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Tree Species Vary Widely in Their Tolerance for Liana Infestation: A Case Study of Differential Host Response to Generalist Parasites

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Abstract

1. Lianas are structural parasites of trees and reduce individual host tree growth, survival and fecundity. Thus, liana infestation is expected to affect tree population growth rates, with potentially different effects in different species depending on the frequency of liana infestation and the impact of liana infestation on population growth rates. Previous studies have documented the myriad negative effects of lianas on trees and variation in liana infestation among tree species; however, no study has quantified the impact of liana infestation on individual tree species population growth rates. Lianas are increasing in abundance in multiple Neotropical sites, which may have profound consequences for tree species composition if lianas differentially affect host tree species population growth.

2. Here, we use long-term data to evaluate the effects of liana infestation on the reproduction, growth, survival and ultimately population growth rates of dozens of tree species from Barro Colorado Island, Panama. We then test whether liana infestation affects tree species differentially with respect to two axes of life-history variation: adult stature and position along the fast–slow axis, a measure of shade tolerance.

3. Liana infestation decreased tree growth, survival and reproduction, with the strongest effects on survival in fast-growing, light-demanding species and on reproduction in large-statured species. In combination, these effects reduced tree population growth rates such that liana-infested populations declined by an average of 1.4% annually relative to conspecific liana-free populations. The reduction in population growth rates was greatest among fast-growing species and smaller in slow-growing species.

4. Synthesis. Our results demonstrate that liana infestation has strong negative effects on tree population growth rates, which vary systematically among tree species with tree life history. The finding that liana infestation is more harmful to fast-growing tree species appears to be at odds with the general expectations in the literature. We propose that this is likely due to survivorship bias, as infestation greatly decreases survival in fast-growing species such that the observable sample is biased towards those that survived and liana-free. In combination with data on how tree species vary in liana infestation rates, these results provide a basis for predicting the impacts of changes in liana abundance on tree species composition.

1 INTRODUCTION

Lianas are an important component of tropical forests, where they frequently occur in the crowns of more than 50% of canopy trees (Ingwell, Wright, Becklund, Hubbell, & Schnitzer, **2010**; Putz, **1984**; van der Heijden &

Phillips, **2009**). Lianas are macro-parasites that do not invest in structural support, relying instead on tree hosts to access canopy light while simultaneously usurping resources that would otherwise be available to their host (e.g. Stevens, **1987**). As a consequence, lianas typically reduce reproduction, growth and survival of individual host trees (Clark & Clark, **1990**; Ingwell et al., **2010**; Peña-Claros et al., **2008**; Phillips, Martínez, Mendoza, Baker, & Vargas, **2005**; Schnitzer & Carson, **2010**; Wright, Sun, Pickering, Fletcher, & Chen, **2015**; Wright, Jaramillo, et al., **2005**). Liana abundance varies widely across tropical forests in relation to climate and disturbance history (Schnitzer, **2005**) and has increased dramatically in recent decades at a number of tropical sites (reviewed in Wright, Sun, et al., **2015**). This raises the question of how changing liana abundance might alter tree communities.

If the detrimental effects of lianas differ among tree species, changes in liana abundance will favour some tree species over others and might alter tree community composition, causing additional indirect effects on ecosystem functioning (Schnitzer, Bongers, & Wright, **2011**; van der Heijden, Powers, & Schnitzer, **2015**). The response of tree species to infestation will depend on two factors: the proportion of the population that is infested by lianas (liana prevalence) and how tolerant a given tree species is to infestation (host tolerance, see Figure **1**). Previous studies have shown that tree species can differ strongly in liana prevalence, and suggested that this variation is associated with tree stature and shade tolerance. Because most lianas grow towards full sunlight (Putz, **1984**), lianas might colonize large-statured tree species located in canopy sites having full sun exposure preferentially (Phillips et al., **2005**). In contrast, tree traits associated with light-demanding species— rapid growth rates, large leaves, few branches, smooth bark and long straight boles—are often associated with lower proportions of trees infested (Clark & Clark, **1990**; Putz, **1984**). These observations led to the expectation that lianas will have stronger negative effects on shade-tolerant, slow-growing tree species (Schnitzer & Bongers, **2002**; Schnitzer & Carson, **2010**). However, this expectation does not consider the sensitivities of tree species once infested. In short, there is evidence that liana prevalence varies among tree species, but no evidence as to whether tree species differ in their tolerance of infestation.
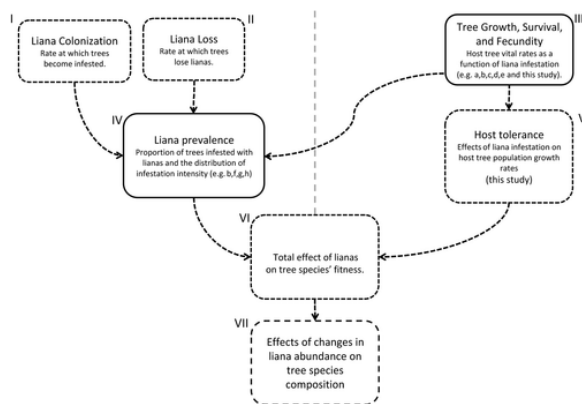

