

# Infestation of trees by lianas in a tropical forest in Amazonian Peru

van der Heijden, Geertje M.F.<sup>1\*</sup>; Healey, John R.<sup>2,3</sup> & Phillips, Oliver L.<sup>1,4</sup>

<sup>1</sup>Earth and Biosphere Institute, School of Geography, University of Leeds, Leeds, LS2 9JT, UK;

<sup>2</sup>School of the Environment and Natural Resources, Bangor University, Bangor, LL57 2UW, UK;

<sup>3</sup>E-mail j.healey@bangor.ac.uk; <sup>4</sup>E-mail: o.phillips@leeds.ac.uk;

\*Corresponding author; E-mail g.m.f.vanderheijden04@leeds.ac.uk

## Abstract

**Question:** In Amazonian moist forest, four questions arose:

1. Do tree species differ in their susceptibility to lianas? 2. What host tree traits (branch-free bole height, growth rate, bark type, leaf length and adult stature) are correlated with the susceptibility of tree species to lianas infesting the trunk and the crown? 3. To what extent do spatial variables (proximity to liana-infested trees and the light environment of the tree crown) affect the likelihood of liana infestation? 4. Are spatial variables or tree traits relatively more important in influencing the susceptibility of trees to lianas? We address all questions separately for trunk and crown infestation.

**Location:** Tambopata Nature Reserve, Peru.

**Methods:** We collected information on liana infestation, tree morphological traits, growth, light-environment and position for 3675 trees in seven 1-ha permanent sample plots. We separated trunk from crown infestation and used correlation and logistic regression analyses for tree species and individual tree-level analyses, respectively.

**Results:** Half of all trees were colonised by at least one liana. Of 41 relatively common dicot tree species, at least five have significantly greater and three significantly lower crown infestation rates than expected by chance. Trunk and crown infestation are influenced by different host traits – trunk infestation was only affected by bark type, while crown infestation is reduced when trees are fast-growing, tall, have low-density wood, long branch-free boles and long leaves. The likelihood of both trunk and crown infestation increases for trees growing in close proximity to another liana-infested tree, but is invariant with the light environment of tree crowns.

**Conclusion:** Crown and trunk infestation have not been properly distinguished before; it is important to do so as the factors determining the different modes of infestation differ fundamentally. The association between crown infestation and tree traits suggests that increases in liana dominance in Amazonian forests could cause changes in forest composition, including favouring faster growing tree species with low density wood, potentially reducing the carbon stored by mature forests.

**Keywords:** Bark type; Branch-free bole height; Carbon; Crown illumination index (CII); Palm; Spatial pattern; Tree growth rate; Vine.

**Nomenclature:** We used current nomenclature at the time of analysis as provided at TROPICOS <http://www.tropicos.org/>

## Introduction

By suppressing tree growth and increasing mortality risks, lianas (woody climbers) are potentially detrimental to the trees that support them (Clark & Clark 1990; Phillips et al. 2005). Trees that remain free of lianas may therefore have a competitive advantage (Putz 1984a; Hegarty 1991). Several studies have indicated that some tree species are less affected by lianas than others (e.g. Putz 1984a, b; Campbell & Newbery 1993; Schnitzer et al. 2000; Alvira et al. 2004). These taxa may have certain traits that prevent lianas from infesting them (Putz 1984a; Hegarty 1991), notably, the possession of fast diameter growth rates, flexible stems, long leaves, long branch-free boles, and smooth bark (Putz 1980, 1984a; Balfour & Bond 1993; Campbell & Newbery 1993; Carsten et al. 2002). In addition, other tree features may be important. For example, Clark & Clark (1990) suggested that adult stature might be important, but did not investigate this in detail.

Lianas can infest a host tree by climbing the trunk, by growing up together with the tree or by laterally growing into the tree crown from a neighbouring tree (Putz 1984a; Campbell & Newbery 1993). Lianas infesting the trunk may proceed to grow on into the crown of the same host tree, so repelling or avoiding lianas infesting the trunk may therefore also protect against crown infestation. However different tree traits may limit these routes of infestation; consequently, some may be more strongly associated with lianas growing into the crown and others more associated with lianas climbing the trunk. Most previous studies, however, examined the association between lianas and tree traits without specifically taking the site of infestation (i.e. trunk or crown) into account (Putz 1984a; Campbell & Newbery 1993; Carsten et al. 2002).

Several studies have failed to find any associations between lianas and tree traits, suggesting that, instead, spatial factors may influence the susceptibility of trees to lianas (Carse et al. 2000; Pérez-Salicrup et al. 2001; Malizia & Grau 2006). For example, as most lianas seem

to proliferate in high light conditions, well-lit crowns may consequently be at higher risk of liana infestation (Malizia & Grau 2006). Also, trees growing in close proximity to others already supporting lianas may be more prone to liana infestation as lianas often grow from one tree to another (Putz 1984b). Liana infestation may also be especially prevalent in small patches with a high abundance of regenerating lianas, such as in canopy gaps (Putz 1984b; Carse et al. 2000; Malizia & Grau 2006).

Recent work suggests that lianas are increasing in dominance in mature Neotropical forests (e.g. Phillips et al. 2002; Wright et al. 2004). This could be driven by the increasing concentration of atmospheric CO<sub>2</sub>, which disproportionately benefits liana growth (e.g. Granados & Körner 2002), by increased tree turnover (Phillips & Gentry 1994; Phillips et al. 2004), the recent warming of the tropics (Malhi & Wright 2004) or even by increases in hunting intensity, which could benefit lianas at the expense of trees (Wright et al. 2007). Whatever the driver(s), increasing dominance of lianas could in turn impact on the carbon balance of tropical forests, whether directly by decreasing tree growth rate and increasing tree mortality (Putz 1984b; Clark & Clark 1990; Phillips et al. 2002, 2005), or indirectly by favouring more liana-resistant tree species, especially if these include fast-growing taxa with low-density wood that store less carbon per unit basal area.

To help predict how the increased dominance of lianas might influence tropical forest biodiversity and carbon balance, better understanding of factors which facilitate or inhibit liana incidence and which tree species are affected is required. Although Amazonia represents a globally significant store of carbon and biodiversity, little research has focussed on factors affecting liana infestation. Here we report findings from an intensely-studied forest site in Amazonian Peru. We ask (1) whether tree species differ in their susceptibility to lianas; (2) whether host tree traits (branch-free bole height, growth rate, bark type, leaf length and adult stature) are correlated with the susceptibility of tree species to lianas infesting the trunk and the crown; (3) to what extent spatial variables (proximity to liana-infested trees and the light environment of the tree crown) affect the likelihood of liana infestation, and (4) whether spatial variables or tree traits are relatively more important in influencing the susceptibility of trees to lianas. We address all questions separately for trunk and crown infestation. A tree species-level analysis is performed to address the first two questions. As a tree's spatial environment depends on the interaction with surrounding trees and is therefore unique for each tree, an individual tree-level approach is adopted to address questions 3 and 4.

## Methods

### *Study site*

This study was conducted in seven 1-ha (100 m × 100 m) permanent sample plots of the RAINFOR project (Red Amazónica de Inventarios Forestales; Amazon Forest Inventory Network; Malhi et al. 2002), spread across the Tambopata Nature Reserve, Madre de Dios, Peru, in southwestern Amazonia (12°48' S, 69°43' W). The plots receive a mean annual rainfall of 2248 mm, with three months averaging below 100 mm, and are located mainly on clay and sandy-clay ultisols and inceptisols, at approximately 260 m a.s.l. (Phillips et al. 2002). One plot contains a permanent swamp area which is seasonally flooded to a depth of up to 2 m. Most of the plots were established in 1983, and have 140–180 species of tree ≥ 10 cm diameter (Gentry 1988). Complete tree censuses have been carried out every three to five years, with the most recent measurements between November 2005 and April 2006 (for details on tree census methodology see e.g. Baker et al. 2004a).

### *Data collection*

The liana census took place between September 2005 and January 2006, approximately three months before the latest full tree census. For each tree ≥ 10 cm diameter at breast height (DBH) growing within the seven plots, we recorded the presence or absence of lianas ≥ 1.30 m tall. Hemi-epiphytes, rattans and climbing Poaceae, Araceae and Cyclanthaceae were excluded (cf. Gerwing et al. 2006). We did not separate woody from non-woody climbers, because of the difficulties in distinguishing juvenile lianas from herbaceous climbers. Trees were considered to be 'trunk-infested' when lianas surrounded the trunk or were attached to the trunk by adventitious roots or tendrils and 'crown-infested' when lianas were attached to or present above the first branch of the tree.

For each tree, we also assembled information on selected traits. Leaf length was determined by measuring the length of a freshly fallen leaf (cf. Putz 1984a). Branch-free bole height (i.e. the height to the first branch) was estimated by the same person (G. van der Heijden). The visual estimates were validated by measuring the height to the first branch of 100 randomly-selected trees using a clinometer. As the slope of the regression line between the estimated and measured branch-free bole height did not differ from 1 (95% confidence interval of slope: 0.961 - 1.051 with intercept = 0), the visual estimates are used without any corrections in subsequent analyses. Bark texture was classified using four categories (cf. Campbell & Newbery 1993): (1) smooth, (2) slightly rough – the

surface being any combination of small dimples, scales or shallow fissures, (3) rough – the surface being large scales or fissures, and (4) trees with spines. If the bark had a tendency to flake, we recorded this separately. The amount of solar radiation received by the tree crown was estimated using the Crown Illumination Index (CII) (Clark & Clark 1992), recorded independently by two observers. The CII consists of an ordinal scale of 1 to 5, with high CII values indicating high light levels. The two observers' estimates of the CII were highly correlated and did not differ significantly (Kendall's index of concordance = 0.91,  $P < 0.001$ ). For subsequent analyses, where they differed we used the lower CII estimate to be more conservative. Trait data for tree species with  $\geq 15$  individuals are reported in App. 1.

For five of the seven plots, we collected new data (or supplemented existing data) on tree coordinates for all trees  $\geq 10$  cm dbh growing within the plot and within a 10 m buffer zone surrounding the plot. For these trees, we also assembled data on liana infestation following the method described above.

Species-specific wood density values were obtained from Chave et al. (2006). When unavailable, genus- or family-level mean values were used, following convention (e.g. Baker et al. 2004b). For the 13 individual trees (0.59%) with no family-level wood density data, we applied the overall species mean for Tambopata of  $0.64 \text{ g.cm}^{-3}$ . Tree species' maximum height (i.e. adult stature) data were extracted from the RAINFOR Functional Traits database (Peacock et al. 2007). Maximum height was not known for all species and can vary substantially between closely related species. Using genus or family averages is therefore inappropriate. Tree species-level analyses on maximum height were only carried out using species for which we had these data available, and maximum height was excluded as a variable from all individual tree-level analyses.

