



# Environmental effects on Neotropical liana species richness

Geertje M. F. van der Heijden\* and Oliver L. Phillips

Ecology and Global Change, School of  
Geography, University of Leeds, Leeds, UK

## ABSTRACT

**Aim** Lianas differ physiologically from trees, and therefore their species-richness patterns and potential climate-change responses might also differ. However, multivariate assessments of spatial patterns in liana species richness and their controls are lacking. Our aim in this paper is to identify the environmental factors that best explain the variation in liana species richness within tropical forests.

**Location** Lowland and montane Neotropical forests.

**Methods** We quantified the contributions of environmental variables and liana and tree-and-shrub abundance to the species richness of lianas, trees and shrubs  $\geq 2.5$  cm in diameter using a subset of 65 standardized (0.1 ha) plots from 57 Neotropical sites from a global dataset collected by the late Alwyn Gentry. We used both regression and structural equation modelling to account for the effects of environmental variables (climate, soil and disturbance) and liana density on liana species richness, and we compared the species-richness patterns of lianas with those of trees and shrubs.

**Results** We found that, after accounting for liana density, dry-season length was the dominant predictor of liana species richness. In addition, liana species richness was also related to stand-level wood density (a proxy for disturbance) in lowland forests, a pattern that has not hitherto been shown across such a large study region. Liana species richness had a weak association with soil properties, but the effect of soil may be obscured by the strong correlation between soil properties and climate. The diversity patterns of lianas and of trees and shrubs were congruent: wetter forests had a greater species richness of all woody plants.

**Main conclusions** The primary association of both liana and tree-and-shrub species richness with water availability suggests that, if parts of the Neotropics become drier as a result of climate change, substantial declines in the species richness of woody plants at the stand level may be anticipated.

## Keywords

Disturbance, liana species richness, Neotropics, rainfall, seasonality, soil, structural equation modelling, tree species richness.

\*Correspondence: Geertje M. F. van der Heijden, School of Geography, University of Leeds, Leeds LS2 9JT, UK.  
E-mail: g.m.f.vanderheijden@googlemail.com

## INTRODUCTION

Tropical forests are the most species-rich vegetation type on Earth (Gentry & Dodson, 1987; Gentry, 1988a). However, plant diversity in tropical forests is highly variable (Gentry, 1992). Numerous studies have attempted to explain this variability across broad spatial scales (e.g. Gentry, 1982, 1988a,b, 1992; Phillips *et al.*, 1994; Clinebell *et al.*, 1995;

Givnish, 1999; ter Steege *et al.*, 2000, 2003; Parmentier *et al.*, 2007).

In general, plant diversity in the tropics is strongly correlated with moisture supply (e.g. Hawkins *et al.*, 2003; Currie *et al.*, 2004), with dry-season length being identified as the main driver of vascular plant richness in the Neotropics (Gentry, 1988a,b; Clinebell *et al.*, 1995; ter Steege *et al.*, 2003). Several mechanisms have been hypothesized

esized to underlie this pattern (e.g. Wright, 1983; Givnish, 1999; Whittaker *et al.*, 2001; O'Brien, 2006). However, the main process or processes responsible for the covariance between diversity and water availability remain unknown (Currie *et al.*, 2004). Soil fertility has also been suggested as a driver of species richness (at least on local and landscape scales), but its role is contested (cf. Huston, 1980, 1994; Gentry, 1982, 1988a; Tilman, 1982; Wright, 1992) and may be much less important than that of climate (Clinebell *et al.*, 1995). Plant diversity is also thought to be higher in more productive and disturbed forests (Phillips *et al.*, 1994). The relationships among climate, soil, productivity and disturbance, however, are complex and often confounded, so it is necessary to disentangle the direct and indirect effects of these variables on diversity in order to develop the most insightful explanatory models.

An assessment of the relationships between diversity and environmental variables is clearly important for understanding why the diversity of tropical forests varies so much, as well as for helping to identify biodiversity hotspots and areas important for conservation. The emerging patterns may also contribute to more accurate predictions of the consequences of changing climatic conditions for diversity (Kerr *et al.*, 2007). Human-induced climate change is expected to alter the physiology, phenology and distribution of plants species considerably, so influencing the diversity of ecosystems and species (Hughes, 2000; Lovejoy & Hannah, 2005), and may become the leading cause of species extinctions this century (Thomas *et al.*, 2004).

Efforts to examine the drivers of plant diversity in tropical forests have focused mainly on woody plants in general (Clinebell *et al.*, 1995; Currie *et al.*, 2004) or on trees in particular (Gentry, 1988b; Phillips *et al.*, 1994; ter Steege *et al.*, 2000, 2003; Parmentier *et al.*, 2007). Lianas – woody climbers that rely on other plants for support – have been largely ignored in diversity research, although they are an important and characteristic component of tropical forests, where they can contribute up to 25% of the number of species (Gentry & Dodson, 1987) and up to 40% of the leaf productivity (Hegarty & Caballé, 1991). With their thin stems, wide vessels, deep root systems and relatively high leaf-area : basal-area ratio (Putz, 1983; Ewers *et al.*, 1990), lianas differ physiologically from trees, and therefore the macroecology of the two life-forms could also be divergent (Gentry, 1982). For example, pantropical liana abundance may actually increase with increasing dry-season length (Schnitzer, 2005; but see van der Heijden & Phillips, 2008). As plant abundance is strongly related to plant species richness, this might also indicate that liana species richness is positively rather than negatively correlated with dry-season length, as is found for many other plant life-forms. To date, a limited number of studies have focused on landscape-scale variation in liana diversity (Ibarra-Manríquez & Martínez-Ramos, 2002; DeWalt *et al.*, 2006; Macía *et al.*, 2007), in which climatic conditions are largely controlled for. Liana studies on a broader geographical scale mainly consider

one variable at a time (Gentry, 1982, 1991). A broad-scale multivariate analysis of liana species richness is lacking.

To this end, we quantify the contributions of environmental variables and liana, tree and shrub abundance to the species richness of lianas, trees and shrubs  $\geq 2.5$  cm in diameter [maximum diameter for lianas, and diameter at breast height (d.b.h.) for trees and shrubs] using a Neotropical subset of a global dataset collected by the late Alwyn Gentry using a standardized sampling methodology. Specifically, we focus on studying (1) the environmental variables potentially representing the main drivers of liana species richness (i.e. climate, soil or disturbance) in Neotropical forests, and (2) whether the species-richness patterns of lianas and their response to environmental variables are comparable to those of trees and shrubs. As Gentry specifically designed this dataset to address questions of forest community assembly, diversity, function and structure on a broad scale by sampling across the full global gradient of forest climate and soil conditions, it is well suited for this type of research and has been widely used for continental- and global-scale analyses (e.g. Gentry, 1982, 1988a, 1991; Clinebell *et al.*, 1995; Givnish, 1999; Phillips *et al.*, 2002; Currie *et al.*, 2004).

