above 7000 mm year^{-1}, MAP^2 and MAP were no longer predictors of liana basal area.

Structural equation modelling

Consistent with the regression results, the best-fitting SEM model for liana density in lowland forests showed that the only variable directly related to liana density was tree density of stems ≥ 10 cm diameter (Fig. 4a). This relationship, however, was marginally insignificant after the ML bootstrap correction and explained only 7% of the variation.

For liana basal area, the best-fitting SEM model for the lowland data set suggested that the relationships of wood density

and tree basal area of stems ≥ 10 cm diameter (all positive) and copper (negative) with liana basal area were all direct and explained 24% of the variation in liana basal area (Fig. 4b). The effects of MAP, DSL, elevation and the other soil axes on liana basal area appeared to be indirect via their effect on either wood density or tree basal area of stems ≥ 10 cm diameter. However, an alternative model, similar to the results from the regression analysis, fitted the data equally well (Fig. 4c). This model explained slightly more of the variation in liana basal area (26%), but most paths leading to liana basal area were marginally insignificant after ML bootstrapping. After exclusion of the two extreme rainfall sites, MAP^2 was no longer a predictor of liana basal area in the alternative model (P = 0.45). Nevertheless, both models fit the truncated data set equally well, although the variance in liana basal area explained by the alternative model was slightly lower than that of the first model (21% vs. 23%).

DISCUSSION

To our knowledge, this is the first attempt to combine soil nutrients, climate and structural forest characteristics in explaining how liana density and basal area vary across Neotropical forests.
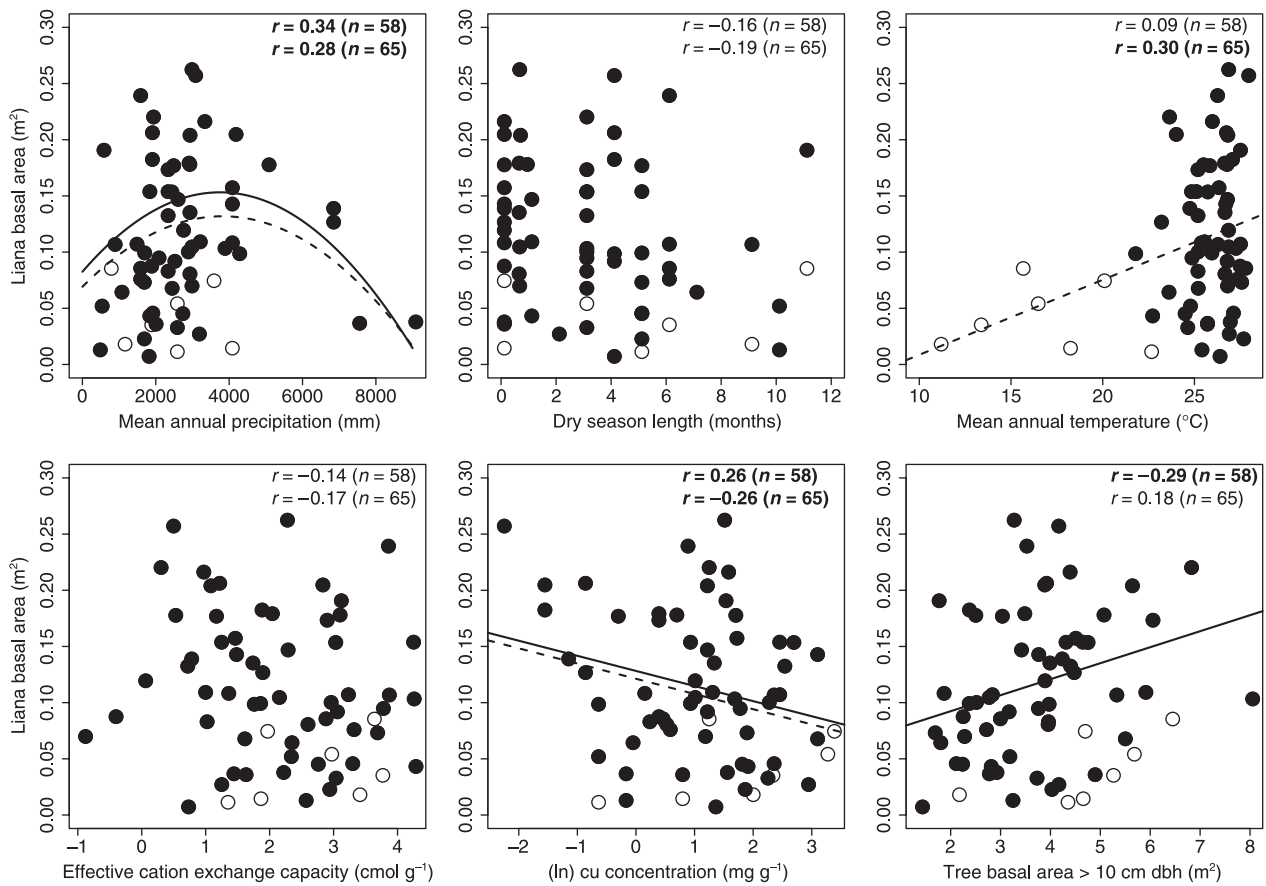
Figure 3 Bivariate relations between liana basal area and the three climate variables, the effective cation exchange capacity (as an indicator of soil fertility) and the most influential soil and structural forest variables. Closed circles indicate lowland sites (≤ 1000 m a.s.l.), open circles montane forests (> 1000 m a.s.l.). Lines of best fit are only indicated for associations which were significant before Bonferroni correction, with a continuous line for lowland forests and a dashed line for the data set including montane forests. Bold correlation coefficients are significant before sequential Bonferroni correction (none are significant after this correction).