### Statistical analyses

Liana infestation rates per species and per plot were calculated for three categories: (1) all infested trees (regardless of infestation site); (2) trees with lianas infesting the trunk (regardless of crown infestation); and (3) trees with lianas infesting the crown (regardless of trunk infestation). We also calculated tree species' liana infestation rates for three different tree diameter size-classes (10-19.9 cm, 20-39.9 cm,  $\geq 40$  cm), because larger trees may be at higher risk of liana infestation (Pérez-Salicrú et al. 2001).

We performed  $\chi^2$ -tests to determine whether each tree species had a significantly higher or lower infestation rate than expected based upon overall infestation rates for all plots combined (for palms and for dicot trees separately, as appropriate). To ensure that test assump-

tions were not violated, we only included tree species with  $\geq 15$  monitored individuals. No tree species had  $\geq 15$  individuals in the  $\geq 40$  cm size-class.

Simple correlations were used to explore the association between dicot tree species' rates of liana infestation in each of its three categories and their measured traits. For each tree species with  $\geq 15$  individuals, mean branch-free bole height and leaf length were calculated for all sizes combined and separately by size-class to account for possible ontogenetic changes. Since lianas are known to reduce tree growth rate (e.g. Clark & Clark 1990), using species-specific growth rate averages based on trees both with and without lianas may confound results. We therefore used maximum potential growth rate ( $\text{mm.a}^{-1}$ ) – the mean of five liana-free individuals with the highest growth rates (cf. Clark & Clark 1999) for the period 2003-2006 – as our measure of species-specific growth rate. Data from trees across the size classes were combined when insufficient liana-free individuals were available per size-class. Liana infestation rates were arcsin-square root transformed and leaf length was transformed using the natural log to meet the normality assumption.

Mann-Whitney  $U$ -tests were employed to test if liana infestation rates differ between rough- and smooth-barked dicot tree species. Bark type averages for each tree species were divided into two groups: those  $< 1.5$  were classified as smooth-barked, those  $\geq 1.5$  as rough-barked. Insufficient species were classified as having a rough bark in the 20-39.9 cm size-class.

An individual tree-level analysis was carried out to test the extent to which spatial variables affect the likelihood of liana infestation and their relative importance compared with measured tree traits. We used binary logistic regression to examine which variables influence the likelihood that an individual tree will be infested with lianas. The logistic model can be written as:

$$P(i) = \frac{1}{1 + \exp[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_n X_n)]} \quad (1)$$

where  $P(i)$  is bound between 0 and 1 and represents the predicted probability that a tree is infested by lianas,  $\beta_0$  is the constant,  $\beta_n$  represent the model coefficients estimated from the data, and  $X_n$  represent the independent predictor variables. All models included tree stem diameter and plot code to control for tree size and possible plot effects, and CII and distance to nearest infested neighbour as spatial variables. Only traits specifically related to trunk or crown infestation were included in the site-specific models. For this analysis, we used all individual trees (thus not only those species used in the tree species-level analysis) for which coordinates were available (five plots), and excluded trees for which data on any of the variables were missing.

We calculated distance to the nearest liana-infested neighbour, including infested trees in the plot buffer zones, for these five plots. For crown infestation and liana infestation regardless-of-site, we used all infested neighbour trees because lianas climbing the trunk or infesting the crown of a neighbouring tree can potentially enter the crown of the target tree. For trunk infestation, however, we only calculated the distance to the nearest trunk-infested neighbour, because lianas in the crown rarely proceed to infest the trunk of another tree (G. van der Heijden pers. obs.).

Bark type, bark flakiness, CII and plot number were included in the model as categorical variables. To meet the linearity assumption of logistic regression, stem diameter and the distance-to-infested-neighbour measures were natural log-transformed (Hosmer & Lemeshow 2000). We examined model goodness-of-fit using the Hosmer-Lemeshow test (Hosmer & Lemeshow 1980) and by assessing the squared standardized residuals, which should be normally distributed with 95% of the values between  $-2$  and  $+2$  (Menard 2006).

Individual tree diameter growth rates cannot be included in the models, because it is difficult to disentangle whether lianas are more likely to infest slow-growing trees or whether trees grow slower due to liana infestation. However, in general, faster-growing tree species have low-density wood, suggesting that wood density may be an indicator of species-specific growth rate (e.g. Muller-Landau 2004) and wood density is a heritable variable that is generally conservative within species (Chave et al. 2006). We analysed all records for which both wood density and maximum potential growth rate data were available ( $n = 1137$ ) to test this suggestion. In models including both variables, growth rate was significantly associated with crown infestation rate ( $P < 0.001$ ), but wood density was not ( $P = 0.212$ ). However, wood density was a significant predictor ( $P = 0.036$ ) in models where growth rate was excluded, indicating that it captures variation otherwise explained by maximum potential growth rate. We therefore used wood density as a proxy for species-specific growth rate.

We used the information-theoretic approach described by Burnham & Anderson (2002) to identify for each of the three liana infestation categories which model best supports the data, from amongst the possible candidate models: 15 for trunk-, 31 for crown- and 127 for liana infestation regardless of site. Models were ranked based on their Akaike Information Criterion (AIC) values. We used Akaike weights ( $\omega_i$ ), the probability that model  $i$  is the best model for the observed data given the candidate set of models, to assess which model(s) were most likely to be best, and selection probabilities for each variable ( $\omega_{i+}(j)$ ), the sum of  $\omega_i$  of all models containing that variable, to assess the importance of the variables.

For both the tree species- and individual tree-level analyses, we omitted all trees growing in permanently water-logged conditions and all palms. Gentry (1991) noted that liana densities are generally lower in more extreme environments (8.1% in swamp vs 53.2% in dry part of the same plot;  $\chi^2 = 151.71$ ,  $P \leq 0.001$ ); including this unusual habitat would therefore confound our results. Palms were excluded because they differ morphologically and ontologically from dicot tree species by having extremely long leaves, long unbranched boles, and lacking diameter growth after the initial establishment period (Tomlinson 1979).

Statistical analyses were carried out with SPSS 14.0 (SPSS-Inc. 2005). R 2.4.0 (Anon. 2006) with the 'Spatstat' package (Baddeley & Turner 2005) was used to calculate the distance to nearest infested neighbour.

## Results

### *Plot level liana infestation*

In total 3675 trees  $\geq 10$  cm DBH (700 palms and 2975 trees) were censused within the seven 1-ha plots (excluding 0.4 ha of swamp), representing ca. 800 different tree species (including 11 palms). Of these trees, half (49.8%) carry lianas, 21.0% have lianas infesting the trunk, and 43.6% bear lianas in the crown (Table 1). When palms are excluded, plot-level infestation rates are very similar ( $57 \pm 5\%$ ; App. 2).

### *Palms versus dicot trees*

Liana infestation rates for palms are lower than for trees in all liana infestation categories (trunk-infested:  $P \leq 0.001$ ; crown-infested:  $P \leq 0.001$ ; regardless-of-site:  $P \leq 0.001$ ). Palms bear lianas on the trunk more often than in the crown, whereas dicot trees have greater crown than trunk infestation rates. Liana infestation rate of dicot trees, but not of palms, increases with increasing host-diameter up to the  $\geq 40$  cm class (trees:  $\chi^2 = 33.12$ ,  $P < 0.001$ ; palms:  $\chi^2 = 0.58$ ,  $P = 0.44$ ). Similar patterns are found when only trees with lianas infesting the crown are considered ( $\chi^2 = 43.21$ ,  $P < 0.001$ ); however, trunk infestation of trees is independent of host size ( $\chi^2 = 2.07$ ,  $P = 0.35$ ; Table 1).

### *Liana infestation of tree species*

Of the six palm species with  $\geq 15$  individuals, *Oenocarpus bataua* supports more lianas in the crown and *Socratea exorrhiza* more on the trunk compared to the overall palm infestation rate (Table 2, App. 1). Of the 41 dicot tree species with  $\geq 15$  individuals, three (*Symphonia globulifera*, *Tachigali polyphylla*, and *Pourouma*

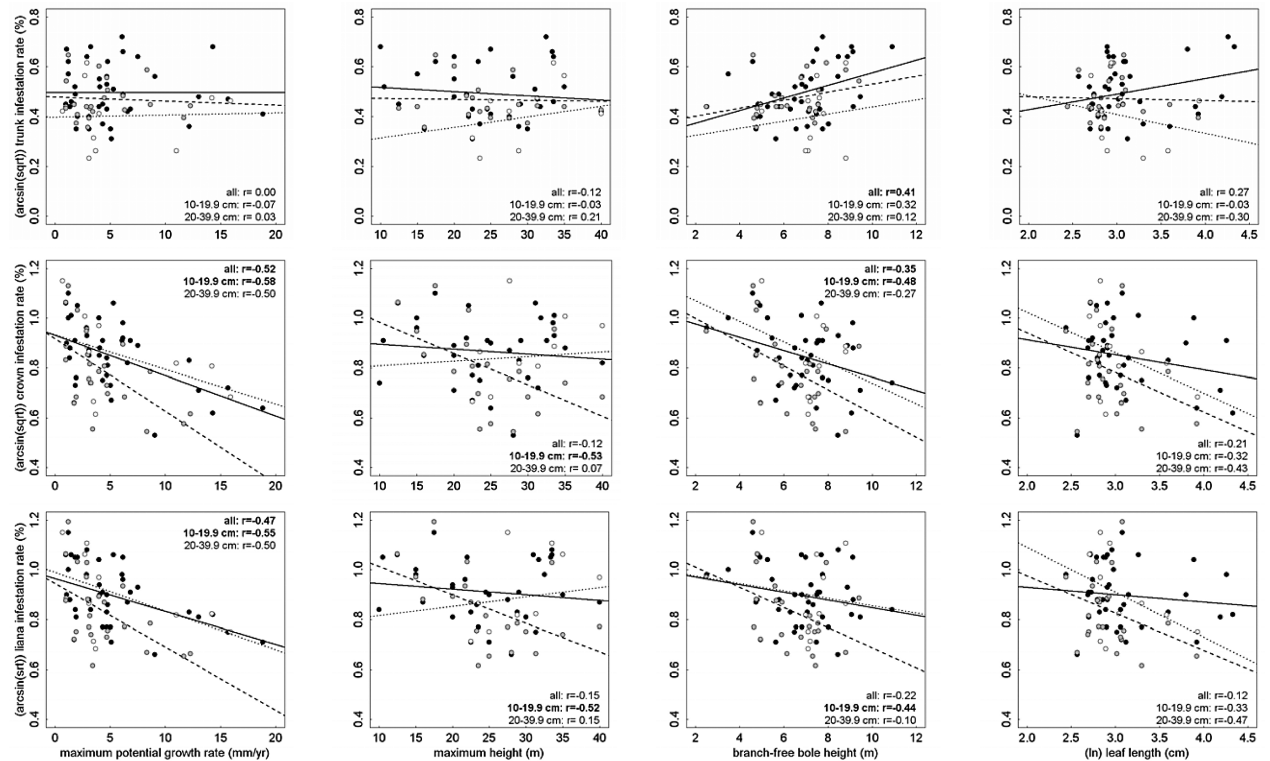
**Table 1.** Liana infestation rates for all plots combined (excluding the seasonally flooded swamp) calculated for all infested trees, and separately for trees with lianas growing on the trunk and for trees with lianas infesting the crown, and by diameter size-class (10-19.9 cm, 20-39.9 cm,  $\geq 40$  cm).