## MATERIALS AND METHODS

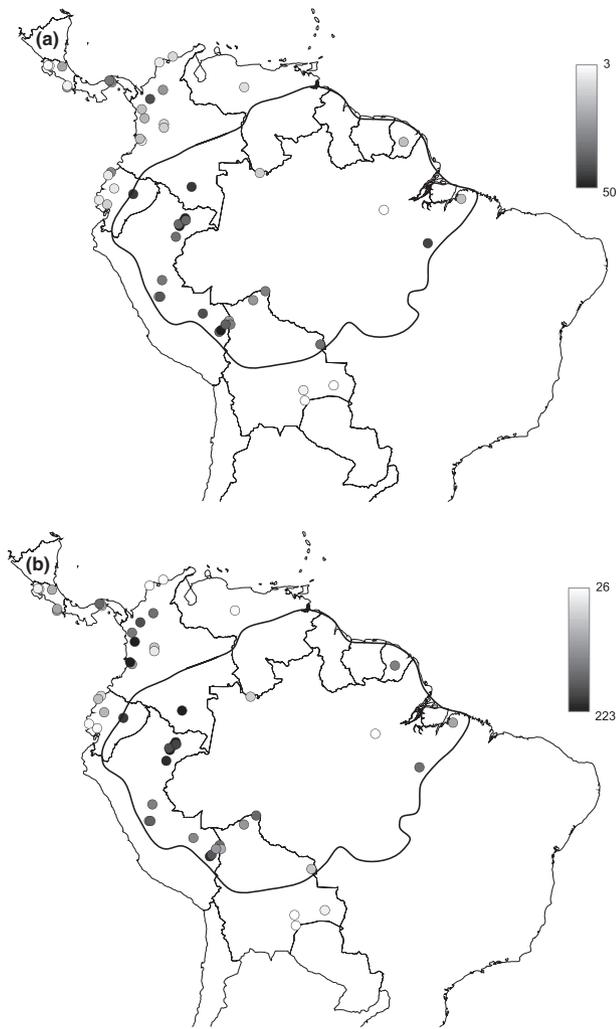
### Study sites and data collection

In 0.1 ha plots of mature homogenous forests world-wide, Gentry measured all trees, lianas, hemi-epiphytes and shrubs with stems  $\geq 2.5$  cm in diameter rooted within the transect area [for a detailed methodology see Phillips & Miller (2002); data available from <http://www.mobot.org/MOBOT/Research/gentry/transect.shtml>]. The plots were composed of 10  $2 \times 50$  m transects, distributed semi-randomly in zig-zag fashion across an area of several hectares. Site homogeneity was maximized by constraining the plot within a narrow elevational range and one soil type, and by avoiding anthropogenic edges and successional habitats. By using ten different lines that traverse a wide area, Gentry's 0.1 ha plots were intended to be representative of the whole forest community under study, and not be unduly influenced by small-scale patchiness in forest structure and composition.

From this dataset we selected 65 plots from 57 Neotropical sites for which accurate and standardized data for both climate and soil nutrients were available (Fig. 1). Three sites had more than one plot; as these were located on contrasting soil types they were assumed to represent independent sampling points. As the plots are principally from the western half of the Neotropics, the models presented here may not necessarily give an accurate prediction of the liana species richness in the central and eastern parts of Amazonia.

### Diversity measures

We updated nomenclature using the TROPICOS database, with family-level taxonomy following the Angiosperm Phy-



**Figure 1** Location of the Neotropical sites and observed species richness per 0.1 ha site ( $n = 58$ ) for (a) lianas and (b) trees and shrubs. Sites with multiple transects are represented by a single dot and the mean species richness for the sites (for the purposes of the map only, transects are treated as independent sampling points in the analyses). The area enclosed by the line represents Amazonia.

logeny Group (APG, 2002). Nomenclature for individuals represented by more than one voucher was updated only when all vouchers had the same species determination. We followed Gentry's habit category concepts (trees and shrubs, lianas, and hemi-epiphytes) and in cases where habit codes for lianas and hemi-epiphytes were ambiguous we referred to local flora and field guides (e.g. Gentry, 1993) to confirm their habit. (Hemi-)epiphytic climbers, and climbing palms and Poaceae were not considered to be lianas. We used species richness (i.e. the number of species per site) as our measure of liana and tree-and-shrub diversity (Appendix S1). For five plots for which  $< 0.1$  ha was inventoried (0.08 ha for three and 0.06 ha for two plots), we estimated the species richness in 0.1 ha using the mean species-accumulation curve generated for each site using 100 randomizations (R package 'vegan').

### Climatic and edaphic variables

Mean annual precipitation (MAP) and dry-season length (DSL) – the number of consecutive months of rainfall averaging  $< 100$  mm per month – were interpolated from rainfall maps (by Gentry) or derived from atlases (Clinebell *et al.*, 1995) and supplemented by data from local weather stations where possible. Mean annual temperature (MAT) for each site was derived from the Climatic Research Unit (CRU) observed climatology database (New *et al.*, 2002) and adjusted with a lapse rate of  $0.006^{\circ}\text{C m}^{-1}$  (Barry, 1992) when the elevation of the site differed from that of the CRU estimate. Although interpolation might have affected the values of the climate variables for the individual plots slightly, it is unlikely to have seriously undermined the analyses and results presented here.

Soil data were obtained from Clinebell *et al.* (1995). For each 0.1 ha plot, top soil (0–10 cm) was collected at three randomly located points within the plot area and the composite 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  $\text{cmol kg}^{-1}$ ) and the aluminium saturation  $[(\text{Al}/\text{ECEC}) \times 100]$ .

### Disturbance

The disturbance history of most of the sites is generally not well known, and we have turnover data, a direct measure of long-term disturbance, for trees  $\geq 10$  cm d.b.h. ( $\% \text{ year}^{-1}$ ) in only 20 lowland plots (published in Londoño & Jimenez, 1999; Baker *et al.*, 2004a,b; Lewis *et al.*, 2004; Phillips *et al.*, 2004). However, we might expect that more disturbed forests are likely to be relatively more dominated by light-demanding tree species, resulting in a lower stand-level wood density (Baker *et al.*, 2004b; Phillips *et al.*, 2004). As anticipated, tree turnover for the 20 plots was correlated with stand-level wood density ( $r = -0.65$ ,  $P = 0.001$ ), and we therefore used wood density as a disturbance proxy for all 65 plots. Wood density data were derived from Chave *et al.* (2006) and Baker *et al.* (2004b). Where species-specific wood densities were unavailable, generic (56% of the species) or familial (15% of the species) mean values, or an overall species mean of  $0.63 \text{ g cm}^{-3}$  (2.3% of the species), were used. Cyatheaceae (1% of the species) are treated here as monocots and were allocated the Arecaceae family mean of  $0.41 \text{ g cm}^{-3}$ . Average wood densities per plot were weighted by basal area (cf. Baker *et al.*, 2004b) and calculated for stems  $\geq 10$  cm in diameter only, to exclude shrub species for which no wood density data were available. Wood density and climate and soil variables are reported in Appendix S2.