Figure 1 Schematic representation of the pathways by which lianas impact tree species composition (VII). All pathways and interactions can be grouped into two categories: (1) those concerning the abundance of lianas (liana prevalence) and (2) those concerning how sensitive hosts are to infestation (host tolerance). The net impact of lianas on tree species composition depends on how lianas affect host species fitness (VI), which in turn depend on how tree species differ in liana infestation frequency/intensity (IV) and in the effects of liana infestation on host population growth rates (V). The frequency and distribution of liana infestation within a tree species depends on liana colonization (I), liana loss (II), host tree survival as a function of liana infestation (III), and the rate of recruitment of new hosts, which are initially liana-free (III). The effect of liana infestation on host population growth rates depends on how liana infestation affects tree growth, survival and fecundity (III). Quantification of all boxes and links must be achieved before the net effects of changes in liana abundance on tree communities can be predicted (VII) but previous work has only focused on a few aspects of the system. Solid lines indicate rates and statistics that have been quantified previously, dashed lines indicate rates, statistics and links that are essentially unknown, being rarely if ever quantified. Letters refer to studies by van der Heijden and Phillips (**2009**) (a), Ingwell et al. (**2010**) (b), Martinez-Izquierdo et al. (**2016**) (c), Wright, Jaramillo, et al. (**2005**) (d), Wright, Sun, et al. (**2015**) (e), Clark and Clark (**1990**) (f), Perez-Salicrup, Sork, and Putz (**2001**) (g) and van der Heijden, Healey, and Phillips (**2008**) (h)

Accurate estimation of host tree tolerance requires integrating the effects of lianas over the entire life cycle to calculate the total consequences of liana infestation for host tree population growth rate, something that has never previously been done for even a single species. Studies of effects at a single life stage and vital rate, such as several recent studies finding no differences among tree species (Álvarez-Cansino, Schnitzer, Reid, & Powers, **2015**; Martinez-Izquierdo, Muriel-Garcia, Powers, & Schnitzer, **2016**; Schnitzer, Kuzee, & Bongers, **2005**), are unlikely to parallel total net effects on fitness for two reasons (Caswell, **1983**; Ehrlén, **2003**; Metcalf & Pavard, **2007**). First, the relative importance of particular vital rates and stages to overall population growth varies among species (de Kroon, Plaisier, van Groenendael, & Caswell, **1986**; de Kroon, van Groenendael, & Ehrlén, **2000**). Thus, similar absolute effects on vital rates may translate into dissimilar effects on population growth rates for species with different life histories. For example, the same absolute decrease in growth rate may be more detrimental for fast-growing species than for slow-growing species. Second, effects at one life stage or vital rate may be offset or magnified by effects at another (Visser et al., **2016a**). Hence, the potential for lianas to alter host tree species composition remains unknown.