	No. of trees	All % trunk infested	All % crown infested	All % infested	No. of dicots infested	Dicots % trunk infested	Dicots % crown infested	Dicots % infested	No. of palms infested	Palm % trunk infested	Palm % crown infested	Palm % infested	
All plots	All sizes	3675	21.0	43.6	49.8	2975	22.6	52.6	57.7	700	14.0	5.1	16.4
	10-19.9	2233	22.0	42.0	48.9	1896	23.0	48.6	54.4	337	16.3	4.5	17.5
	20-39.9	1211	18.3	41.7	47.2	848	21.1	57.1	60.9	363	11.8	5.8	15.4
	$\geq 40$	231	25.1	68.8	72.7	231	25.1	68.8	72.7	0	0.0	0.0	0.0

*minor*) are less likely and five (*Lindackeria paludosa*, *Amaioua corymbosa*, *Oxandra riedeliana*, *Micropholis guyanensis* and *Iryanthera juruensis*) more likely to have lianas infesting the crown than expected from overall tree crown infestation rates. Only *Siparuna decipiens* supports fewer and *Guarea gomma* more lianas on the trunk than expected (Table 2, App. 1). Although only eight out of 41 dicot species differed significantly ( $P \leq 0.05$ ) in crown infestation rate, the crown infestation rate of these species ranged from 25 to 79% (Table 2). Due to the very high species diversity and relatively low sample size for many species, there is considerable potential for Type II error – we may be unable to reject the null hypothesis of

no difference in some cases even when a difference exists. This is potentially an important effect: simulations of effect size versus sample size suggest that if sample size were increased to 100 individuals for all species and the same infestation rates reported, we would expect to find 18 of the 41 dicot species to be either under- or over-infested relative to the overall crown infestation rate (App. 4).

For these 41 most frequent dicot tree species, trunk infestation is invariant with most tree traits, except for a positive association with branch-free bole height (Fig. 1). Rough-barked trees generally support lianas on the trunk more often than smooth-barked trees, although the difference is not significant for trees 10-19.9 cm dbh (all sizes



**Fig. 1.** Bivariate relations between the liana infestation rate for trunk and crown infestation separately, and for infestation regardless-of-site, and the continuous tree traits of tree species with  $\geq 15$  individuals. All trees ( $n = 41$ ), trees with 10-19.9 cm DBH ( $n = 24$ ) and 20-39.9 cm DBH ( $n = 10$ ) are indicated by, respectively, black, grey and white circles, with continuous, dashes and dotted lines of best fit. Significant correlations ( $P \leq 0.05$ ) are indicated in bold.

**Table 2.** Liana infestation rate (%) regardless-of-site of infestation, trunk infested and crown infested, for tree species with  $\geq 15$  individuals in all size-classes, sorted by crown infestation rate. Differences from the overall infestation rate for palms or dicot trees, as appropriate, are indicated in bold ( $P \leq 0.05$ ) and italic ( $0.1 > P > 0.05$ ).

		No. of trees	% infested	% trunk infested	% crown infested
<b>Palms</b>					
Arecaceae	<i>Oenocarpus mapora</i>	16	0.0	0.0	0.0
Arecaceae	<i>Euterpe precatoria</i>	89	12.4	12.4	3.4
Arecaceae	<i>Iriartea deltoidea</i>	440	13.0	10.9	3.4
Arecaceae	<i>Astrocaryum gratum</i>	20	15.0	15.0	5.0
Arecaceae	<i>Socratea exorrhiza</i>	98	<b>34.7</b>	<b>31.6</b>	9.2
Arecaceae	<i>Oenocarpus bataua</i>	28	17.9	3.6	<b>14.3</b>
<b>Dicots</b>					
Clusiaceae	<i>Symphonia globulifera</i>	35	<b>37.1</b>	28.6	<b>25.7</b>
Fabaceae	<i>Sclerolobium bracteosum</i>	15	53.3	40.0	33.0
Fabaceae	<i>Tachigali polyphylla</i>	45	<b>42.2</b>	15.6	<b>35.6</b>
Malvaceae	<i>Matisia ochrocalyx</i>	16	43.8	18.8	37.5
Linaceae	<i>Hebepetalum humiriifolia</i>	21	42.9	9.5	38.1
Urticaceae	<i>Pourouma cecropiifolia</i>	19	52.6	21.1	42.1
Urticaceae	<i>Pourouma minor</i>	160	<b>46.3</b>	20.6	<b>43.1</b>
Moraceae	<i>Brosimum lactescens</i>	25	48.0	12.0	44.0
Moraceae	<i>Helicostylus tomentosa</i>	18	55.6	22.2	44.4
Euphorbiaceae	<i>Mabea nitida</i>	20	55.0	40.0	45.0
Moraceae	<i>Pseudolmedia macrophylla</i>	39	48.7	12.8	46.2
Apocynaceae	<i>Aspidosperma tambopatense</i>	17	52.9	11.8	47.1
Sabiaceae	<i>Meliosma herbertii</i>	27	48.1	25.9	48.1
Myristicaceae	<i>Iryanthera laevis</i>	70	54.3	17.1	48.6
Myristicaceae	<i>Virola sebifera</i>	23	57.1	33.3	52.4
Moraceae	<i>Pseudolmedia laevis</i>	65	58.5	16.9	53.8
Urticaceae	<i>Pourouma guianensis</i>	33	54.5	12.1	54.5
Bixaceae	<i>Bixa arborea</i>	18	61.1	27.8	55.6
Ochnaceae	<i>Ouratea</i> sp.	27	57.1	18.5	55.6
Monimiaceae	<i>Siparuna decipiens</i>	75	58.7	<b>12.0</b>	56.0
Linaceae	<i>Roucheria punctata</i>	37	64.9	27.0	56.8
Violaceae	<i>Leonia glycyarpa</i>	98	59.2	15.3	58.2
Moraceae	<i>Pseudolmedia laevigata</i>	44	61.4	25.0	59.1
Euphorbiaceae	<i>Drypetes gentryi</i>	22	59.1	18.2	59.1
Lauraceae	<i>Ocotea bofo</i>	25	64.0	36.0	60.0
Euphorbiaceae	<i>Hevea guianensis</i>	18	61.1	38.9	61.1
Chrysobalanaceae	<i>Licania heteromorpha</i>	29	62.1	17.2	62.1
Clusiaceae	<i>Calophyllum brasiliense</i>	16	62.5	18.8	62.5
Meliaceae	<i>Guarea gomma</i>	16	68.8	<b>43.8</b>	62.5
Olacaceae	<i>Heisteria acuminata</i>	16	75.0	25.0	62.5
Myristicaceae	<i>Iryanthera juruensis</i>	113	<b>67.3</b>	22.1	<b>63.7</b>
Lecythidaceae	<i>Eschweilera coriacea</i>	31	<b>77.4</b>	35.5	64.5
Violaceae	<i>Rinorea viridifolia</i>	45	68.9	17.8	66.7
Salicaceae	<i>Laetia procera</i>	16	75.0	37.5	68.8
Burseraceae	<i>Tetragastris altissima</i>	27	74.1	18.5	70.4
Euphorbiaceae	<i>Sagotia racemosa</i>	24	70.8	29.2	70.8
Sapotaceae	<i>Pouteria torta</i>	25	76.0	20.0	72.0
Rubiaceae	<i>Amaioua corymbosa</i>	21	76.2	19.0	<b>76.2</b>
Annonaceae	<i>Oxandra riedeliana</i>	20	75.0	15.0	<b>75.0</b>
Sapotaceae	<i>Micropholis guyanensis</i>	17	<b>76.5</b>	23.5	<b>76.5</b>
Salicaceae	<i>Lindackeria paludosa</i>	24	<b>83.3</b>	33.3	<b>79.2</b>

$P = 0.038$ ; 10-19.9 cm,  $P = 0.340$ ). Crown infestation, on the other hand, is significantly negatively associated in the 10-19.9 cm class (but not in the 20-39.9 cm class) with branch-free bole height, maximum potential growth rate and maximum height, but not with leaf length (Fig. 1). Results for liana infestation regardless-of-site are generally comparable to crown infestation for the continuous traits (Fig. 1) and to those for trunk infestation for bark type (all sizes  $P = 0.019$ ; 10-19.9 cm  $P = 0.325$ ). These results are not driven by the disproportional effect of any one plot (App. 3).

#### Liana infestation of individual trees

There is considerable model uncertainty for trunk infestation, reflected by the low Akaike weights ( $\omega_i \leq 0.40$ ) for the five models within the 90% confidence set of models (i.e. cumulative  $\omega \geq 90$ ; Table 3a). However, the high selection probabilities of distance-to-infested neighbour and bark type ( $\geq 0.90$ ) compared with those of bark flakiness and wood density ( $< 0.40$ ) suggests that the former two variables are important for predicting the likelihood of trunk infestation, with smooth-barked

trees having a lower and trees growing in proximity of another trunk-infested tree having a higher liana infestation risk.

For crown infestation, the model with the lowest AIC has considerable support from the Akaike weight ( $\omega_i=0.84$ ), indicating that this model is likely to be best given the candidate set of models (Table 3b). The model with the lowest AIC shows that trees with long branch-free boles, long leaves, and low wood density are less likely and trees growing in close proximity to an infested tree are more likely to have lianas in the crown. With a selection probability of 0.06 compared with  $\geq 0.94$  for the other variables, there is no support for CII as a predictor of crown infestation.

For liana infestation regardless-of-site, the ten models within the 90% confidence set all have low Akaike weights ( $\omega \leq 0.21$ ), therefore no model can be considered the best (Table 3c). The selection probabilities for the variables indicate that distance to the nearest liana-infested neighbour, branch-free bole height and wood density were important predictor variables of overall liana infestation ( $\omega_i=1.00$ ), while there was comparatively less support for bark type, leaf length and bark flakiness ( $0.39 \leq \omega_i \leq 0.66$ ), and hardly any support for CII ( $\omega_i = 0.16$ ).