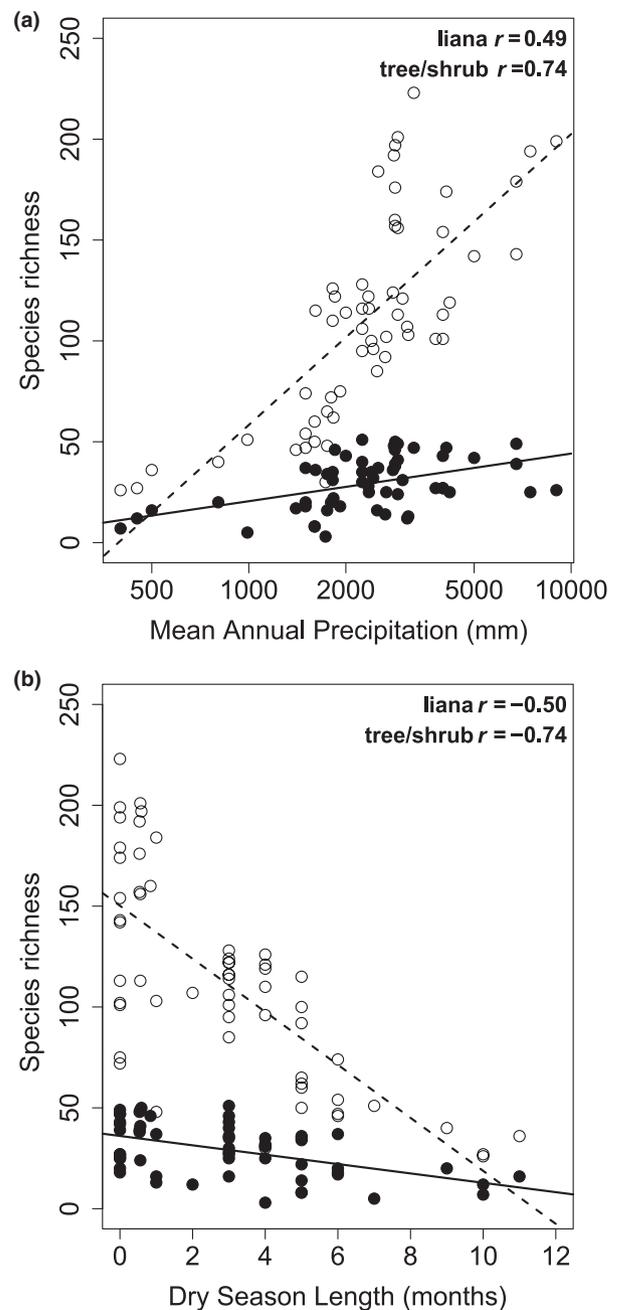
### Data analysis

We employed best-subsets regression and structural equation modelling to investigate whether soil, climate and/or distur-

bance predict liana and tree-and-shrub species richness. We selected best-fitting models using ordinary least squares (OLS) regression, with (1) only soil, (2) only climate, and (3) all climate, soil and disturbance variables included. Species richness is strongly correlated with the number of individuals in a plot – the probability of encountering a greater number of species increases with the number of individuals in an area. We therefore included either liana density or tree-and-shrub density in all models as an extra explanatory variable of species richness. Thus, any effect of environment on species richness indicates a direct effect, as the potential indirect effects via stem density are now separated.

The efficacy of the various 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), and model fit was assessed by comparing the standardized residuals with the fitted values and with each significant variable (cf. Crawley, 1993). Spatial autocorrelation of the residuals was evaluated using the Moran's  $I$  test for residual autocorrelation and by assessing the semi-variograms of each model (Cliff & Ord, 1981). As spatial autocorrelation was present in all models, generalized least squares (GLS) regression was used to account for this. Model selection was based upon assessment of the Akaike information criterion (AIC), whereby models with a lower AIC fit the data better (Burnham & Anderson, 2002). Finally, the residuals (observed minus predicted values) of the 'best' models were evaluated to determine where the model over- or under-predicts to give an indication of which other factors may need to be considered in the models.

We used structural equation modelling (SEM) to disentangle direct and indirect relationships between the variables (e.g. Shipley, 2000). Hypothesized models of the interactions between environmental variables, liana or tree-and-shrub density and wood density and their effect upon liana and tree-and-shrub species richness were based on previous knowledge and on discussion with soil experts (J. Lloyd and C. Quesada, pers. comm.) and were developed *a priori* (Appendix S3). AMOS 5.0.1 (Arbuckle, 2003) was used to evaluate the degree of model fit by comparing the model-implied covariance matrix with the covariance matrix obtained from the data and to determine path coefficients and their standard errors using the maximum likelihood method. We assessed general model goodness-of-fit using the chi-square ( $\chi^2$ ) statistic and closeness-of-fit using the comparative fit index (CFI) and the root mean square error of approximation (RMSEA), which perform better than other fit indices when sample sizes are small (Fan *et al.*, 1999). Models with a CFI > 0.95 and a RMSEA  $\leq$  0.05 are generally considered to be good fits (Browne & Cudeck, 1989; Hu & Bentler, 1995). We applied bootstrapping with 2000 iterations to correct the chi-square statistic and the confidence intervals of the parameter estimates for non-normality (Bollen & Stine, 1993; West *et al.*, 1995). As we used SEM in a 'model-generating' context, the original models have been subject to evaluation and modifica-



**Figure 2** Bivariate relationships of liana and tree-and-shrub species richness per 0.1 ha Neotropical site ( $n = 58$ ) with (a) mean annual precipitation and (b) dry-season length. Closed circles represent lianas, open circles represent trees and shrubs. Linear regression lines of best fit are indicated with a continuous line for lianas and a dashed line for trees and shrubs.

tion. We removed insignificant paths one by one to assess whether including those paths in the model significantly improved model fit. Models were compared by assessing the AIC, which penalizes model complexity. As the AIC is defined as twice the number of parameters minus the log-likelihood of the model, the AIC is also based upon a maximum likelihood method (Burnham & Anderson, 2002). Appendix S4 incorporates the correlation matrix for all variables included in the SEM.

Instead of including separate soil variables in the multivariate analyses, we incorporated four major soil axes derived from principal components analysis (PCA) (PC-ORD, McCune & Mefford, 1995) in the regression and SEM analyses. This reduces the number of soil variables in the analyses to ensure that the analyses do not suffer from multi-collinearity and it reduces the risk of spurious associations (Legendre & Legendre, 1998). To ensure that normality and linearity assumptions were met for both the regression and the SEM analyses, we transformed MAP using the natural log (Fig. 2). All other significant relationships between variables were linear. Analyses were carried out on the full dataset of 65 plots (lowland and montane) as well as on a subset of 58 lowland forests ( $\leq 1000$  m a.s.l.). As results for both the full and the lowland dataset were similar, we focus here on the results for lowland forests. Results for the full dataset are shown in Appendix S5. All analyses, except SEM, were carried out in R 2.6.0 (R Development Core Team, 2007).