In this study, we evaluated the effect of liana infestation on population dynamics of tropical tree species on Barro Colorado Island, Panama through analyses of large, long-term datasets spanning 28 years. We estimated the effects of liana infestation on all key aspects of a tree's life cycle, and compared the differential effects of lianas on the population growth rates of 33 tree species. We quantified the tolerance/sensitivity of each host species to liana infestation as the difference between liana-free population growth rates and heavily infested population growth rates. Finally, we evaluated interspecific relationships between tolerance of liana infestation and two important axes of life-history variation among tropical tree species: adult stature and position on the growth-survival trade-off (Kohyama, Suzuki, Partomihardjo, Yamada, & Kubo, **2003**; Wright et al., **2010**). We show that lianas have strong negative effects on tree species population growth rates, and that these effects are stronger in faster growing tree species.

2 MATERIALS AND METHODS

2.1 Study site

BCI is a 1,562-ha island covered with lowland moist tropical forest located in Gatun Lake in central Panama (9°9′N, 79°51′W). Annual rainfall averages 2,632 mm (1929–2014), and there is a distinct dry season between January and April (Leigh, **1999**). Croat (**1978**) and Leigh (**1999**) provided detailed descriptions of BCI.

2.2 Datasets

We used seven datasets that covered all life-history stages and two key functional traits.

2.2.1 Dataset 1

Tree growth and survival from censuses of one 50-ha plot and five 4-ha plots. In the 50-ha forest dynamics plot (FDP), all free-standing woody plants with diameter at 1.3 m height (DBH) ≥1 cm have been mapped, measured for diameter and identified to species in 1980–1982, 1985, 1990, 1995, 2000, 2005 and 2010 (Condit, **1998**). The same methods were used to census all trees ≥20 cm DBH in the five 4-ha plots in 2003–2004 and 2014.

2.2.2 Dataset 2

Tree reproductive status and proportion of the canopy covered by lianas (liana load) in the FDP. We assessed 3,520 trees of 30 species in 1996 and 2007 (Ingwell et al., **2010**; Wright, Muller-Landau, Calderón, & Hernandez, **2005**) and an additional 18,157 trees of 129 species between March 2010 and October 2014. We assessed a size-stratified sample of individuals during the reproductive season of each species. The size-stratified samples included equal numbers of individuals from three size classes of equivalent DBH width, with the upper

and lower limits being the largest individual and the largest size at which no individuals reproduce (as assessed by field observations) respectively. We quantified liana load and reproductive status from the ground, using binoculars for the taller crowns. We scored both liana load and reproductive status on a five-point scale with zero indicating a liana-free or reproductively sterile tree and scores 1–4 indicating trees with 1%–25%, 26%–50%, 51%–75% and 76%–100% of the crown-bearing lianas or reproductive structures (flowers and/or fruits). For reproductive status, we located the approximate centre of a projection onto the ground for each crown, used this central point to divide each crown into four quarter-sections, and scored each quarter separately. For dioecious species, we also visually determined sex expression (male/female) from the ground or from abscised flowers collected beneath each individual. For liana load, we recorded a single score for the entire crown. These methods produce repeatable scores for liana load and reproductive status (Ingwell et al., **2010**; Wright, Sun, et al., **2015**). Ground observations on how tree reproduction is affected by liana infestation could be biased if the ability to observe reproductive parts in the canopy from the ground decreased with infestation. We believe this potential bias is minimal based on our own experience, previous studies in which observers climbed into the tree crowns to verify ground observations (Stevens, **1987**) and experimental liana-removal studies (Kainer, Wadt, & Staudhammer, **2014**).

2.2.3 Dataset 3
Liana load for all trees (3,312 total) in the five 4-ha plots between 2005 and 2006, using the methods described for dataset 2. Lianas found in the crowns of trees were identified to species by experienced botanists (Schnitzer et al., **2012**).

2.2.4 Dataset 4
Seed production, quantified weekly since January 1987 using 200 0.5-m^2 seed traps located within the FDP (Wright, Muller-Landau, et al., **2005**).

2.2.5 Dataset 5
Seedling establishment, growth and survival for individuals <1 cm DBH monitored annually since 1994 in 600 1-m^2 plots, with three plots paired with each seed trap (Wright, Muller-Landau, et al., **2005**).

2.2.6 Dataset 6
Growth, mortality and recruitment of seedlings ≥20 cm tall and <1 cm DBH monitored annually or biannually since 2001 in 20,000 1-m^2 plots located in a uniform design throughout the FDP (Comita, Aguilar, Pérez, Lao, & Hubbell, **2007**).