Table 1 Best regression models explaining the variation in liana density and basal area (ba) in lowland forests (≤ 1000 m a.s.l., $n = 58$). See Appendix S7 for the direction of the effects of nutrients in the principal components analysis (PCA) axes.

	Cation axis	Cu axis	MAP	MAP²	No. of stems ≥ 10	Tree & shrub ba	Tree & shrub ba ≥ 10 cm	R^2	P
Liana density									
PCA only								–	–
PCA & climate								–	–
PCA, climate & forest*								–	–
PCA, climate & forest†					+			0.067	0.051
PCA, climate & forest‡								–	–
Liana basal area									
PCA only								–	–
PCA & climate		+	+	–				0.190	0.010
PCA, climate & forest*	+	+	–			+		0.247	0.005
PCA, climate & forest†	+	+	–				+	0.248	0.005
PCA, climate & forest‡		+	+	–				0.190	0.010

+ and – signs indicate the direction of the relationship. MAP, mean annual precipitation; MAP², second-order term of MAP.
*Wood density, total tree and shrub stem density and basal area.
†Wood density, tree and shrub stem density and basal area for size classes 2.5–10 cm and ≥10 cm.
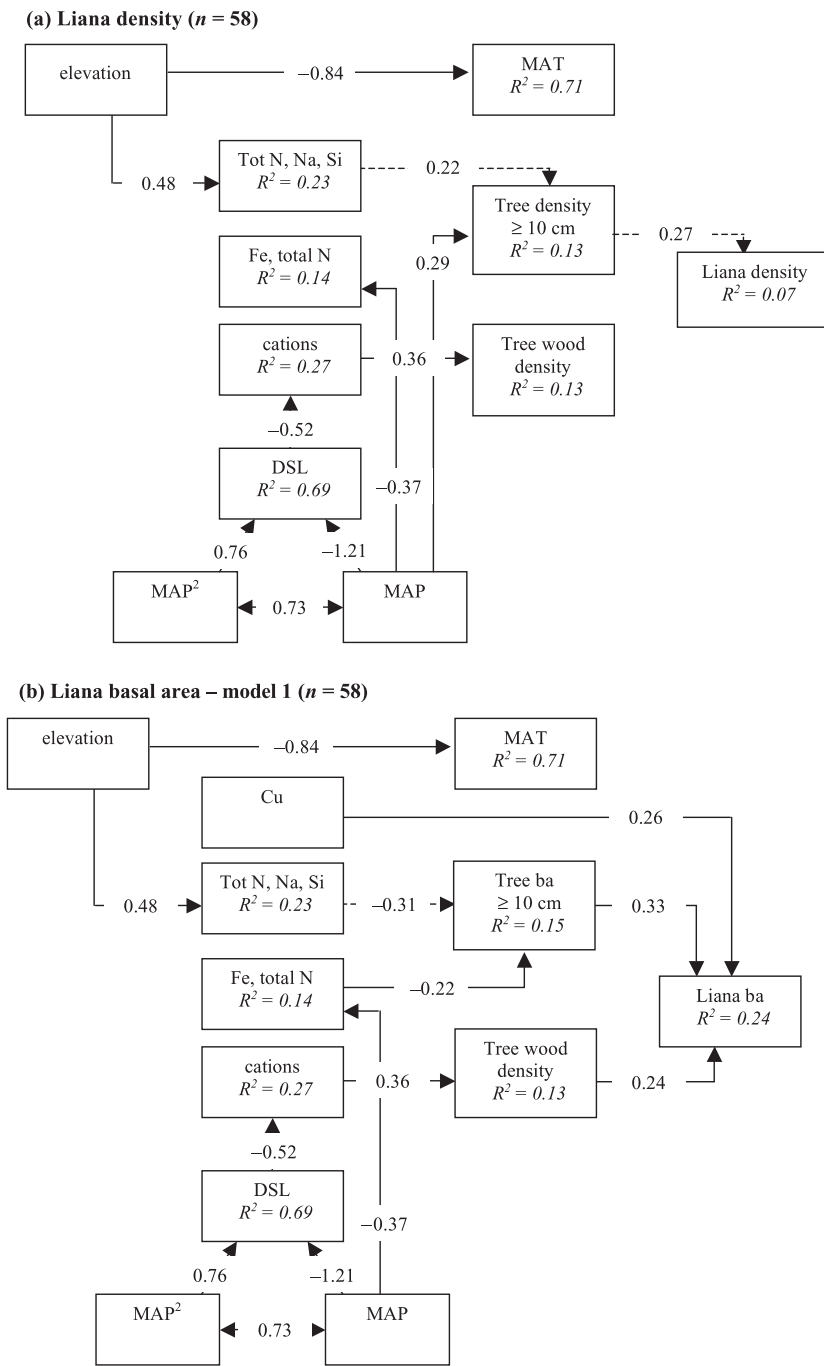‡Wood density and total tree and shrub basal area:stem density ratio.