## RESULTS

### Variation in species richness

Both liana and tree-and-shrub species richness varied greatly among the Neotropical plots (Fig. 1). Liana species richness ranged from 3 to 51 and averaged 27 ( $\pm 13$  SD) species per 0.1 ha. Tree-and-shrub species richness was substantially higher, ranging from 26 to 223 species and averaging 106 per 0.1 ha ( $\pm 51$  SD).

### Principal components analysis

Ordination of the soil variables revealed four main linear combinations of soil properties with eigenvalues  $> 1$ , which

together account for approximately 82% of the variation between the sites. These major axes are: (1) a gradient from high levels of Al and Al saturation to high cation concentrations (Cation axis); (2) a gradient of increasing concentrations of Fe and total N (Fe & total N axis); (3) a gradient from high Si concentrations to high Cu concentrations (Cu & Si axis); and (4) a gradient of increasing concentrations of Si and Na (Si & Na axis) (Appendix S6).

### Liana species richness

OLS and GLS regression analyses and SEM showed that the model incorporating liana density (positive effect), DSL (negative effect) and wood density (indicating a positive effect of disturbance) best explained the variation in the species richness of lianas  $\geq 2.5$  cm in diameter (Table 1). Models with MAP (positive effect) generally fit the data less well, as is indicated by the higher AIC value compared with models with DSL. The SEM models indicated that the effect of soil fertility on liana species richness is indirect, rather than direct, via its effect on wood density (Fig. 3a).

The distribution of the residuals from the GLS model for the 'best' liana species-richness model ('all variables' model, Table 1) indicated that, although most residuals are  $< 2$  RMSE (indicating reasonable to good fit), the model generally under-predicted liana species richness in the Amazon region and over-predicted it in Central America and in Chocó forests west of the Andes (Fig. 4a).

### Tree-and-shrub species richness

The optimal variable subset predicting the species richness of trees and shrubs  $\geq 2.5$  cm in diameter incorporated MAP and tree density (Table 1, Fig. 3b). Selection of DSL instead of

**Table 1** Best regression models explaining variation in (a) liana and (b) tree-and-shrub species richness of 0.1 ha plots from Neotropical lowland forests ( $\leq 1000$  m a.s.l.;  $n = 58$ ).

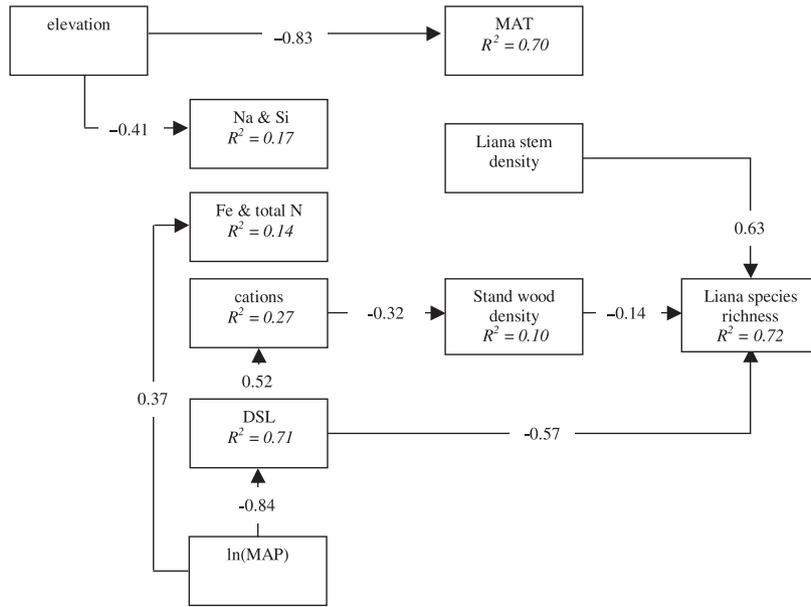
Model	Cation axis		Wood density	Liana tree-and-shrub density	OLS				GLS	
	DSL	ln(MAP)			$R^2$	$R^2_{adj}$	AIC	Moran's $I$	AIC	
(a) Liana species richness										
Only soil	–			+	0.494	0.476	430.4	<b>0.110</b>	425.5	
Only climate (1)		+		+	0.617	0.603	414.3	<b>0.211</b>	402.7	
Only climate (2)		–		+	0.678	0.667	404.2	0.108	400.9	
All variables	–		–	+	0.698	0.681	402.5	0.081	397.5	
(b) Tree-and-shrub species richness										
Only soil	–			+	0.440	0.419	593.4	<b>0.199</b>	581.7	
All variables (1)		–		+	0.624	0.610	570.3	0.070	568.1	
All variables (2)		+		+	0.643	0.630	567.4	<b>0.246</b>	551.0	

+ and – signs indicate the direction of the relationship of the environmental variables with species richness. Fit of the ordinary least squares (OLS) models is indicated by the  $R^2$ , adjusted  $R^2$  and Akaike information criterion (AIC). Models with bold Moran's  $I$  values exhibit spatial autocorrelation in the residuals. In the generalized least squares (GLS) analyses the spatial structure of the residuals was incorporated using a Gaussian function, and the fit of the GLS models is indicated by the AIC. Models with only climate variables were not included in the table when results were similar to those of the 'all variable' models (see Materials and Methods). Numbers indicate competing models.

DSL, dry-season length; MAP, mean annual precipitation.

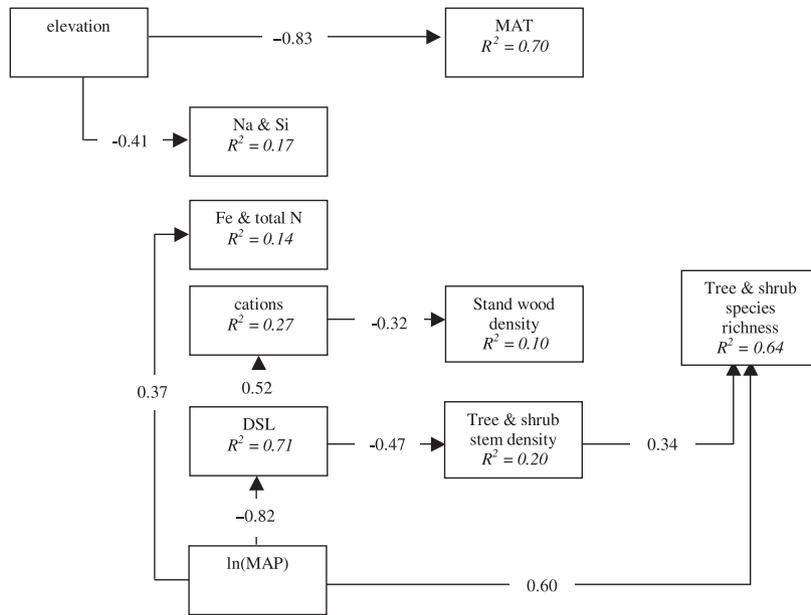
**(a) Liana species richness – lowland (n = 58)**