2.2.7 Dataset 7
Previously published species trait data. As a measure of adult stature we used H_{max}, defined as the mean height of the six largest diameter individuals in the 50-ha plot in 2007/2008 (Wright et al., **2010**). As a proxy for a species' position along the growth–survival trade-off (hereafter slow–fast axis), we used the first principal component factor score of a principal components analysis including the mortality and mean relative growth rate (obtained from Condit et al., **2006**) for trees >10 cm DBH, with higher values indicating higher growth and lower survival. A species' position on the slow–fast axis is an excellent estimate of shade tolerance with greater values indicating increasing light requirements (Wright et al., **2010**). The first PCA axis explains 61% of the variation (eigenvalue 1.2099, among 229 species). H_{max} and factor scores on the slow–fast axis were independent of each other ($r = .04$, n.s.).

2.3 Study species
We used different, but overlapping, sets of tree species in our analyses. First, we evaluated community-level mean effects of liana load on tree reproduction, growth and survival in hierarchical analyses (one analysis per vital rate). We included tree species with at least 15 individuals for the relevant vital rate to ensure reasonable

precision for species-specific estimates (rarer species comprised 1%–5% of the data). The 15-individual criterion resulted in 91, 61, 57 and 62 tree species for analyses of liana effects on reproductive probability, proportion of crown-bearing fruit, growth and survival respectively (Table **S1.1**). Each species had at least one infested individual, 97% had 5 or more, and 90% had 10 or more infested individuals.

Second, we constructed species-specific integral projection models (IPMs; see below) to quantify how lianas affect population growth rates. We included only those species with sufficient data for liana infestation (datasets 2 and 3) in addition to all other life-history stages and vital rates. Vital rates included seed production (dataset 4), seedling recruitment (dataset 5), seedling and tree growth and survival (datasets 1, 5 and 6), and reproduction (datasets 2 and 3). There were sufficient data for all life stages and vital rates for 33 species (Table **S1.2**). We provide an example R-code, and an unofficial r package for building the IPMs (Appendix **S2**).

2.4 Liana effects on tree growth, survival and reproduction

We quantified how lianas affected tree growth, survival and reproduction (datasets 1–3) by fitting generalized linear mixed models. Growth, survival and reproduction were first expressed as functions of individual size (DBH in mm), after which the liana infestation level (hereafter **L**) was included as a factor. We evaluated alternative models that included main effects of **L** and interactions between size and **L**. All models included random slopes and intercepts for species and, if individuals were measured multiple times in repeated censuses, additional random intercepts for individual. The exact model formulations are presented in Tables **S4.3–7**, but in all cases the most complex model had the following form:

$$Y_{si} \sim (\beta_0 + \varepsilon_s + \varepsilon_i) + (\beta_1 + \mu_s)S_i + (\beta_2 + \gamma_s)\mathbf{L}_i + \beta_3\mathbf{L}_iS_i \text{ (1)}$$

where Y_{si} represents the annual growth rate, survival state or reproductive status of individual i from species s, β_0 the intercept, ε_s a species random effect, ε_i an individual random effect (where appropriate), β_1 the main effect of individual tree size S_i, μ_s the random species effect of size, $\boldsymbol{\beta_2}$ a 4 × 1 vector for the main effects of different levels of the factor **L**, $\boldsymbol{\gamma_s}$ a 4 × 1 vector for random effects of factor **L** on species s, and $\boldsymbol{\beta_3}$ a 4 × 1 vector of the interactions between size and factor **L**. **L** is a vector of zeros and ones denoting the liana infestation score of individual i. A vector of four zeros represents a liana-free individual, while vectors with three zeros and a one in position 1, 2, 3 or 4 represent an individual with the corresponding level of infestation. All other models were simpler subsets of Equation [1]. Models were fit using the Laplace approximation of the true likelihood with the lme4 R package (Bates, Mächler, & Bolker, **2014**). All models share the same random effect structure, and model selection was based on the Akaike information criterion (AIC). More details on the estimation of vital rates are given below.