**Table 3.** Model selection results for liana infestation of tree (a) trunk, (b) crown, and (c) regardless-of-site. Only dicot trees are considered. For each model, we indicate the variables included: the number of estimated parameters (K), the Akaike Information Criterion (AIC), the differential AIC ( $\Delta_i$ ), the Akaike weight ( $\omega_i$ ), the cumulative  $\omega_i$ , and Hosmer-Lemeshow statistics with associated *P*-value. Only models within the 90% confidence set of models (i.e. cumulative  $\omega_i \geq 0.90$ ) are shown. The importance of each variable in the model is indicated by the selection probability ( $\omega_+(j)$ ).  $d_{trunk}$  is the distance to the nearest trunk-infested neighbour and  $d_{all}$  the distance to the nearest liana infested neighbour. + indicates a positive relationship, - indicates a negative relationship, and n.t. indicates no general trend. Total sample size is 2218. For more information see methods. Note that all models additionally include stem diameter and plot code to control for tree size and possible plot effects.

<b>(a) Trunk infestation</b>														
Model	Wood density (g.cm <sup>-3</sup> )	Bark type	Bark flakiness	$d_{trunk}$ (m)	K	AIC	$\Delta_i$	$\omega_i$	cum. $\omega$	Hosmer-Lemeshow statistic	<i>P</i>			
1		+		-	9	2386.602	0.000	0.40	0.40	14.277	0.075			
2		+	-	-	10	2387.494	0.892	0.26	0.66	13.080	0.109			
3		+		-	10	2388.597	1.995	0.15	0.80	15.748	0.046			
4		+	-	-	11	2389.494	2.892	0.09	0.90	13.080	0.109			
$\omega_+(j)$	0.27	0.90	0.40	1.00										
<b>(b) Crown infestation</b>														
Model	Branch-free bole height (m)	Leaf length (cm)	Wood density (g.cm <sup>-3</sup> )	CII	$d_{all}$ (m)	K	AIC	$\Delta_i$	$\omega_i$	cum. $\omega$	Hosmer-Lemeshow statistic	<i>P</i>		
1	-	-	+		-	10	2960.427	0.000	0.84	0.84	4.292	0.830		
2	-	-	+	n.t.	-	16	2965.871	5.444	0.06	0.90	4.631	0.796		
3	-	-			-	9	2966.006	5.579	0.05	0.95	3.473	0.901		
$\omega_+(j)$	1.00	0.96	0.95	0.06	1.00									
<b>(c) Infestation regardless of site</b>														
Model	Branch-free bole height (m)	Leaf length (cm)	Wood density (g.cm <sup>-3</sup> )	Bark type	Bark flakiness	CII	$d_{all}$ (m)	K	AIC	$\Delta_i$	$\omega_i$	cum. $\omega$	Hosmer-Lemeshow statistic	<i>P</i>
1	-		+	+			-	11	2933.721	0.000	0.21	0.21	1.707	0.989
2	-		+	+	+		-	12	2934.435	0.714	0.15	0.35	1.267	0.996
3	-	-	+	+			-	9	2934.845	1.124	0.12	0.47	6.010	0.646
4	-		+				-	12	2934.886	1.165	0.12	0.59	3.829	0.872
5	-	-	+	+	+		-	13	2935.668	1.947	0.08	0.67	3.099	0.928
6	-	-	+				-	10	2935.866	2.145	0.07	0.74	5.516	0.000
7	-		+		+		-	10	2936.070	2.349	0.06	0.80	3.401	0.907
8	-		+	+		n.t.	-	17	2936.956	3.235	0.04	0.84	11.073	0.198
9	-	-	+		+		-	11	2937.142	3.421	0.04	0.88	3.874	0.868
10	-		+	+	+	n.t.	-	18	2937.708	3.987	0.03	0.91	3.520	0.898
$\omega_+(j)$	1.00	0.36	1.00	0.66	0.39	0.15	1.00							

## Discussion

In Tambopata half of trees  $\geq 10$  cm DBH and 58% of non-palms  $\geq 10$  cm DBH host one or more lianas. Comparison with other studies in tropical rainforests is marginally complicated by methodological differences in the tree and liana diameters considered (trees  $\geq 10$  cm DBH infested by lianas  $> 1.3$  m in height in this study). Nonetheless, our results parallel the infestation rates reported in some other neotropical studies (Putz 1983; 1984a), but are lower than those found in 'liana forests' (Pérez-Salicrup et al. 2001).

In general, our results are consistent with previous studies showing that tree species with the least liana infestation tend to be fast-growing, have flexible trunks, low-density wood, long branch-free boles, long leaves and a smooth bark (Putz 1980, 1984a; Balfour & Bond 1993; Campbell & Newbery 1993). Studies failing to find evidence for liana-tree associations (Carse et al. 2000; Pérez-Salicrup et al. 2001; Malizia & Grau 2006) were mostly carried out in areas with recent or nearby disturbance, which may have led to near saturation of the host community (infestation rates of 77, 83 and 65% respectively). As pointed out by Pérez-Salicrup et al. (2001), insight into liana-tree interactions is most likely to be gained from sites with lower liana incidence.

This is the first study to quantitatively assess the relationship between adult stature and liana infestation rate. Adult stature was indeed negatively correlated with crown infestation rate, but only in the 10–19.9 cm size-class (Fig. 1). Understory species, which probably are only represented in the smaller size-classes, may be more prone to liana infestation since lianas generally climb on successively taller trees to reach the canopy (Putz 1995). This result also emphasizes the importance of separately assessing the association between liana infestation and tree traits for different size-classes.

Previous research has suggested that as most lianas infest a tree trunk by surrounding it, but are generally restricted by a maximum host diameter that they can encircle (Putz 1984b; Putz & Chai 1987; DeWalt et al. 2000; Nabe-Nielsen 2001), so trees may prevent trunk infestation by reaching this maximum diameter quickly (Putz 1980, 1984a). However, these studies did not separate infestation of the trunk from that of the crown. For our Amazonian site, when these routes of infestation were separated, maximum potential growth rate actually had no effect on trunk infestation, but showed instead a strong negative association with crown infestation (Table 3a, b; Fig. 1). However, surprisingly, even though rapid stem thickening did not influence the likelihood of trunk infestation, the proportion of trunk-infested trees did not differ among the diameter size-classes either (Table 1, 2). This indicates that a tree is unlikely to get infested with trunk-borne lianas if it avoids trunk infestation at the vulnerable juvenile stage.

An explanation for the strong relationship between growth rate and crown infestation, on the other hand, may

be that, as faster growing tree species tend to have longer leaves ( $r > 0.45$ ) and branch-free boles ( $r > 0.30$ ), it may represent a combined effect of leaf length and branch-free bole height (and possible other traits not included in this study, e.g. trunk flexibility (Putz 1984a)) rather than an independent effect of growth alone. This is reflected at the individual tree level, where wood density (used as a proxy for growth rate), branch-free bole height and leaf length are all important predictors of the likelihood of crown infestation (Table 3b). The independent effect of each trait, however, is difficult to distinguish.

By separating lianas infesting the trunk from those infesting the crown, we are able to show for the first time that these different routes of infestation are influenced by different tree traits. Our results indicate that:

1. Combining crown and trunk infestation may confound understanding of liana-tree interactions (Table 3c, Fig. 1). To be able to correctly determine the influence a tree trait has on liana incidence, these infestation sites should be treated separately.
2. Avoiding or dislodging lianas infesting the crown may be more important to a tree than avoiding lianas infesting the trunk, as is indicated by the variety of tree traits which apparently reduce the likelihood of crown infestation compared with the sole trait found to reduce trunk infestation (Table 3, Fig. 1). Competition for light in the canopy between lianas and trees can be severe and canopy liana load is much more likely to generate sufficient force to cause mechanical failure than trunk-borne liana load (Putz 1984b; Clark & Clark 1990; Phillips et al. 2002).

Generally, trees growing near another infested tree are at higher risk of liana infestation (Table 3). However, as we did not record whether the target tree was infested with the same liana as a neighbouring tree, there are two possible explanations for the observed pattern:

1. Lianas spread from tree to tree, increasing the risk of infestation of nearby trees (Putz 1984b; Pérez-Salicrup et al. 2001; Pérez-Salicrup & de Meijere 2005); and
2. A locally high abundance of lianas, e.g. in canopy gaps, results in high infestation rates for trees growing in and near these patches (Putz 1984b; Carse et al. 2000; Malizia & Grau 2006). These explanations are not mutually exclusive.

The amount of light that tree crowns receive does not appear to affect the likelihood of liana infestation in the crown (Table 3b), however liana infestation of trees with exposed crowns may be more intense than those with shaded crowns (Wright et al. 2005; Malizia & Grau 2006). Our findings differ from those in a subtropical montane forest in Argentina, where trees with well-lit crowns were at higher risk of liana infestation (Malizia & Grau 2006).

Overall, we show that for a western Amazonian forest



fast-growing tree species which are tall as adults, have low-density wood, long branch-free boles, long leaves, and a smooth bark are less likely to support lianas. By reducing the growth (e.g. Clark & Clark 1990) and fitness (e.g. Kainer et al. 2006), and increasing the mortality risk of hosts (Putz 1984b; Phillips et al. 2005), lianas may affect the outcome of competition amongst different tree species by favouring those with traits that make them less susceptible to liana infestation. Although this remains to be tested, we speculate that if the associations between liana infestation and host tree traits we found are representative of the wider Amazonian region, a continued increase in liana dominance could drive a basin-wide shift in tree species composition towards fast-growing tree taxa with low-density wood. On average, liana-free trees in Tambopata store 25% less carbon per unit basal area than liana-infested trees store ( $6.47 \pm 0.07$  vs.  $8.52 \pm 0.10$  Mg-C.m<sup>-2</sup> tree basal area, using biomass allometry from Chave et al. (2005)). Liana-driven tree compositional changes could therefore affect the ability of tropical forests to store carbon, and could cause a substantial impact on the rate of increase in atmospheric carbon dioxide and of climate change by releasing some of the  $\approx 90$  Pg C currently stored in Amazonian trees (Malhi et al. 2006).

**Acknowledgements.** We thank Tatiana Boza Espinoza for help with data collection, James Gibbons for statistical advice, and Emanuel Gloor and Julie Peacock for comments on earlier versions of this manuscript. This research was possible through grants from the Explorer's Club, the Coalbourn Trust, and the Alberta Mennega Foundation, financial support from the University of Leeds and logistic support from the Instituto Nacional para Recursos Naturales (INRENA) and Peruvian Safaris S.A.. O.L.P. was supported by a NERC Grant and a Leverhulme Trust Research Fellowship.