$\chi^2_{(36)} = 33.3, P = 0.60, \text{Bollen-Stine } P = 0.75, \text{CFI} = 1.00, \text{RMSEA} < 0.0001$



**(b) Tree and shrub species richness – lowland (n = 58)**

$\chi^2_{(36)} = 32.9, P = 0.62, \text{Bollen-Stine } P = 0.77, \text{CFI} = 1.00, \text{RMSEA} < 0.0001$



**Figure 3** Structural equation models of (a) liana and (b) tree-and-shrub species richness for 58 0.1 ha plots from Neotropical lowland forests. Single-headed arrows indicate ‘causal’ relationships. Path coefficients are standardized regression weights (standardized by the standard deviation). Paths indicate  $P \leq 0.05$ . Variances ( $R^2$ ) explained by the model are italicized. Residual error variables are omitted for simplicity. MAP, mean annual precipitation; MAT, mean annual temperature; DSL, dry-season length; CFI, comparative fit index; and RMSEA, root mean square error of approximation. Insignificant paths are not included in the final model. Note: see Appendix S6 for correlations of the soil nutrient variables with the axes resulting from principal components analysis.

MAP led to a model that fitted the data less well. As with the model for liana species richness, the ‘best’ model for tree species richness [‘only climate (2)’] also generally over-predicted in Central America and west of the Andes and under-predicted in Amazonia (Fig. 4b).

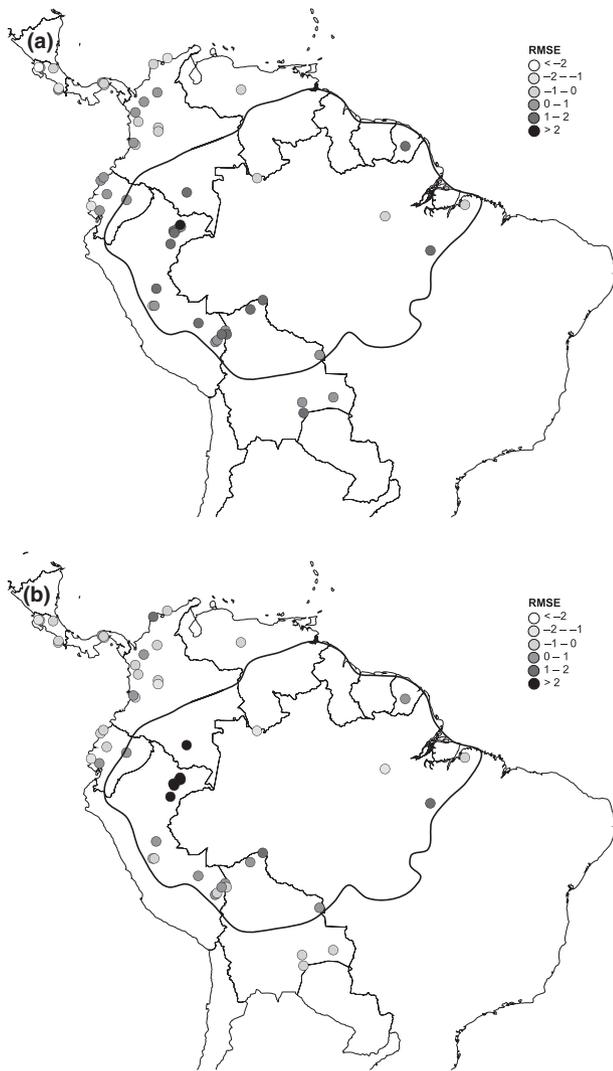
**DISCUSSION**

To our knowledge, this is the first attempt to combine stem density, disturbance, and climatic and edaphic variables in one analysis to explain the variability in liana species richness across Neotropical forests.

**Environmental associations with liana species richness**

*Climate*

Of the environmental variables considered here, DSL has the highest power to explain the variation in species richness of lianas  $\geq 2.5$  cm in diameter in the Neotropics (Table 1, Fig. 3a). Generally, areas with evenly distributed rainfall have more liana species than those with a pronounced dry season. This result is consistent with several other studies that also found dry-season length in particular (Gentry, 1988a,b; Clinebell *et al.*, 1995; ter Steege *et al.*, 2003), and water- and



**Figure 4** Spatial distribution of the residuals for the (a) 'all variables' model for liana species richness and (b) 'only climate (2)' model for tree-and-shrub species richness (Table 1). Residuals are shown according to the size of the error relative to the root mean square error (RMSE), with residuals  $> 2$  RMSE representing gross errors of fit. Under-prediction of the model is indicated by positive errors (dark colours), over-prediction by negative errors (light colours). Sites with more than one transect are represented by the mean residuals. The area indicated by the line represents Amazonia.

humidity-related variables in general (Gentry, 1982; Hawkins *et al.*, 2003; Currie *et al.*, 2004), to be the main correlates with plant and tree diversity in the Neotropics.

Several mechanisms have been proposed to explain these water availability–diversity relationships, some trying to explain the origin and others the maintenance of diversity (e.g. Givnish, 1999; Currie *et al.*, 2004). One historically popular mechanism is species–energy theory, which was first proposed by Wright (1983) and later extended by others (e.g. Hawkins *et al.*, 2003; Storch *et al.*, 2005). This theory states that a high net primary productivity (NPP) will lead to a high

number of individuals, high speciation and low extinction rates and consequently to a high number of species. The impact of the availability of water on species richness is proposed to be indirect by its positive influence on NPP (i.e. influencing also abundance). A slightly different hypothesis is that a high or evenly distributed moisture supply allows plants to survive at lower light intensities, increasing plant density and therefore the number of species (Huston, 1994; Givnish, 1999). However, for lianas there is no support for either of these above-mentioned hypotheses. Liana species richness is strongly correlated with liana density (and therefore with productivity), but liana density itself is unrelated to water availability (Fig. 3a; van der Heijden & Phillips, 2008). These findings contrast with those of Schnitzer (2005), who found that liana density actually increased in areas with a pronounced dry season – contrary to the hypotheses advanced above – possibly as a result of the inclusion of African and Asian plots, where tree and liana biogeographical factors differ markedly compared to those in Amazonia. Finally, Givnish (1999) hypothesized that the level of density-dependent mortality caused by plant pathogens and/or herbivores, which results in a higher turnover and therefore in a higher species richness, increases with increasing rainfall and decreasing seasonality. However, our results show that, although disturbance (as inferred by the wood density proxy) is associated with liana species richness, it is not correlated with rainfall or seasonality (Fig. 3a).

It is more likely that the negative relationship between DSL and liana diversity may have resulted from one or a combination of the following. First, the liana species pool will be depleted as lianas face a physiological challenge – lianas have wide vessels and narrow, uninsulated stems and are therefore prone to drought-induced embolism (Ewers *et al.*, 1990). Only liana species adapted to cope with these conditions may be expected to survive in areas with a pronounced dry season (but see Currie *et al.*, 2004). Second, a longer dry season shortens the growing season, which affects survival and establishment rates, which in turn may decrease the number of potential co-existing functional types, and hence the number of liana species (Kleidon & Mooney, 2000).