(a) Liana density (*n* = 58)

(b) Liana basal area – model 1 (*n* = 58)

Figure 4 Structural equation models of: (a) liana density (lowland); $\chi^2 = 37.21$, d.f. = 44, $P = 0.76$, Bollen–Stine $P = 0.83$, CFI = 1.00, RMSEA < 10^{-4}; (b) liana basal area (lowland; model 1); $\chi^2 = 48.90$, d.f. = 53, $P = 0.64$, Bollen–Stine $P = 0.80$, CFI = 1.00, RMSEA $\leq 10^{-4}$; and (c) liana basal area (lowland; alternative model); $\chi^2 = 45.34$, d.f. = 52, $P = 0.73$, Bollen–Stine $P = 0.84$, CFI = 1.00, RMSEA $\leq 10^{-4}$. Single-headed arrows indicate 'causal' relationships, double-headed arrows are free correlations. Path coefficients are standardized regression weights (standardized by the standard deviation). Variances (R^2) explained by the model are italicized. Paths with ML bootstrapping corrected $P < 0.05$ are represented by a continuous line, paths with $0.05 > P \leq 0.10$ by a dashed line. Residual error variables are omitted for simplicity. Note: signs of the soil nutrients in the PCA axes are reported in Appendix S7. MAP, mean annual precipitation; MAP^2, second-order term of MAP; DSL, dry season length; MAT, mean annual temperature; ba, basal area.

Climate

The most striking finding is that neither annual rainfall nor rainfall seasonality are related to liana density and basal area in Neotropical forests (Table 1, Figs 2 and 4). Several previous studies have suggested that liana densities are highest in tropical forests with a pronounced dry season (Gentry, 1991; Parthasarathy *et al.*, 2004; Schnitzer, 2005). Schnitzer (2005) in particular hypothesized that liana densities were higher in seasonal forests and ascribed this to them having a competitive advantage over other life-forms as they do not suffer as much from water stress