## References

- Anon. 2005. *SPSS*. SPSS-Inc. Chicago, IL, US.
- Anon. (R Development Core Team) 2006. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.
- Alvira, D., Putz, F.E. & Fredericksen, T.S. 2004. Liana loads and post-logging liana densities after liana cutting in a lowland forest in Bolivia. *Forest Ecology and Management* 190: 73-86.
- Baddeley, A. & Turner, R. 2005. Spatstat: an R package for analyzing spatial point patterns. *Journal of Statistical Software* 12: 1-42.
- 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., Silva, J.N.M. & Vásquez Martínez, R. 2004a. Increasing biomass in Amazonian forest plots. *Philosophical Transactions of the Royal Society of London. Series B* 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., Monteagudo, A., Neill, D., Patino, S., Pitman, N., Silva, J.N.M. & Vásquez-Martinez, R. 2004b. Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology* 10: 545-562.
- Balfour, D.A. & Bond, W.J. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81: 91-100.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Science, New York, NY, US.
- Campbell, E.J.F. & Newbery, D.M. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology* 9: 469-490.
- Carse, L.E., Fredericksen, T.S. & Licona, J.C. 2000. Liana-tree species associations in a Bolivian dry forest. *Tropical Ecology* 41: 1-10.
- Carsten, L.D., Juola, F.A., Male, T.D. & Cherry, S. 2002. Host associations of lianas in a south-east Queensland rain forest. *Journal of Tropical Ecology* 18: 107-120.
- Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eames, D., Folster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riera, B. & Yamakura, T. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87-99.
- 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.
- Clark, D.A. & Clark, D.B. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs* 62: 315-344.
- Clark, D.A. & Clark, D.B. 1999. Assessing the growth of tropical rain forest trees: Issues for forest modelling and management. *Ecological Applications* 9: 981-997.
- Clark, D.B. & Clark, D.A. 1990. Distribution and effects on tree growth of lianas and woody hemi-epiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6: 321-331.
- DeWalt, S.J., Schnitzer, S.A. & Denslow, J.S. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* 16: 1-19.
- Gentry, A.H. 1988. 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. 1991. Distribution and evolution of climbing plants. In: Putz, F.E. & Mooney, H.A. (eds.) *Biology of vines*, pp. 3-49. Cambridge University Press, Cambridge, UK.
- Gerwing, J.J., Schnitzer, S.A., Burnham, R.J., Bongers, F., Chave, J., DeWalt, S.J., Ewango, C.E.N., Foster, R.B., Kenfack, D., Martinez-Ramos, M., Parren, M.P.E., Pérez-Salicipur, D.R., Putz, F.E. & Thomas, D.W. 2006. A standard protocol for liana censuses. *Biotropica* 38: 256-261.
- Granados, J. & Körner, C. 2002. In deep shade, elevated CO<sub>2</sub> increases the vigor of tropical climbing plants. *Global Change Biology* 8: 1109-1117.
- Hegarty, E.E. 1991. Vine-host interactions. In: Putz, F.E. & Moo-

- ney, H.A. (eds.), *Biology of Vines*, pp. 357-375. Cambridge University Press, Cambridge, UK.
- Hosmer, D.W. & Lemeshow, S. 1980. A goodness-of-fit test for the multiple logistic regression. *Communications in Statistics* A10: 1043-1069.
- Hosmer, D.W. & Lemeshow, S. 2000. *Applied logistic regression*. John Wiley & Sons, New York, NY, US.
- Kainer, K.A., Wadt, L.H.O., Gomes-Silva, D.A.P. & Capanu, M. 2006. Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. *Journal of Tropical Ecology* 22: 147-154.
- Malhi, Y. & Wright, J. 2004. Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London. Series B*: 359: 311-329.
- Malhi, Y., Phillips, O.L., Lloyd, J., Baker, T.R., Wright, J., Almeida, S., Arroyo, L., Fredericksen, T.S., Grace, J., Higuchi, N., Killeen, T., Laurence, W.F., Leano, C., Lewis, S.L., Meir, P., Monteagudo, A., Neill, D., Núñez Vargas, P., Panfill, S.N., Silva, N., Silveira, M., Sombroek, W.G., Valencia, R., Vásquez, R.M., Vieira, I.C.G. & Vinceti, B. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science* 13: 439-450.
- Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., 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., Quesada, C.A., Slalomao, R., Silva, J.N.M., Torres Lezama, A., Terborgh, J.W., Vásquez Martínez, R. & Vinceti, B. 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. *Global Change Biology* 12: 1107-1138.
- Malizia, A. & Grau, H.R. 2006. Liana-host tree associations in a subtropical montane forest of north-west Argentina. *Journal of Tropical Ecology* 22: 331-339.
- Menard, S. 2006. *Applied logistic regression analysis*. Sage Publications, London, UK.
- Muller-Landau, H.C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20-32.
- Nabe-Nielsen, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. *Journal of Tropical Ecology* 17: 1-19.
- Peacock, J., Baker, T.R., Lewis, S.L., Lopez-Gonzalez, G. & Phillips, O.L. 2007. The RAINFOR database: monitoring forest biomass and dynamics. *Journal of Vegetation Science* 18: 535-542.
- Pérez-Salicrup, D.R. & de Meijere, W. 2005. Number of lianas per tree and number of trees climbed by lianas in Los Tuxtlas, Mexico. *Biotropica* 37: 153-156.
- 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. & Gentry, A.H. 1994. Increasing turnover through time in tropical forests. *Science* 263: 954-958.
- Phillips, O.L., Martinez, R.V., 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., Martinez, R.V., Mendoza, A.M., Baker, T.R. & Núñez Vargas, P. 2005. Large lianas as hyperdynamic elements of the tropical forest canopy. *Ecology* 86: 1250-1258.
- Phillips, O.L., Baker, T.R., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W.F., Lewis, S.L., Lloyd, J., Terborgh, J., Vasquez-Martinez, 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., Patino, 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 of London Series B*: 359: 381-407.
- Putz, F.E. 1980. Lianas vs. trees. *Biotropica* 12: 224-225.
- Putz, F.E. 1983. Liana biomass and leaf area of a "Tierra Firme" forest in the Rio Negro Basin, Venezuela. *Biotropica* 15: 185-189.
- Putz, F.E. 1984a. How trees avoid and shed lianas. *Biotropica* 16: 19-23.
- Putz, F.E. 1984b. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65: 1713-1724.
- Putz, F.E. 1995. Vines in treetops: consequences of mechanical dependence. In: Lowman, M.D. & Nadkarni, N.M. (eds.) *Forest canopies*, pp. 311-324. Academic Press Limited, London, UK.
- Putz, F.E. & Chai, P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75: 523-531.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* 88: 655-666.
- Tomlinson, P.B. 1979. Systematics and ecology of the Palmae. *Annual Review of Ecology and Systematics* 10: 85-107.
- Wright, S.J., Calderón, O., Hernández, A. & Paton, S. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. *Ecology* 85: 484-489.
- Wright, S.J., Hernandez, A. & Condit, R. 2007. The bushmeat harvest alters seedling banks by favouring lianas, large seeds and seed dispersed by bats, birds, and wind. *Biotropica* 39: 363-371.
- Wright, S.J., Jaramillo, M.A., Pavon, J., Condit, R., Hubbell, S.P. & Foster, R.B. 2005. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* 21: 307-315.

Received 13 August 2007;

Accepted 31 December 2007;

Co-ordinating Editor: P.S. White.

For App. 1, see below (online version)

also available at JVS/AVS Electronic Archives;

[www.opuluspress.se/](http://www.opuluspress.se/)

**App. 1.** Infestation rate and traits for tree species with  $\geq 15$  individuals in the seven plots combined (excluding trees growing in the seasonally-flooded swamp area). Means ( $\pm$ SE) are given for branch-free bole height and leaf length. Bark type: 1 = smooth, 2 = slightly rough and 3 = rough. Leaf form: c = compound leaves, s = simple leaves. Maximum potential growth rate is the average of the five fastest-growing non-infested trees. Maximum height and wood density values are obtained from the literature and the RAINFOR functional traits database (Chave et al. 2006; Peacock 2007). Differences from the overall infestation rate for palms or dicot trees, as appropriate, are indicated in bold ( $P < 0.05$ ).