#### Disturbance

Apart from DSL, disturbance, as inferred from the wood density proxy, is a significant predictor of species richness of lianas  $\geq 2.5$  cm in diameter per 0.1 ha plot on a Neotropical scale (Table 1, Fig 3a). More disturbed sites have a higher liana species richness, a relationship previously not documented across such an extensive geographical region, but which is well established on both local and landscape scales (Schnitzer & Carson, 2000; Laurance *et al.*, 2001; Ibarra-Manríquez & Martínez-Ramos, 2002). The contribution of the independent effect of disturbance, however, is relatively small, as excluding the disturbance proxy from the OLS model (although it was significant in the model) reduced the  $R^2_{adj}$  by only 1.4%. There are at least two explanations for the relatively weak relationship between disturbance and liana species richness. First, although

wood density is correlated with disturbance, it is not a perfect proxy for disturbance. The relationship between species richness and disturbance indicated by the model may be stronger in reality. Second, the results may reflect the spatial bias of the dataset towards western Amazonia, which generally has high turnover rates and low wood density compared with stands in eastern Amazonia (Baker *et al.*, 2004b; Phillips *et al.*, 2004), where comparative liana data are lacking. We speculate that the inclusion of eastern Amazonian forests might make the effect of disturbance on liana species richness more pronounced. Furthermore, as disturbance also seems to affect liana stem density (van der Heijden & Phillips, 2008), disturbance may also indirectly affect liana species richness through its effect on liana density, which in turn is strongly related to liana richness (Fig. 3a).

As stand wood density is highly correlated with both turnover (i.e. disturbance) and productivity across Amazonia (Baker *et al.*, 2004b; Malhi *et al.*, 2004; Phillips *et al.*, 2004), a low stand wood density may not necessarily indicate high disturbance levels. However, high-productivity sites, at least in Amazonia, are almost always high-turnover sites. Although causal relationships are of course difficult to ascertain and may involve feedbacks, it is reasonable to infer that a high-turnover (high-disturbance) environment favours liana growth – because lianas tend to proliferate in high-light conditions (e.g. Putz, 1984; Schnitzer *et al.*, 2000) – and that thriving lianas in turn may accelerate turnover – because Amazon lianas are known to promote tree death (Phillips *et al.*, 2005).

### Soil

Soil fertility is significantly related to liana species richness in models in which only soil variables and liana density are accounted for (Table 1). However, as the relationship between soil fertility and liana species richness disappears when climate variables are also included, this is probably an artefact of the strong correlation of soil fertility with precipitation and is therefore more likely to indicate an effect of moisture rather than an effect of fertility itself on liana species richness (Fig. 3a). SEM also indicated that neither fertility nor any of the other soil gradients are directly related to the species richness of lianas  $\geq 2.5$  cm in diameter. The effect of soil fertility seems to be indirect via its effect on disturbance (as inferred from the wood density proxy) – forests growing on more fertile soils have a higher tree turnover and are more dynamic (Phillips *et al.*, 1994, 2004). The apparent lack of an association between liana diversity and soil properties has been previously noted on more local scales (Burnham, 2002; Ibarra-Manríquez & Martínez-Ramos, 2002; Macía *et al.*, 2007). However, although soil fertility might not have a general effect on liana species richness, there is some evidence that soil fertility affects liana species richness in extreme cases. For example, in plots located on white sand soils, which are very nutrient-poor, the observed liana species richness is about 25% lower than that predicted by the model. Moreover, as a result of the strong correlations between climate and soil, experi-

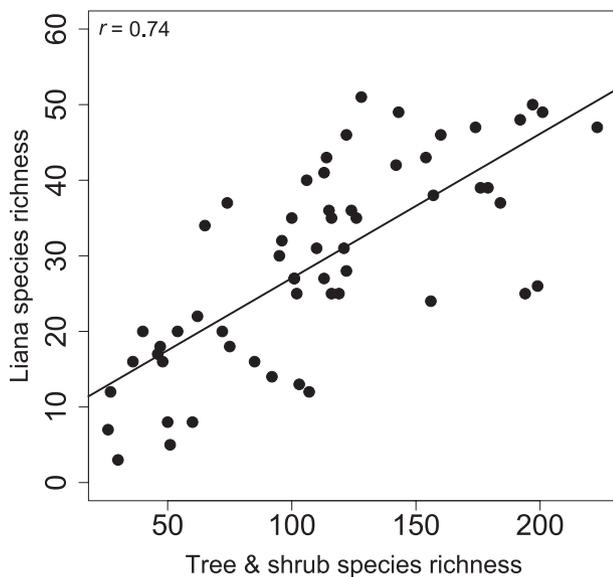
mental validation or more extensive sampling is necessary to assess in more detail whether the relationship between climate and species richness can be attributed to climate alone or whether some of the variance may be explained by soil properties.

### Other factors

The residual plots of our GLS models show that, in general, species richness was under-predicted for plots located in the Amazon basin and over-predicted for plots located in the forested area of Central America and those west of the Andes (Fig. 4). This pattern in the residuals may be explained by other factors than soil, climate or disturbance, such as an effect of area and/or regional history. The forested area within Central America and that west of the Andes are each considerably smaller than and are almost separated (although not completely 'species-tight') from the Amazon forests. Larger areas (i.e. Amazonia) should have more species, because of higher speciation and lower extinction rates (Rosenzweig, 1995). Furthermore, speciation rates in Amazonia may be higher owing to differences in regional histories between the areas (e.g. Latham & Ricklefs, 1993; Ricklefs *et al.*, 1999). As a consequence of differences in size and/or regional history, plots inventoried in the Amazon may harbour more species than plots in tropical forests outside this region, regardless of any effects of the environment: a phenomenon that has also been demonstrated for trees (Phillips *et al.*, 1994).

### Liana vs. tree-and-shrub species richness

Apart from the effect of stem density, MAP is the other best explanatory variable of species richness in trees and shrubs  $\geq 2.5$  cm in diameter (Table 1, Fig. 3b). Dry-season length, which has a direct effect on liana diversity, indirectly influences tree-and-shrub diversity via its effect on tree-and-shrub density. Liana and tree-and-shrub density in the Neotropics are therefore both driven by the availability of water. The similarity in their response to moisture supply may be the cause of the congruent diversity patterns of lianas and trees and shrubs (Fig. 5) – areas with a high number of tree and shrub species tend to have a high number of liana species. Macía *et al.* (2007) found similar diversity patterns of lianas and trees in Amazonian Bolivia. Outliers for this relationship between liana and tree diversity, however, are the so-called liana forests, which are relatively more diverse in lianas than in trees (Pérez-Salicrup *et al.*, 2001). The congruent pattern between liana and tree-and-shrub diversity may indicate that similar evolutionary and ecological processes underlie the diversity patterns of these plant life-forms. The dependence of both liana and tree-and-shrub species richness on water availability suggests that if parts, or all, of the Neotropics dry up to a significant degree this century, as predicted (e.g. Costa & Foley, 2000; Cox *et al.*, 2004; Li *et al.*, 2006), substantial declines in the species richness of woody plants at the stand level may be anticipated.