during the dry season. The apparent discrepancy between our work and that of Schnitzer (2005), who also used the Gentry data set, remains unresolved, but may be due to the different geographical regions considered (Neotropical forests in our study, pantropics in Schnitzer's work); we speculate that the relationship between liana density and annual rainfall in Schnitzer's work may be driven by the inclusion of African and Asian samples, where factors such as tree and liana biogeography also differ markedly. We also assessed if the relative liana density [liana density/(liana density + total tree and shrub density)] and basal area (ba) [liana ba/(liana ba + total tree and shrub ba)] of
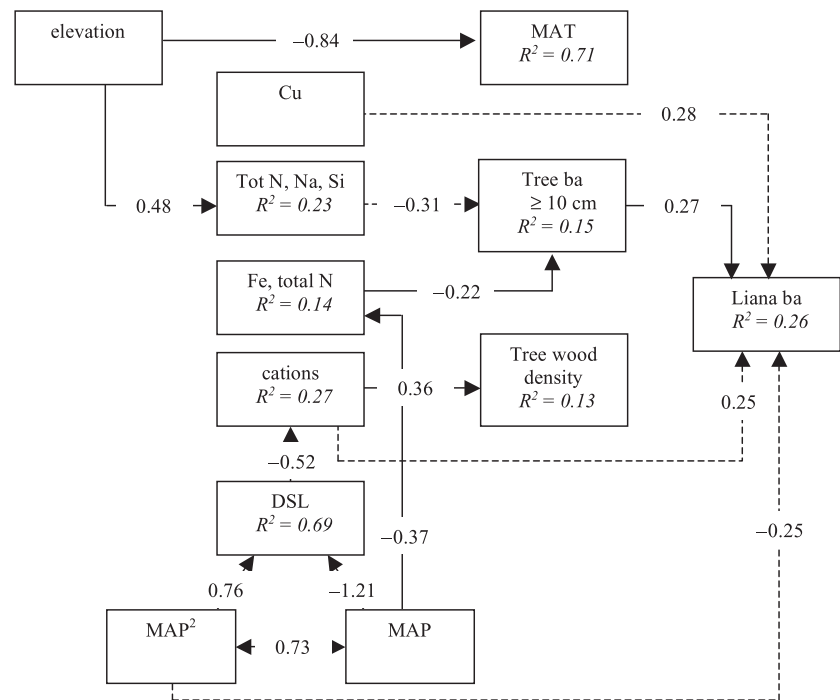
(c) Liana basal area – alternative model (*n* = 58)

Figure 4 *Continued*

lowland forests are related to dry season length and annual rainfall, but rejected this possibility as the results were insignificant. Sites at the climatic extremes offer some support for the moisture effect on lianas – the site with the highest liana density (Galerazamba, Colombia) occurred in an area with the longest dry season and a very low annual rainfall, and the two sites with an annual rainfall > 7000 mm have very low liana basal area (Fig. 3). But across the vast majority of Neotropical climates liana success is invariant with respect to rainfall regimes.

Although no effect of temperature is apparent in lowland forests, temperature is negatively associated with both liana density and basal area when montane forests are included (Figs 2 and 3) due to the reduced dominance of lianas in the seven high-altitude transects. Although research on the direct effect of temperature on liana density and basal area is scarce (Molina-Freaner *et al.*, 2004), several other studies have found a negative relationship between liana density and altitude (e.g. Putz & Chai, 1987; Parthasarathy *et al.*, 2004).

Soil

In general, our study shows that liana density is unrelated to soil fertility or to other soil gradients (Table 1, Figs 2 and 4). This is consistent with findings from some other studies (DeWalt & Chave, 2004; Balfour & Bond, 1993), although some researchers (mostly working on a landscape scale) have found greater liana abundance on more fertile soils (Proctor *et al.*, 1983; Putz & Chai, 1987; Laurance *et al.*, 2001; DeWalt *et al.*, 2006). Balfour and Bond (1993) have suggested that liana density may be determined by structural forest variables, in particular host tree characteristics, rather than soil nutrient availability.

The effect of soil fertility on liana basal area is less clear. SEM models illustrate that soil fertility may negatively influence liana basal area either directly (Table 1, Fig. 4c) or indirectly via its effect on tree wood density (Fig. 4b). However, since soil fertility may have an impact on several forest attributes (e.g. forest turnover rates (Phillips *et al.*, 2004)), the former might still indicate an indirect effect of soil fertility on liana basal area via a variable not included in the model. Of the soil factors tested the copper axis appears to have the strongest influence on liana basal area (Table 1, Fig. 4). As the copper concentrations in the sample are generally low (< 30 mg kg^{-1}), this is unlikely to be a toxicity effect and may simply reflect a weak association with another soil variable not included in the analysis. Unfortunately, although the soil analyses incorporate a wide range of macro- and micro-nutrients and potentially deleterious elements, they did not report pH, soil C, soil texture, soil organic matter and water holding capacity, which complicates interpretation.