		Size-class	No. of trees	Branch-free bole height (m)	Leaf length (cm)	Leaf form	Bark type	Wood density (g.m <sup>-3</sup> )	Maximum potential growth rate (mm yr <sup>-1</sup> )	Maximum height (m)	% trunk infested	% crown infested	% infested
<b>Palms</b>													
Arecaceae	<i>Astrocaryum gratum</i>	all sizes	20	7.2 ( $\pm 0.9$ )	565 ( $\pm 15$ )	c	2	n/a	n/a	n/a	15.0	5.0	15.0
		10-19.9	15	7.4 ( $\pm 0.9$ )			2				13.3	0.0	13.3
Arecaceae	<i>Euterpe precatoria</i>	all sizes	89	10.5 ( $\pm 0.3$ )	378 ( $\pm 5$ )	c	1	n/a	n/a	n/a	12.4	3.4	12.4
		10-19.9	89	10.5 ( $\pm 0.3$ )			1				12.4	3.4	12.4
Arecaceae	<i>Iriartea deltoidea</i>	all sizes	440	11.0 ( $\pm 0.2$ )	406 ( $\pm 1$ )	c	1	n/a	n/a	n/a	10.9	3.4	13.0
		10-19.9	107	6.5 ( $\pm 0.3$ )			1				9.3	2.8	<b>10.3</b>
		20-39.9	333	12.4 ( $\pm 0.3$ )			1				11.4	3.6	13.8
Arecaceae	<i>Oenocarpus bataua</i>	all sizes	28	7.7 ( $\pm 0.8$ )	548 ( $\pm 19$ )	c	1	n/a	n/a	n/a	3.6	<b>14.3</b>	17.9
		20-39.9	23	8.2 ( $\pm 0.9$ )			1				0.0	<b>17.4</b>	17.4
Arecaceae	<i>Oenocarpus mapora</i>	all sizes	16	8.5 ( $\pm 0.7$ )	394 ( $\pm 15$ )	c	1	n/a	n/a	n/a	0.0	0.0	0.0
		10-19.9	16	8.5 ( $\pm 0.7$ )	394 ( $\pm 15$ )	c	1				0.0	0.0	0.0
Arecaceae	<i>Socratea exorrhiza</i>	all sizes	98	11.6 ( $\pm 0.4$ )	392 ( $\pm 3$ )	c	4/1 <sup>a</sup>	n/a	n/a	n/a	<b>31.6</b>	9.2	<b>34.7</b>
		10-19.9	98	11.6 ( $\pm 0.4$ )			4/1 <sup>a</sup>				<b>31.6</b>	<b>9.2</b>	<b>34.7</b>
<b>Dicots</b>													
Annonaceae	<i>Oxandra riedeliana</i>	all sizes	20	4.9 ( $\pm 0.5$ )	16 ( $\pm 0.6$ )	s	1	0.77	2.0	22.0	15.0	<b>75.0</b>	75.0
		10-19.9	19	4.7 ( $\pm 0.5$ )			1		2.0		15.8	<b>73.7</b>	73.7
Apocynaceae	<i>Aspidosperma tambopatense</i>	all sizes	17	7.8 ( $\pm 0.5$ )	15 ( $\pm 0.7$ )	s	1	0.75	1.9	30.0	11.8	47.1	52.9
		10-19.9	15	7.4 ( $\pm 0.5$ )			1		1.9		13.3	40.0	46.7
Bixaceae	<i>Bixa arborea</i>	all sizes	18	6.8 ( $\pm 0.5$ )	23 ( $\pm 1.4$ )	s	2	0.36	4.7	x	27.8	55.6	61.1
Burseraceae	<i>Tetragastris altissima</i>	all sizes	27	5.3 ( $\pm 0.4$ )	49 <sup>b</sup>	c	1	0.71	4.0	31.7	18.5	70.4	74.1
Chrysobalanaceae	<i>Licania heteromorpha</i>	all sizes	29	7.6 ( $\pm 0.5$ )	15 ( $\pm 0.8$ )	s	1	0.82	6.9	24.5	17.2	62.1	62.1
		10-19.9	17	6.0 ( $\pm 0.4$ )			1		3.2		17.6	52.9	52.9
Clusiaceae	<i>Calophyllum brasiliense</i>	all	16	7.6 ( $\pm 0.5$ )	15 ( $\pm 0.8$ )	s	3	0.56	4.3	29.0	18.8	62.5	62.5
Clusiaceae	<i>Symphonia globulifera</i>	all sizes	35	8.5 ( $\pm 0.5$ )	13 ( $\pm 0.5$ )	s	1	0.60	9.0	28.0	28.6	<b>25.7</b>	<b>37.1</b>
		10-19.9	26	7.3 ( $\pm 0.4$ )			1		8.3		30.8	<b>26.9</b>	38.5
Euphorbiaceae	<i>Drypetes gentryi</i>	all sizes	22	9.1 ( $\pm 0.7$ )	18 ( $\pm 0.9$ )	s	2	0.69 <sup>c</sup>	1.4	n/a	18.2	59.1	59.1
		10-19.9	15	7.8 ( $\pm 0.5$ )			2		1.0		26.7	60.0	60.0
Euphorbiaceae	<i>Hevea guianensis</i>	all sizes	18	7.5 ( $\pm 0.6$ )	45 ( $\pm 1.0$ )	c	2	0.56	1.1	25.0	38.9	61.1	61.1
Euphorbiaceae	<i>Mabea nitida</i>	all sizes	20	10.9 ( $\pm 0.8$ )	18 ( $\pm 1.7$ )	s	1	0.65	3.2	10.0	40.0	45.0	55.0
Euphorbiaceae	<i>Sagotia racemosa</i>	all sizes	24	3.5 ( $\pm 0.2$ )	20 ( $\pm 0.9$ )	s	2	0.58	1.2	15.0	29.2	70.8	70.8
Fabaceae	<i>Sclerolobium bracteosum</i>	all sizes	15	9.1 ( $\pm 0.7$ )	76 ( $\pm 5.6$ )	c	1	0.56	14.3	n/a	40.0	33.3	53.3
Fabaceae	<i>Tachigali polyphylla</i>	all sizes	45	7.5 ( $\pm 0.4$ )	51 ( $\pm 1.7$ )	c	1	0.64	18.8	25.0	15.6	<b>35.6</b>	<b>42.2</b>
		10-19.9	27	7.3 ( $\pm 0.4$ )			1		11.6		14.8	<b>29.6</b>	<b>37.0</b>
		20-39.9	15	7.1 ( $\pm 0.6$ )			1		15.9		20.0	40.0	46.7
Lauraceae	<i>Ocotea bofo</i>	all sizes	25	8.9 ( $\pm 0.5$ )	18 ( $\pm 1.4$ )	s	2	0.54 <sup>c</sup>	7.5	20.0	36.0	60.0	64.0
Lecythidaceae	<i>Eschweilera coriacea</i>	all sizes	31	8.5 ( $\pm 0.4$ )	19 ( $\pm 1.1$ )	s	2	0.84	2.9	33.5	35.5	64.5	<b>77.4</b>
		10-19.9	15	7.7 ( $\pm 0.4$ )			2		2.9		33.3	66.7	73.3
		20-39.9	15	8.8 ( $\pm 0.5$ )			2		2.9		33.3	60.0	80.0
Linaceae	<i>Hebepetalum humiriifolia</i>	all sizes	21	5.6 ( $\pm 0.3$ )	23 ( $\pm 1.0$ )	s	2	0.87	5.1	22.5	9.5	38.1	42.9

**App. 1-4.** Internet supplement to: van der Heijden, G.M.F.; Healey, J.R. & Phillips, O.L. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru *Journal of Vegetation Science* 11: 747-756; doi: 10.3170/2008-8-18459

## II

## App. 1, cont.

		Size-class	No. of trees	Branch-free bole height (m)	Leaf length (cm)	Leaf form	Bark type	Wood density (g.m <sup>-3</sup> )	Maximum potential growth rate (mm yr <sup>-1</sup> )	Maximum height (m)	% trunk infested	% crown infested	% infested
Linaceae	<i>Roucheria punctata</i>	all sizes	37	7.2 (±0.3)	19 (±0.6)	s	1	0.83 <sup>c</sup>	4.0	20.0	27.0	56.8	64.9
		10-19.9	28	7.1 (±0.2)			1		4.0		32.1	50.0	60.7
Malvaceae	<i>Matisia ochrocalyx</i>	all sizes	16	4.9 (±0.4)	22 (±1.3)	s	1	0.57	1.7	n/a	18.8	37.5	43.8
		10-19.9	16	4.9 (±0.4)			1		1.7		18.8	37.5	43.8
Meliaceae	<i>Guarea gomma</i>	all sizes	16	7.8 (±0.5)	71 (±4.3)	c	2	0.65	6.1	32.5	<b>43.8</b>	62.5	68.8
Monimiaceae	<i>Siparuna decipiens</i>	all sizes	75	4.7 (±0.2)	17 (±1.1)	s	1	0.64	3.1	16.0	<b>12.0</b>	56.0	58.7
		10-19.9	74	4.7 (±0.2)			1		3.0		<b>12.2</b>	56.8	59.5
Moraceae	<i>Brosimum lactescens</i>	all sizes	25	6.6 (±0.4)	18 (±1.1)	s	1	0.66	5.0	41.7	12.0	44.0	48.0
		20-39.9	15	7.1 (±0.6)			1		3.7		6.7	33.3	40.0
Moraceae	<i>Helicostylus tomentosa</i>	all sizes	18	5.8 (±0.3)	21 (±0.9)	s	1	0.69	1.9	x	22.2	44.4	55.6
Moraceae	<i>Pseudolmedia laevigata</i>	all sizes	44	6.5 (±0.3)	15 (±0.9)	s	1	0.63	4.1	35.0	25.0	59.1	61.4
		10-19.9	22	5.4 (±0.2)			1		3.3		18.2	45.5	45.5
		20-39.9	21	7.5 (±0.4)			1		2.7		28.6	71.4	76.2
Moraceae	<i>Pseudolmedia laevis</i>	all sizes	65	7.1 (±0.2)	17 (±0.5)	s	1	0.64	6.6	40.0	16.9	53.8	58.5
		10-19.9	35	6.5 (±0.3)			1		6.3		17.1	40.0	48.6
		20-39.9	25	7.8 (±0.4)			1		4.0		16.0	68.0	68.0
Moraceae	<i>Pseudolmedia macrophylla</i>	all sizes	39	8.0 (±0.3)	27 (±1.1)	s	1	0.66	4.3	23.5	12.8	46.2	48.7
		10-19.9	18	7.0 (±0.4)			1		3.4		16.7	27.8	33.3
		20-39.9	19	8.8 (±0.5)			1		3.1		5.3	57.9	57.9
Myristicaceae	<i>Iryanthera juruensis</i>	all sizes	113	5.5 (±0.2)	16 (±0.4)	s	3	0.66	6.2	21.7	22.1	<b>63.7</b>	<b>67.3</b>
		10-19.9	102	5.4 (±0.2)			3		6.2		21.6	<b>60.8</b>	<b>64.7</b>
Myristicaceae	<i>Iryanthera laevis</i>	all sizes	70	6.3 (±0.3)	17 (±0.6)	s	1	0.63	4.7	22.5	17.1	48.6	54.3
		10-19.9	48	5.7 (±0.3)			1		4.5		20.8	52.1	58.3
		20-39.9	21	7.2 (±0.5)			1		3.5		9.5	38.1	42.9
Myristicaceae	<i>Virola sebifera</i>	all sizes	23	7.3 (±0.6)	22 (±1.4)	s	1	0.46	4.8	23.3	33.3	52.4	57.1
		10-19.9	19	6.8 (±0.6)			1		4.8		23.5	41.2	47.1
Ochnaceae	<i>Ouratea</i> sp.	all sizes	27	5.8 (±0.3)	16 (±1.0)	s	2	0.76 <sup>c</sup>	1.3	n/a	18.5	55.6	57.1
		10-19.9	22	5.6 (±0.3)			2		1.0		18.2	54.5	47.1
Olacaceae	<i>Heisteria acuminata</i>	all sizes	16	7.0 (±0.5)	18 (±0.9)	s	2	0.71	1.8	10.5	25.0	62.5	75.0
Rubiaceae	<i>Amaioua corymbosa</i>	all sizes	21	4.8 (±0.6)	15 (±0.2)	s	2	0.77 <sup>c</sup>	1.0	12.5	19.0	<b>76.2</b>	<b>76.2</b>
		10-19.9	17	4.9 (±0.4)			2		1.0		17.6	<b>76.5</b>	76.5
Sabiaceae	<i>Meliosma herbertii</i>	all sizes	27	6.8 (±0.3)	21 (±0.8)	s	2	0.42	4.7	n/a	25.9	48.1	48.1
		10-19.9	18	6.4 (±0.4)			2		4.7		27.8	44.4	44.4
Salicaceae	<i>Laetia procera</i>	all sizes	16	9.1 (±0.7)	18 (±1.0)	s	2	0.64	6.2	33.3	37.5	68.8	75.0
Salicaceae	<i>Lindackeria paludosa</i>	all sizes	24	4.6 (±0.4)	22 (±1.0)	s	1	0.56	1.2	17.5	33.3	<b>79.2</b>	<b>83.3</b>
		10-19.9	22	4.4 (±0.4)			1		1.2		36.4	<b>81.8</b>	<b>86.4</b>
Sapotaceae	<i>Micropholis guyanensis</i>	all sizes	17	7.7 (±0.6)	18 (±2.3)	s	1	0.66	5.3	31.0	23.5	<b>76.5</b>	<b>76.5</b>
Sapotaceae	<i>Pouteria torta</i>	all sizes	25	6.8 (±0.7)	26 (±2.0)	s	2	0.77	1.5	33.5	20.0	72.0	76.0
Urticaceae	<i>Pourouma cecropiifolia</i>	all sizes	19	9.5 (±0.9)	66 (±0.9)	s	1	0.38	13.0	20.0	21.1	42.1	52.6
Urticaceae	<i>Pourouma guianensis</i>	all sizes	33	7.1 (±0.4)	36 (±2.2)	s	1	0.38	12.1	28.8	12.1	54.5	54.5
		10-19.9	16	7.1 (±0.5)			1		8.6		18.8	50.0	50.0
		20-39.9	15	7.0 (±0.5)			1		11.0		6.7	53.3	53.3