**Figure 5** Bivariate relationship between liana and tree-and-shrub species richness of 0.1 ha sites from Neotropical lowland forests ( $n = 58$ ).

#### ACKNOWLEDGEMENTS

We thank J. Lloyd and C. Quesada for useful discussions on tropical soils, and J. Lloyd, H. Keeling, M. Huston and J. Chave for comments on earlier versions of the manuscript. The University of Leeds provided financial support. O. L. Phillips was supported by a NERC grant and by a Leverhulme Trust Research Fellowship. This work was made possible by the drive and vision of the late Alwyn Gentry.

#### REFERENCES

APG (2002) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society*, **141**, 399–436.

Arbuckle, J. (2003) *Amos, 5.0*. Smallwaters, Chicago, IL.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Natalino, M., Silva, J. & Vásquez Martínez, R. (2004a) Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 353–365.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D., Patiño, S., Pitman, N., Silva, J.N.M. & Vásquez Martínez, R. (2004b) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.

Barry, R.G. (1992) *Mountain weather and climate*, 2nd edn. Routledge, London.

Belsey, D.A., Kuh, E. & Welsch, R.E. (1980) *Regression diagnostics: identifying influential data and sources of collinearity*. John Wiley and Sons, New York.

Bollen, K.A. & Stine, R.A. (1993) Bootstrapping goodness-of-fit measures in structural equation models. *Testing structural equation models* (ed. by K.A. Bollen and J.S. Long), pp. 111–135. SAGE Publications, Newbury Park, CA.

Browne, M.W. & Cudeck, R. (1989) Single sample cross-validation indices for covariance structures. *Multivariate Behavioral Research*, **24**, 445–455.

Burnham, R.J. (2002) Dominance, diversity and distribution of lianas in Yasuni, Ecuador: who is on top? *Journal of Tropical Ecology*, **18**, 845–864.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science, New York.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2,456 Neotropical tree species. *Ecological Applications*, **16**, 2356–2367.

Cliff, A.D. & Ord, J.K. (1981) *Spatial processes*. Pion, London.

Clinebell, R.R., Phillips, O.L., Gentry, A.H., Stark, N. & Zuuring, H. (1995) Predictions of Neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56–90.

Costa, M.H. & Foley, J.A. (2000) Combined effects of deforestation and doubled atmospheric CO<sub>2</sub> concentrations on the climate of Amazonia. *Journal of Climate*, **13**, 18–34.

Cox, P.M., Betts, R.A., Collins, M., Harris, P.P., Huntingford, C. & Jones, C.D. (2004) Amazonian forest dieback under climate-carbon cycle projections for the 21st century. *Theoretical and Applied Climatology*, **78**, 137–156.

Crawley, M.J. (1993) *GLIM for ecologists*. Blackwell Scientific Publications, Oxford.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

DeWalt, S.J., Ickes, K., Nilus, R., Harms, K.E. & Burslem, D.F.R.P. (2006) Liana habitat associations and community structure in a Bornean lowland tropical forest. *Plant Ecology*, **186**, 203–216.

Draper, N.R. & Smith, H. (1998) *Applied regression analysis*. Wiley, New York.

Ewers, F.W., Fisher, J.B. & Chiu, S.T. (1990) A survey of vessel diameter in stems of tropical lianas and other growth forms. *Oecologia*, **84**, 544–552.

Fan, X., Thompson, B. & Wang, L. (1999) Effects of sample size, estimation method, and model specification on structural equation modeling fit indexes. *Structural Equation Modeling*, **6**, 56–83.

Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1–84.

Gentry, A.H. (1988a) Changes in plant community diversity and floristic composition on environmental and

- geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.
- Gentry, A.H. (1988b) Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of the Sciences USA*, **85**, 156–159.
- Gentry, A.H. (1991) Distribution and evolution of climbing plants. *Biology of vines* (ed. by F.E. Putz and H.A. Mooney), pp. 3–49. Cambridge University Press, Cambridge.
- Gentry, A.H. (1992) Tropical forest biodiversity: distributional patterns and their conservational significance. *Oikos*, **63**, 19–28.
- Gentry, A.H. (1993) *A field guide to the families and genera of woody plants of northwest South America (Colombia, Ecuador, Peru)*. University of Chicago Press, Chicago, IL.
- Gentry, A.H. & Dodson, C. (1987) Contribution of nontrees to species richness of a tropical rain forest. *Biotropica*, **19**, 149–156.
- Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *The Journal of Ecology*, **87**, 193–210.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hegarty, E.E. & Caballé, G. (1991) Distribution and abundance of vines in forest communities. *Biology of vines* (ed. by F.E. Putz and H.A. Mooney), pp. 313–335. Cambridge University Press, Cambridge.
- van der Heijden, G.M.F. & Phillips, O.L. (2008) What controls liana success in Neotropical forests? *Global Ecology and Biogeography*, **17**, 372–383.
- Hu, L. & Bentler, P.M. (1995) Evaluating model fit. *Structural equation modeling: concepts, issues and applications* (ed. by R.H. Hoyle), pp. 76–99. Sage Publications, Thousand Oaks, CA.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.
- Huston, M. (1980) Soil nutrients and tree species richness in Cost Rican forests. *Journal of Biogeography*, **7**, 147–157.
- Huston, M. (1994) *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Ibarra-Manríquez, G. & Martínez-Ramos, M. (2002) Landscape variation of liana communities in a Neotropical rain forest. *Plant Ecology*, **160**, 91–112.
- Kerr, J.T., Kharaouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science*, **316**, 1581–1584.
- Kleidon, A. & Mooney, H.A. (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology*, **6**, 507–523.
- Latham, R.E. & Ricklefs, R.E. (1993) Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *Oikos*, **67**, 325–333.
- Laurance, W.F., Pérez-Salicrup, D., Delemônica, P., Fearnside, P.M., D'Angelo, S., Jerzolimski, A., Pohl, L. & Lovejoy, T.E. (2001) Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology*, **82**, 105–116.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn. Elsevier B.V., Amsterdam.
- Lewis, S.L., Malhi, Y. & Phillips, O.L. (2004) Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 437–462.
- Li, W., Fu, R. & Dickinson, R.E. (2006) Rainfall and its seasonality over the Amazon in the 21st century as assessed by the coupled models for the IPCC AR4. *Journal of Geophysical Research*, **111**, D02111.
- Londoño, C. & Jimenez, E. (1999) Efecto del tiempo entre los censos sobre la estimación de las tasas anuales de mortalidad y de reclutamiento de árboles. *Cronica Forestal y del Medio Ambiente No. 14*, **199**, 41–57.
- Lovejoy, T.E. & Hannah, L. (2005) *Climate change and biodiversity*. Yale University Press, New Haven, CT.
- Macía, M.J., Ruokolainen, K., Tuomisto, H., Quisbert, J. & Cala, V. (2007) Congruence between floristic patterns of trees and lianas in a southwest Amazonian rain forest. *Ecography*, **30**, 561–577.
- Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez-Buylla, E.R., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Mercado Montoya, L.M., Monteagudo, A., Neill, D., Núñez Vargas, P., Patino, S., Pitman, N., Quesada, C.A., Salomao, R., Macedo Silva, J.N., Torres Lezama, A., Vásquez Martínez, R., Terborgh, J., Vinceti, B. & Lloyd, J. (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global Change Biology*, **10**, 1–29.
- McCune, B. & Mefford, M.J. (1995) *PC-ORD: multivariate analysis of ecological data*. MjM Software, Gleneden Beach, OR.
- New, M., Lister, D., Hulme, M. & Makin, I. (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- O'Brien, E.M. (2006) Biological relativity to water–energy dynamics. *Journal of Biogeography*, **33**, 1868–1888.
- Parmentier, I., Malhi, Y., Senterre, B., Whittaker, R.J., A.T.D.N., Alonso, A., Balinga, M.P.B., Bakayoko, A., Bongers, F., Chatelain, C., Comiskey, J.A., Cortay, R., Djuikouo Kamdem, M.-N., Doucet, J.-L., Gautier, L., Hawthorne, W.D., Issembe, Y.A., Kouame, F.N., Kouka, L.A., Leal, M.E., Lejoly, J., Lewis, S.L., Nusbaumer, L., Parren, M.P.E., Peh, K.S.-H., Phillips, O.L., Sheill, D., Sonke, B., Sosef, M.S.M., Sunderland, T.C.H., Stropp, J., ter Steege, H., Swaine, M.D., Tchouto, M.G.P., van Gemberden, B.S., van Valkenburg, J.L.C.H. & Woll, H. (2007) The odd man out? Might climate explain the lower tree  $\alpha$ -diversity of African rain forests relative to Amazonian rain forests? *The Journal of Ecology*, **95**, 1058–1071.