We plotted model residuals against size to evaluate the appropriateness of the linearity assumptions for each model and found no evidence of nonlinearity (see example R-code in Appendix **S2**). We considered a model to be significantly better than a simpler model only when the ΔAIC >10 (excluding equivalent but more complex models; Bolker et al., **2009**). We calculated R^2 values for mixed models in two ways, using the methods of Nakagawa and Schielzeth (**2013**): marginal values, R^2_m, included only fixed effects; conditional values, R^2_c, included both fixed and random effects.

Species-specific liana infestation coefficients ($\boldsymbol{\beta_2} + \boldsymbol{\gamma_s}$) represent the additive effects of lianas on growth, survival and reproduction relative to the baseline rates of liana-free individuals. When these are negative, lianas have an adverse effect. To test whether the effect of lianas on vital rates are related to tree life-history strategies, we analysed correlations between species-specific liana infestation coefficients (every element of $\boldsymbol{\beta_2} + \boldsymbol{\gamma_s}$) and the two axes of life-history variation (slow–fast and H_{max}). Significance levels were Bonferroni-corrected (α levels given in **Results**). For more on the justification for and interpretation of this hierarchical approach, see Appendix **S3**.

2.5 Liana effects on species population growth rates

We estimated population growth rates (λ) as a function of liana infestation (L) for 33 species by constructing IPMs (Easterling, Ellner, & Dixon, **2000**; Ellner & Rees, **2006**). In IPMs, vital rates are continuous functions of size spanning the entire life cycle, which together create projection kernels that quantify the transitions of existing individuals (growth and survival) and the birth of new individuals in (discrete) time. When the distribution (number of individuals) in a population at time t is described by $W(x,t)$ as a function of size x, then the distribution of individuals sized y at time $t + 1$ is given by:

$$W(y, t + 1) = \int_A^Z P(y, x)W(x, t)dx \quad (2)$$

where the limits $[A, Z]$ represent the minimum and maximum sizes of individuals, respectively, and $P(y,x)$ is a projection kernel that describes the transition of individuals of size x at time t that survive and grow to size y at time $t + 1$, and the production by individuals sized x at time t of new individuals sized y at time $t + 1$. The projection kernel $P(y,x)$ is built from two functions.

Function G relates growth and survival from size x to size y in one time step, and function F quantifies the production of new recruits of size y by individuals of size x. The projection kernel P can then be expressed as:

$$P(y, x) = G(y, x, L) + F(y, x, L) \quad (3)$$

where $G(y,x,L)$ is a transition kernel, constructed using fitted models describing the liana-dependent growth and survival of each species, and $F(y,x,L)$ is a reproduction kernel that describes the distribution of new individuals of size y produced by individuals of size x and liana load L.

We combined data on tree and seedling demography in two-stage IPMs, where size is measured by diameter (d) and height (h) at the tree and seedling stages respectively. The two-stage IPMs in turn consisted of four kernel functions that described all size-dependent transitions between seedlings and trees. These included (1) a function describing reproduction $P_{d\to h}(y_h, x_d, L)$, which incorporates liana effects, (2) a function describing the survival and growth of seedlings (<1 cm DBH) $P_h(y_h, x_h)$, (3) a function quantifying the transition between seedlings and trees $P_{h\to d}(y_d, x_h)$ and (4) a function describing survival and growth of trees $P_d(y_d, x_d, L)$, which also incorporates liana effects. Liana infestation among seedlings was ignored, as smaller seedlings never have lianas, and larger seedlings have them only extremely rarely. Table **1** describes the formulation of each of the four kernels. The four functions are then combined in a mega-matrix (**M**) which describes the transition within and between seedlings and trees:

$$M = \begin{pmatrix} P_h(y, x) & P_{d\to h}(y, x, L) \\ P_h \to d(y, x) & P_d(y, x, L) \end{pmatrix} \quad (4)$$

Table 1. Equations for the transition kernels in the mega-matrix **M**, with definitions of the various vital rate functions and parameters. All transitions are from size x at time t to size y at time $t + 1$, where size is measured in height (h) for seedlings less than 10 mm in diameter at breast height, and in diameter at breast height (d) for larger individuals. The four transition kernels (P_h, $P_{h \to d}$, P_d and $P_{d \to h}$) together form an integral projection model. All functions were fit to data