App. 1-4. Internet supplement to: van der Heijden, G.M.F.; Healey, J.R. & Phillips, O.L. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru *Journal of Vegetation Science* 11: 747-756; doi: 10.3170/2008-8-18459

## App. 1, cont.

		Size-class	No. of trees	Branch-free bole height (m)	Leaf length (cm)	Leaf form	Bark type	Wood density (g.m <sup>-3</sup> )	Maximum potential growth rate (mm yr <sup>-1</sup> )	Maximum height (m)	% trunk infested	% crown infested	% infested
Urticaceae	<i>Pourouma minor</i>	all sizes	160	6.5 (±0.2)	21 (±0.4)	s	1	0.44	15.7	31.3	20.6	<b>43.1</b>	<b>46.3</b>
		10-19.9	87	5.5 (±0.2)			1		12.3		18.4	<b>33.3</b>	<b>37.9</b>
		20-39.9	67	7.6 (±0.3)			1		14.2		20.9	52.2	53.7
Violaceae	<i>Leonia glycyarpa</i>	all sizes	98	4.8 (±0.2)	17 (±0.5)	s	1	0.60	3.1	27.5	15.3	58.2	59.2
		10-19.9	68	4.7 (±0.2)			1		3.1		14.7	47.1	48.5
		20-39.9	30	5.0 (±0.3)			1		0.7		16.7	<b>83.3</b>	<b>83.3</b>
Violaceae	<i>Rinorea viridifolia</i>	all sizes	45	2.5 (±0.3)	11 (±0.2)	s	1	0.52	2.9	15.0	17.8	66.7	68.9
		10-19.9	44	2.5 (±0.3)			1		2.9		18.2	<b>65.9</b>	68.2

<sup>a</sup> *Socratea exorrhiza* has stilt roots with spines (which were considered to be of the 'stem'), but the bark is classified as smooth above the roots;

<sup>b</sup> obtained from local floras;

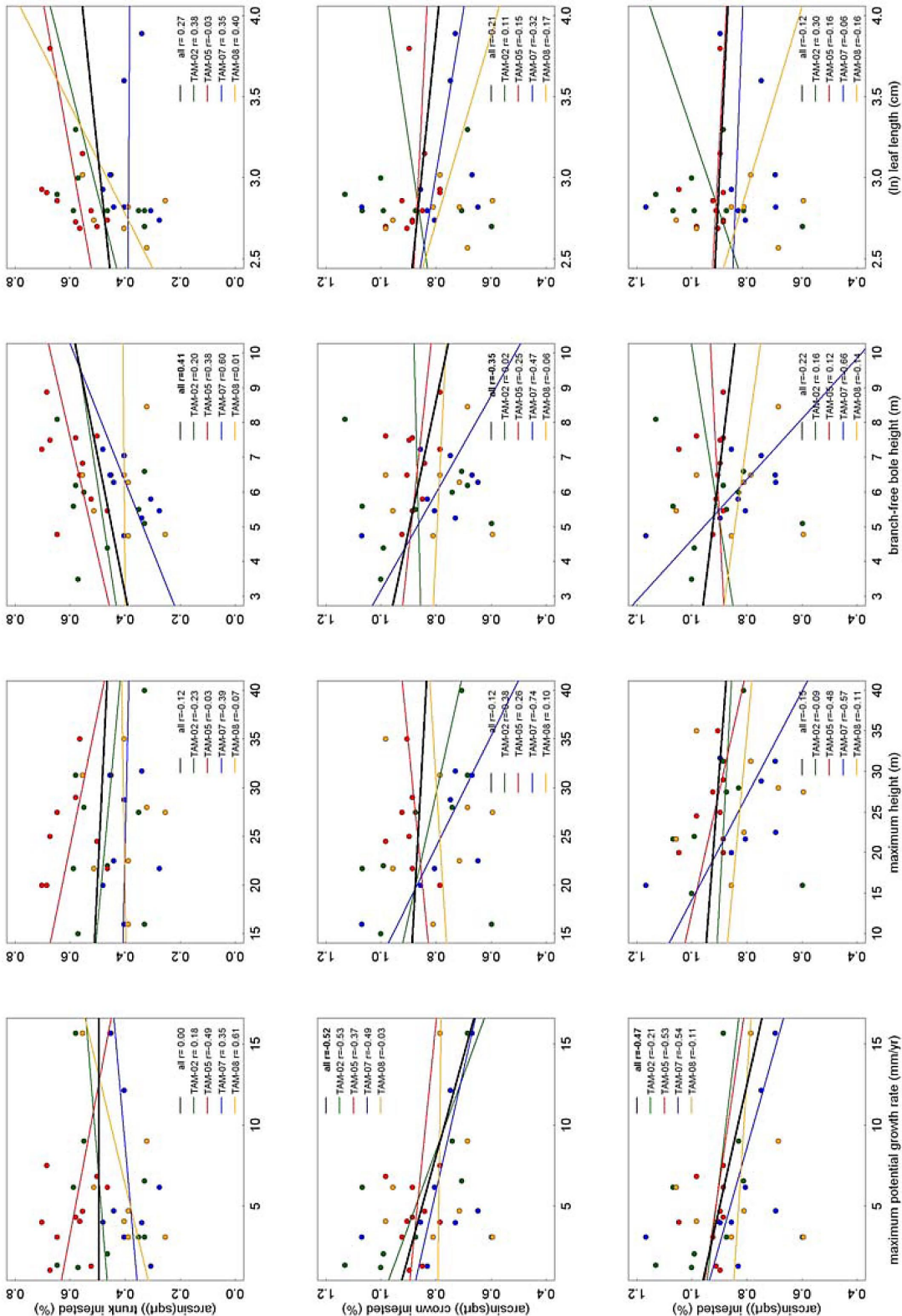
<sup>c</sup> genus average.

## IV

**App. 2.** Liana infestation rates per plot calculated separately for all tree species, dicots and palms, and for trees with trunk infested, crown infested and infestation regardless-of-site, and for the diameter size-classes all sizes, 10-19.9 cm, 20-39.9 cm and  $\geq 40$  cm. TAM-03 is the seasonally flooded swamp area. Note: TAM-03 and TAM-04 together form one 1-ha plot.

		No. of trees	All % trunk infested	All % crown infested	All % infested	No. of dicots infested	Dicots % trunk infested	Dicots % crown infested	Dicots % infested	No. of palms infested	Palm % trunk infested	Palm % crown infested	Palm % infested
<b>TAM-03</b>	All sizes	334	5.1	4.2	8.1	281	5.3	5.0	8.9	53	3.8	0.0	3.8
	10-19.9	106	7.6	5.7	10.4	101	7.9	5.9	10.9	5	0.0	0.0	0.0
	20-39.9	179	3.9	3.4	6.7	131	3.8	4.6	7.6	48	4.2	0.0	4.2
	$\geq 40$	49	4.1	2.0	6.1	49	4.1	2.0	6.1	0	0.0	0.0	0.0
<b>TAM-04</b>	All sizes	280	18.6	48.2	53.2	255	19.2	52.6	56.9	25	12.0	4.0	16.0
	10-19.9	179	19.6	44.1	49.7	166	19.3	47.0	51.2	13	23.1	7.7	30.8
	20-39.9	88	17.1	51.1	54.6	76	19.7	59.2	63.2	12	0.0	0.0	0.0
	$\geq 40$	13	15.4	84.6	92.3	13	15.4	84.6	92.3	0	0.0	0.0	0.0
<b>TAM-01</b>	All sizes	573	14.0	36.3	41.2	394	17.0	50.8	55.1	179	7.3	4.5	10.6
	10-19.9	321	16.2	34.3	41.1	240	17.1	45.0	50.0	81	13.6	2.5	14.8
	20-39.9	216	9.7	35.7	37.0	118	16.1	60.2	61.9	98	2.0	6.1	7.1
	$\geq 40$	36	19.4	58.3	66.7	36	19.4	58.3	66.7	0	0.0	0.0	0.0
<b>TAM-02</b>	All sizes	658	22.0	39.5	47.0	469	25.8	54.8	60.6	189	12.7	1.6	13.2
	10-19.9	400	23.5	41.3	48.3	306	26.5	52.9	58.5	94	13.8	3.2	14.9
	20-39.9	225	18.2	30.7	39.1	130	23.1	53.1	59.2	95	11.6	0.0	11.6
	$\geq 40$	33	30.3	78.8	84.9	33	30.3	78.8	84.9	0	0.0	0.0	0.0
<b>TAM-05</b>	All sizes	520	22.9	56.7	60.4	501	23.6	58.9	62.5	19	5.3	0.0	5.3
	10-19.9	328	22.9	50.6	55.5	316	23.8	52.5	57.6	12	0.0	0.0	0.0
	20-39.9	152	21.7	63.8	65.8	145	22.1	66.9	63.2	7	14.3	0.0	14.3
	$\geq 40$	40	27.5	80.0	80.0	40	27.5	80.0	80.0	0	0.0	0.0	0.0
<b>TAM-06</b>	All sizes	642	30.7	40.7	50.9	440	33.6	55.2	62.1	202	24.3	8.9	26.8
	10-19.9	384	32.3	43.2	54.9	287	33.8	55.1	63.8	97	27.8	8.3	28.9
	20-39.9	212	26.9	32.6	42.0	107	32.7	55.1	58.9	105	21.0	9.5	24.8
	$\geq 40$	46	34.8	56.5	58.7	46	34.8	56.5	58.7	0	0.0	0.0	0.0
<b>TAM-07</b>	All sizes	498	17.3	46.6	50.6	475	18.1	48.8	53.1	23	0.0	0.0	0.0
	10-19.9	308	17.2	40.6	45.5	291	18.2	43.0	48.1	17	0.0	0.0	0.0
	20-39.9	158	16.5	51.3	54.4	152	17.1	53.3	56.6	6	0.0	0.0	0.0
	$\geq 40$	32	21.9	81.3	81.3	32	21.9	81.3	81.3	0	0.0	0.0	0.0
<b>TAM-08</b>	All sizes	504	18.3	41.7	48.4	441	19.1	46.3	52.6	63	12.7	9.5	19.1
	10-19.9	313	18.5	40.3	46.0	290	19.7	43.1	49.3	23	4.4	4.4	4.4
	20-39.9	160	18.1	41.9	50.6	120	18.3	51.7	58.3	40	17.5	12.5	27.5
	$\geq 40$	31	16.1	54.8	61.3	31	16.1	54.8	61.3	0	0.0	0.0	0.0