- Pérez-Salicrup, D., Sork, V.L. & Putz, F.E. (2001) Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica*, **33**, 34–47.
- Phillips, O.L. & Miller, J.S. (2002) *Global patterns of plant diversity: Alwyn H. Gentry's forest transect dataset*. Missouri Botanical Garden Press, St Louis, MI.
- Phillips, O.L., Hall, P., Gentry, A.H., Sawyer, S.A. & Vásquez Martínez, R. (1994) Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of the Sciences USA*, **91**, 2805–2809.
- Phillips, O.L., Vásquez Martínez, R., Arroyo, L., Baker, T.R., Killeen, T., Lewis, S.L., Malhi, Y., Mendoza, A.M., Neill, D., Vargas, P.N., Alexiades, M., Cerón, C., Flora, A.D., Erwin, T., Jardim, A., Palacios, W., Saldias, M. & Vinceti, B. (2002) Increasing dominance of large lianas in Amazonian forests. *Nature*, **418**, 770–774.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W.F., Lewis, S.L., Lloyd, J., Terborgh, J., Vásquez Martínez, R., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J.A., Czimczik, C.I., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S.G., Nascimento, H.E.M., Olivier, J., Palacios, W., Patiño, S., Pitman, N., Quesada, C.A., Saldias, M., Torres Lezama, A. & Vinceti, B. (2004) Pattern and process in Amazon tree turnover, 1976–2001. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359**, 381–407.
- Phillips, O.L., Vásquez Martínez, R., Monteagudo Mendoza, A., Baker, T.R. & Núñez Vargas, P. (2005) Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology*, **86**, 1250–1258.
- 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. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology*, **65**, 1713–1724.
- R Development Core Team (2007) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ricklefs, R.E., Latham, R.E. & Qian, H. (1999) Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *Oikos*, **86**, 369–373.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Schnitzer, S.A. (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *The American Naturalist*, **166**, 262–276.
- Schnitzer, S.A. & Carson, W.P. (2000) Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology*, **82**, 58–64.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (2000) The impact of liana on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology*, **88**, 655–666.
- Shipley, B. (2000) *Cause and correlation in biology. A user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge.
- ter Steege, H., Sabatier, D., Castellanos, H., van Andel, T., Duivenvoorden, J., de Oliveira, A.A., Ek, R., Lilwah, R., Maas, P.J.M. & Mori, S. (2000) An analysis of the floristics composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology*, **16**, 801–828.
- ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., van der Hout, P., Daly, D.C., Silveira, M., Phillips, O.L., Vásquez Martínez, R., van Andel, T., Duivenvoorden, J., Adalardo de Oliveira, A., Ek, R.C., Lilwah, R., Thomas, R., van Essen, J., Baider, C., Maas, P.J.M., Mori, S.A., Terborgh, J., Núñez Vargas, P., Mogollon, H. & Morawetz, W. (2003) A spatial model of tree  $\alpha$ -diversity and tree density for the Amazon. *Biodiversity and Conservation*, **12**, 2255–2277.
- Storch, D., Evans, K.L. & Gaston, K.J. (2005) The species–area–energy relationship. *Ecology Letters*, **8**, 487–492.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- West, S.G., Finch, J.F. & Curran, P.J. (1995) Structural equation models with nonnormal variables. *Structural equation modelling. Concepts, issues and applications* (ed. by R.H. Hoyle), pp. 56–75. Sage Publications Inc., Thousand Oaks, CA.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 495–506.
- Wright, S.J. (1992) Seasonal drought, soil fertility and species density of tropical forest plant communities. *Trends in Ecology and Evolution*, **7**, 260–263.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Location, and liana and tree-and-shrub diversity and density for each of the 65 plots.

**Appendix S2** Climate, soil and disturbance variables for each of the 65 plots.

**Appendix S3** Initial path models for lianas and tree-and-shrub species richness used for structural equation modelling analyses.

**Appendix S4** Correlation matrix for all variables included in the structural equation models for the lowland sites only ( $n = 58$ ) and for both the lowland and montane sites ( $n = 65$ ).

**Appendix S5** Multiple regression and structural equation modelling results for the species richness of lianas and of trees and shrubs for all 65 plots.

**Appendix S6** Principal components analysis axes for soil variables for the full ( $n = 65$ ) and lowland ( $n = 58$ ) datasets.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

## BIOSKETCHES

**Geertje van der Heijden** has recently completed her PhD thesis in tropical ecology at the University of Leeds. She is working on understanding the factors controlling liana success in tropical forests on both Neotropical and local scales.

**Oliver Phillips** is Professor of Tropical Ecology at the University of Leeds. He is working on understanding the factors driving tropical forest composition, biomass, dynamics, and their change through time. He jointly coordinates the Amazon Forest Inventory Network (RAINFOR).

---

Editor: Bradford Hawkins