Construction of the mega-matrix M		
Kernel	Formulation	Description
$P_h(y_h, x_h)$	$= \begin{cases} S_h(x_h)N(y_h, \mu = G_h(x_h), \sigma = \sigma_h) & y_h \leq h_{d=10} \\ 0 & y_h > h_{d=10} \end{cases}$	$S_h()$ and $G_h()$ are height-dependent annual survival and height growth (mm/year) functions for seedlings fit to data, $N()$ denotes the normal distribution, σ_h is the standard deviation of individual height growth and $h_{d=10}$ is the height at which seedling attain a DBH of 10 mm (Figure S11)
$P_{h \to d}(y_d, x_h)$	$= \begin{cases} 0 & y_h \leq h_{d=10} \\ S_h(x_h)A'(y_d)N(A(y_d), \mu = G_h(x_h), \sigma = \sigma_h) & y_h > h_{d=10} \end{cases}$	$A()$ is an allometric function that translates DBH to height (Figure S11). $A'(y_d)$ is the derivative of this function, which is required to translate two continuous random variables
$P_d(y_d, x_d, L)$	$= S_d(x_d)N(y_d, \mu = G_d(x_d, L), \sigma = \sigma_d)$	$S_d()$ and $G_d()$ are diameter-dependent survival and growth functions for trees, fit to data. L is the liana load, σ_d is the standard deviation of individual diameter growth
$P_{d \to h}(y_h, x_d, L)$	$= R(x_d, L)C(x_d, L)F(x_d)S_d(x_d)\phi I(y_h)$	$R()$, $C()$ and $F()$ are the diameter-dependent functions denoting the fraction of individuals that are reproductive, the crown fraction-bearing fruits, and seed production respectively. The seed-to-seedling transition probability is given by ϕ and $I()$ denotes the distribution of initial heights for seedlings (Figures S4 and S5)

The dimensions of **M** were set at 500 × 500 (corresponding to 100 seedling height and 400 tree DBH classes) as further increases in matrix dimensions had a negligible influence on λ (changes <0.0001%).

Using the IPMs, we calculated per capita population growth rates for each species at each level of liana infestation. We use $\lambda_0, \lambda_1, \ldots \lambda_4$ to denote the intrinsic rate of increase for the five infestation categories (free, up to 25%, 26%–50%, 51%–75% and 76%–100% infested) respectively. The intrinsic growth rate is the natural log of the per capita population growth rate, where negative and positive values indicate decreasing and increasing populations respectively. We use λ to denote the intrinsic rate of increase to avoid confusion with the Pearson product-moment correlation coefficient, which we denote with r. To determine which demographic rates contributed most to the negative effect of lianas on tree population growth rates, we iteratively replaced model coefficients with zero values, and recalculated λ. Finally, we conducted a correlation analysis of interspecific variation to evaluate whether changes in λ under heavy infestation ($\lambda_4 - \lambda_0$; or the sensitivity to infestation) were related to either adult stature (H_{max}) or position on the slow–fast axis. Significance levels were Bonferroni-corrected (α-levels given in the results).

We parameterized IPMs by combining the vital rate models fit to all datasets (see Equation **1** and Table **1**), where growth, survival, probability of reproduction and fraction of tree crowns-bearing fruits were related to **L** using general linear mixed effect models (GLMMs) for trees >1 cm DBH (Equation **1**). Details on the procedure for each vital rate are given below. To estimate uncertainty in λ due to uncertainty in fitted model parameter estimates, we sampled from the theoretical "posterior" distributions for all vital rates. In essence, we conducted a parametric bootstrap where we sampled model coefficients from multivariate normal distributions defined by the model coefficients and variance–covariance matrices estimated for each vital rate. We provide all functions used to build the IPMs as an unofficial r package, including an example script with mixed model fitting and the bootstrapping procedure (see Appendix **S2** for details).

The population growth rates reported here are a means to scale up and estimate the net results of all lower level influences of lianas on growth, survival and reproduction. They are an artificial construct as in reality tree populations in different infestation classes are not closed populations: trees will continuously transition among liana infestation classes.