**App. 3.** Bivariate relations per plot between liana infestation (trunk, crown and regardless-of-site) and the continuous tree traits for tree species with  $\geq 10$  individuals (regardless of size-class). Only plots for which enough tree species were available to carry out a correlation analysis are indicated: TAM-02 ( $n=9$ ), TAM-05 ( $n=11$ ), TAM-07 ( $n=8$ ), TAM-08 ( $n=7$ ). Black line indicates the relationship when all plots are combined ( $n=41$ ). Significant correlations ( $P \leq 0.05$ ) are indicated in bold.



**App. 1-4.** Internet supplement to: van der Heijden, G.M.F.; Healey, J.R. & Phillips, O.L. 2008.

**App. 4.** Exploration of Type-I and Type-II errors.

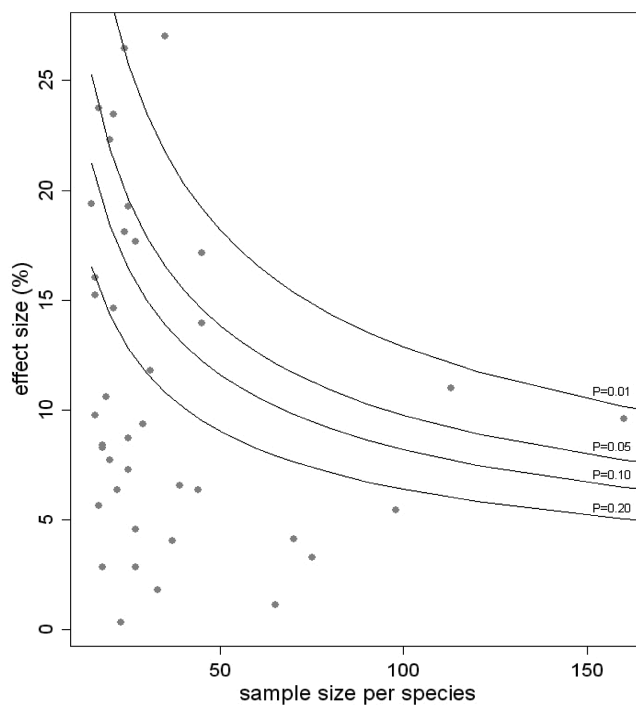
a) We compared the  $P$ -values from the conventional  $\chi^2$ -test with  $P$ -values generated using the following bootstrapping methodology:

- 1) We resampled each of the 41 species as well as the whole dicot tree population based upon their original distribution of crown infested and uninfested trees generating 100 new samples with equal sample size as the original sample.
- 2) For each species, each of the 100 bootstrap samples was subjected to a  $\chi^2$ -test whereby the number of infested and uninfested trees is used as “observed” and the expected proportion is based upon one of the 100 bootstrap samples of the whole dicot tree population.
- 3) For each of these  $\chi^2$ -tests, the probability of finding the ‘observed’ contingency table was calculated by simulating the actual distribution of possible table configurations based upon the data using a Monte Carlo bootstrapping method with 2000 samples. This method is less restrictive in terms of assumptions than the conventional  $\chi^2$ -test, as it does not rely on the chi-square distribution holding.
- 4) For each species, the median  $P$ -value of the  $\chi^2$ -tests of these 100 bootstrap samples was used as the robust  $P$ -value. By comparing the  $P$ -value obtained from the conventional  $\chi^2$ -tests with the  $P$ -value obtained using bootstrapping, we can assess whether the significant differences found by the conventional  $\chi^2$ -test have arisen by chance or are robust. Generally, as is shown below, the results of the conventional  $\chi^2$ -test are very similar to those obtained with the bootstrapping method. Significant correlations ( $P < 0.05$ ) are indicated in bold and those with  $0.05 < P < 0.1$  in italic.

			$N$	% crown	conventional $\chi^2$ $P$ -value	Bootstrapped $P$ -value
Clusiaceae	<i>Symphonia</i>	<i>globulifera</i>	35	25.7	<b>0.001</b>	<b>0.016</b>
Fabaceae	<i>Sclerolobium</i>	<i>bracteosum</i>	15	33.3	0.133	0.197
Fabaceae	<i>Tachigali</i>	<i>polyphylla</i>	45	35.6	<b>0.021</b>	<b>0.038</b>
Malvaceae	<i>Matisia</i>	<i>ochrocalyx</i>	16	37.5	0.223	0.321
Linaceae	<i>Hebepetalum</i>	<i>humirifolia</i>	21	38.1	0.180	0.192
Urticaceae	<i>Pourouma</i>	<i>cecropiifolia</i>	19	42.1	0.354	0.495
Urticaceae	<i>Pourouma</i>	<i>minor</i>	160	43.1	<b>0.015</b>	<b>0.037</b>
Moraceae	<i>Brosimum</i>	<i>lactescens</i>	25	44.0	0.383	0.311
Moraceae	<i>Helicostylis</i>	<i>tomentosa</i>	18	44.4	0.482	0.630
Euphorbiaceae	<i>Mabea</i>	<i>nitida</i>	20	45.0	0.489	0.492
Moraceae	<i>Pseudomedia</i>	<i>macrophylla</i>	39	46.2	0.412	0.518
Apocynaceae	<i>Aspidosperma</i>	<i>tambopatense</i>	17	47.1	0.640	0.463
Sabiaceae	<i>Meliosma</i>	<i>herbertii</i>	27	48.2	0.634	0.687
Myristicaceae	<i>Iryanthera</i>	<i>laevis</i>	70	48.6	0.487	0.410
Myristicaceae	<i>Virola</i>	<i>sebifera</i>	23	52.4	0.715	0.534
Moraceae	<i>Pseudolmedia</i>	<i>laevis</i>	65	53.8	0.856	0.461
Urticaceae	<i>Pourouma</i>	<i>guianensis</i>	33	54.6	0.834	0.600
Bixaceae	<i>Bixa</i>	<i>arborea</i>	18	55.6	0.810	0.503
Ochnaceae	<i>Ouratea</i>	sp.	27	55.6	0.768	0.558
Monimiaceae	<i>Siparuna</i>	<i>decipiens</i>	75	56.0	0.569	0.474
Linaceae	<i>Roucheria</i>	<i>punctata</i>	37	56.8	0.623	0.491
Violaceae	<i>Leonia</i>	<i>glycycarpa</i>	98	58.2	0.280	0.275
Euphorbiaceae	<i>Drypetes</i>	<i>gentryi</i>	22	59.1	0.550	0.459
Moraceae	<i>Pseudolmedia</i>	<i>laevigata</i>	44	59.1	0.397	0.412
Lauraceae	<i>Ocotea</i>	<i>bofo</i>	25	60.0	0.466	0.419
Euphorbiaceae	<i>Hevea</i>	<i>guianensis</i>	18	61.1	0.476	0.470
Chrysobalanaceae	<i>Licania</i>	<i>heteromorpha</i>	29	62.1	0.313	0.362
Clusiaceae	<i>Calophyllum</i>	<i>brasiliense</i>	16	62.5	0.433	0.466
Meliaceae	<i>Guarea</i>	<i>gomma</i>	16	62.5	0.433	0.453
Olacaceae	<i>Heisteria</i>	<i>acuminata</i>	16	62.5	0.433	0.480
Myristicaceae	<i>Iryanthera</i>	<i>juruisensis</i>	113	63.7	<b>0.019</b>	<b>0.011</b>
Lecythidaceae	<i>Eschweilera</i>	<i>coriacea</i>	31	64.5	0.188	0.201
Violaceae	<i>Rinorea</i>	<i>viridifolia</i>	45	66.7	<i>0.061</i>	<i>0.068</i>
Salicaceae	<i>Laetia</i>	<i>procera</i>	16	68.8	0.199	0.226
Burseraceae	<i>Tetragastris</i>	<i>altissima</i>	27	70.4	<i>0.066</i>	<i>0.079</i>
Euphorbiaceae	<i>Sagotia</i>	<i>racemosa</i>	24	70.8	<i>0.076</i>	0.104
Sapotaceae	<i>Pouteria</i>	<i>torta</i>	25	72.0	<i>0.054</i>	<b>0.042</b>
Annonaceae	<i>Oxandra</i>	<i>riedeliana</i>	20	75.0	<b>0.046</b>	<b>0.050</b>
Rubiaceae	<i>Amaioua</i>	<i>corymbosa</i>	21	76.2	<b>0.031</b>	<b>0.042</b>
Sapotaceae	<i>Micropholis</i>	<i>guyanensis</i>	17	76.5	<b>0.049</b>	<b>0.050</b>
Salicaceae	<i>Lindackeria</i>	<i>paludosa</i>	24	79.2	<b>0.009</b>	<b>0.012</b>



**b)** We simulated the effect size (i.e. the difference between the observed infestation rate and the overall crown infestation rate) necessary to obtain  $P$ -values of 0.01, 0.05, 0.1 and 0.2 with increasing sample size. Grey dots represent the 41 dicot species used in this study. Fig. A4.1 shows that for many species we were not able to detect a significant result between observed and expected crown infestation rate due to the small sample sizes involved (Type II error) even if effect sizes were greater than those of species for which we were able to detect a significant difference. However, with a similar effect size and an increased sample size of 100 individuals, we would expect to find a significant difference in crown infestation rate for 44% of the species (i.e. 44% of the species would either have a significantly higher or a lower crown infestation rate compared with the overall crown infestation rate of 52.6%).



**Fig. A4.1.**