Failure to reject the null hypothesis is not equivalent to disproving the alternative hypothesis; the general lack of significant relationships between the soil variables and liana density and basal area therefore poses the question whether the data are adequate for the task in hand. As almost any relationship is likely to be *statistically* significant if the sample size is large enough, we have to determine which are *ecologically* significant. For this reason, we calculated the smallest slope which the data would be able to detect with a power of 0.8 and α of 0.05, whilst keeping the sample size and the variance of the soil and liana variables equivalent to the original data using Lenth's (2006) power calculator. These minimum detectable slopes show that the soil data would be able to detect relatively small effects of soil on liana density or basal area ≥ 2.5 cm (i.e. a two-fold change in liana density and a

three-fold change in liana basal area) (Appendix S8). By comparison, these forests span a 20-fold gradient in liana density and a 50-fold gradient in liana basal area. Any possible effect of soil characteristics, as measured by Clinebell *et al.* (1995), on liana density and basal area ≥ 2.5 cm, is therefore very weak.

Structural forest variables

We expected liana density and basal area to be positively related to disturbance, as reflected by high tree densities, low tree basal area and low wood density. In the lowland sites, liana density indeed increased with density of trees with stems ≥ 10 cm in diameter; however, this relationship was weak. The patterns for liana basal area, however, were opposite to our expectations (Table 1; Fig. 4). To provide independent validation of these results, we also used long-term tree turnover data for trees ≥ 10 cm d.b.h. (% year^{-1}), a direct measure of long-term disturbance, available from permanent plots at 20 of the 58 lowland samples (Londoño & Jimenez, 1999; Baker *et al.*, 2004a,b; Lewis *et al.*, 2004; Phillips *et al.* 2004). The resulting correlations with liana variables were similar (density: $r = 0.243$; basal area: $r = 0.085$) to those obtained using the structural proxies for disturbance.

One explanation for the weak relationship between liana density and disturbance may be that although disturbance may explain liana density locally, it may not be an important predictor of liana density on a broader geographical scale (Schnitzer, 2005). An alternative explanation is that it simply reflects the spatial bias of the data set towards western Amazonia and the Andes. Most eastern Amazonian forests have lower turnover rates and higher wood densities than the western Amazon (Baker *et al.*, 2004b; Phillips *et al.*, 2004), but mostly lack comparable liana data.

Although disturbance may be a driver of liana density on the Neotropical scale, other structural characteristics of the forest may be more important in controlling liana basal area. When lianas reach the canopy, they expand in diameter and invest in leaves and reproductive organs (Putz, 1995). The success of lianas therefore depends upon successful infestation of a host tree. Tree species with high growth rates, low wood density, flexible trunks, long branch-free boles, long leaves and smooth bark, generally succeed in avoiding liana infestation (e.g. Putz, 1984a; Balfour & Bond, 1993) and may prevent lianas from reaching the canopy. Furthermore, large lianas (≥ 10 cm diameter) depend on large trees to support their biomass and to provide access to the high-light conditions in the canopy (Phillips *et al.*, 2005). As approximately 80% of the lianas ≥ 2.5 cm diameter have already reached the canopy (Kurzel *et al.*, 2006), forests with a low abundance of suitable hosts, such as forests with many fast-growing trees and a low density of large trees, may consequently have a low basal area of lianas ≥ 2.5 cm diameter. Host tree characteristics and availability may therefore be more important drivers of liana basal area than disturbance.

CONCLUSION

In Neotropical forests across a 20-fold rainfall gradient and a 150-fold gradient in ECEC, liana density (≥ 2.5 cm diameter) is invariant with respect to climate and soil variables, except for a weak effect of temperature. Similarly, liana basal area (≥ 2.5 cm diameter) does not vary predictably with climate, except for a weak effect of mean annual precipitation. Liana density may be driven by disturbance, but structural characteristics of the forest (tree stem density, basal area and wood density) appear more important in controlling liana basal area. We conclude that tropical climate changes this century may not strongly affect lianas directly, but could have very substantial indirect effects via changes in tree community structure and dynamics.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Liana density, basal area and structural forest variables for each of the 65 0.1-ha samples.

Appendix S2 Location, climate and soil variables for the 65 0.1-ha samples.

Appendix S3 Transformation of the soil variables.

Appendix S4 Initial SEM path diagrams.

Appendix S5 Best regression models for all 65 samples (including both lowland and montane forests).

Appendix S6 Structural equation results for all 65 samples (including both lowland and montane forests).

Appendix S7 Principal components analysis axes.

Appendix S8 Scatter plots with minimum detectable slopes.

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