2.5.1 Probability of reproduction
We estimated the size-dependent probability of reproduction (R) using a GLMM, where tree reproductive status (sterile or reproductive; datasets 2 and 3) was related (logistically) to tree diameter and level of liana infestation (Equation **1**). Reproductive status was dichotomized for the analyses using only sterile trees (score 0) vs. fertile trees with reproductive structures (score 1–4).

2.5.2 Fraction of crown-bearing fruits
We used a linear mixed effect model to model the relationship between the fraction of the crown-bearing reproductive structures (hereafter "crown reproductive fraction"; C) and tree diameter and the level of liana infestation (Equation **1**; datasets 2 and 3).

2.5.3 Seed production
Mean species-specific seed production per m^2 of reproductive basal area (F) was quantified by dividing seed production by reproductive basal area. Reproductive basal area was calculated for each census year as the sum of individual basal areas (dataset 1) weighted by size-dependent reproductive probability and crown reproductive fraction (datasets 2 and 3) and interpolated linearly between census years to obtain yearly values. Yearly seed production equalled plot area multiplied by the density of seeds arriving in the seed traps (dataset 4). Yearly estimates of seed production were divided by yearly estimates of reproductive basal area and averaged to obtain F. This method of estimating seed production yields estimates of F that closely resemble estimates obtained using more complex methods such as inverse modelling (shown in Visser et al., **2016a**).

2.5.4 Seedling establishment

We calculated species-specific mean yearly seedling establishment probability (ϕ) as the density (per area) of newly recruiting seedlings across all seedling plots divided by the density of seeds arriving at all seed traps (datasets 4 and 5).

2.5.5 Initial height of establishing seedlings

The initial height distributions of newly established seedlings (I; dataset 5) were fit to exponential, log-normal and Weibull probability density functions. The Weibull provided the best fit for 31 out of 33 species. We therefore fit Weibull distributions for every species.

2.5.6 Seedling to tree transition

We estimated the height at which tree seedlings entered the FDP census ($h_{d=10}$; 10 mm DBH) with a linear model that related height with DBH for each species using data on height and DBH from dataset 6.

2.5.7 Growth

We modelled size-dependent growth (G) as height growth for seedlings (mm/year) and basal area growth for trees >1 cm DBH (mm^2/year) using linear mixed effect models (Equation **1**). We calculated growth rates as the difference in size divided by the time in years between censuses (datasets 1, 5 and 6). Tree growth rates were related to **L** as shown in Equation **1**. Due to measurement error (Rüger, Berger, Hubbell, Vieilledent, & Condit, **2011**), a tiny fraction of the growth rates (dataset 1) were unrealistically low or high and likely erroneous. We therefore excluded any values greater than four standard deviations from the overall mean (0.4% of all measurements).

2.5.8 Survival

We estimated the size-dependent yearly probability of survival (S) for both seedlings and larger individuals (>1 cm DBH) using logistic mixed effects models (datasets 1, 5 and 6). Survival rates of larger individuals were related to **L** as shown in Equation **1**.

2.5.9 Minimum and maximum sizes

Minimum sizes (A) in the IPM were set to 0 mm height for seedlings and 10 mm DBH for larger trees. Maximum sizes (Z) were the previously estimated species-specific height at which seedlings have 10 mm DBH for seedlings and 110% (sensu Zuidema, Jongejans, Chien, During, & Schieving, **2010**) of the mean DBH of the six largest individuals of each species in the 50-ha plot (dataset 1).

3 RESULTS

3.1 Liana diversity

The 3,312 trees ≥20 cm DBH in the five 4-ha plots (dataset 3) held a total of 144 liana species and 54% of the crowns were infested in 2005–2006. Co-infestation was common; 43.9% of liana-infested individuals hosted two or more liana species. A maximum of 18 lianas species was found on a single *Luehea seemannii* tree (44 cm DBH). Most liana species were rare, with just 50 species (34.7%) responsible for 90% of infestation records. The five most common liana species were *Coccoloba excelsa*, *Doliocarpus major*, *Doliocarpus olivaceus*, *Maripa panamensis* and *Prionostemma aspera*, which together were responsible for 31% of all infestations.

3.2 Effects of lianas on tree vital rates

Tree growth, survival, reproductive probability and crown reproductive fraction were all strongly negatively affected by high liana loads (Figure **2**). The proportion of trees that were reproductive decreased with increasing liana infestation (Figure **2**a), with the best model including size and main effects of *L* but no *L*-size interaction (ΔAIC = 791.19, Table **S4.3**, R^2_m = .26, R^2_c = .68). The fraction of the tree crown-bearing reproductive structures

increased strongly with tree size, with intercepts decreasing with increasing liana infestation (Figure **2**b). Again, the best model included size and main effects of *L* but no *L*-size interaction (ΔAIC = 25.16, Table **S4.4**, R^2_m = .19, R^2_c = .69).
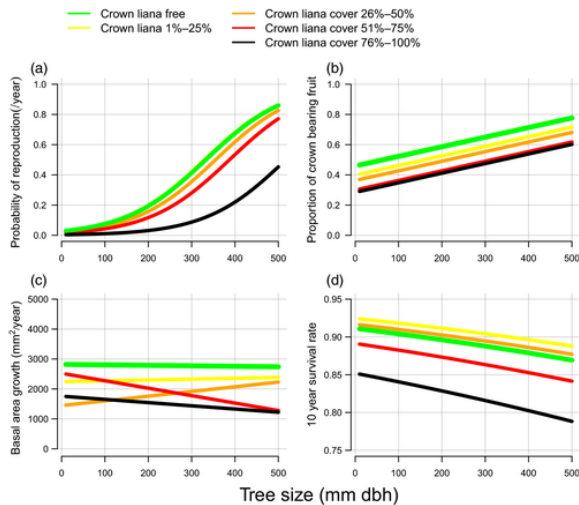

Figure 2 The effects of liana infestation on tropical tree demographic rates as a function of tree size, as estimated by fitted mixed effect models. Estimated effects on the probability of reproduction (a) are based on analyses of 15,140 individuals, effects on the proportion of the crown-bearing fruit (b) on 5,140 individuals, effects on tree growth (c) on 17,770 individuals, and effects on tree survival (d) on 6,547 individual trees

Tree growth was strongly influenced by lianas (Figure **2**c), with the best model including size, main effects of liana load (*L*), and interactions between *L* and size (ΔAIC = 57.0, Table **S4.5**, R^2_m = .03, R^2_c = .43). Tree growth decreased with increasing *L*, with the lowest growth rates when trees were heavily infested (*L* = 4; 75%–100% crown cover). Larger trees were less affected when lianas infested less than 50% (*L* = 1 and 2) of their crowns (see positive slopes of the yellow and orange lines in Figure **1**c).

Tree survival declined noticeably only with *L* values >50% (Figure **2**d), with the best model including size and main effects of *L*, but no *L*-size interaction (ΔAIC = 471.376; Table **S4.6**; R^2_m = .08, R^2_c = .35). Here again, an infestation level of >75% resulted in the most severe decrease in tree survival. Table **S4.7** presents coefficients and standard errors for each model.

3.3 Interspecific variation in the effects of lianas on tree vital rates

We found that tree species differed strongly in how severe infestation (75%–100% of crown infested) affected vital rates, as measured by species-specific liana infestation coefficients (γ_s + β_2). Large adult stature (H_{max}) was associated with increasingly negative effects of severe infestation on the probability of reproduction (Figure **3**a, *r* = −.36, *p* = .0031, Bonferroni-corrected α = 0.00625), crown reproductive fraction (Figure **3**c, *r* = −.32, *p* = .0007) and growth (Figure **3**e, *r* = −.53, *p* = .00001), with a non-significant trend for survival (Figure **3**g, *r* = .11, *p* = .39). Fast-growing species—those with high scores on the slow–fast axis—showed much stronger declines in survival than slower growing species (Figure **3**h, *r* = −.56, *p* < .00001), but no significant differences in growth, reproduction or fecundity (Figure **3**b, d and f; Bonferroni-corrected α = 0.00625). The mixed model vital rate predictions used to parameterize IPMs performed well for all 33 species, reproducing species average rates with an R^2 that ranged over .71–.97 (Figure **S5.3–13**).
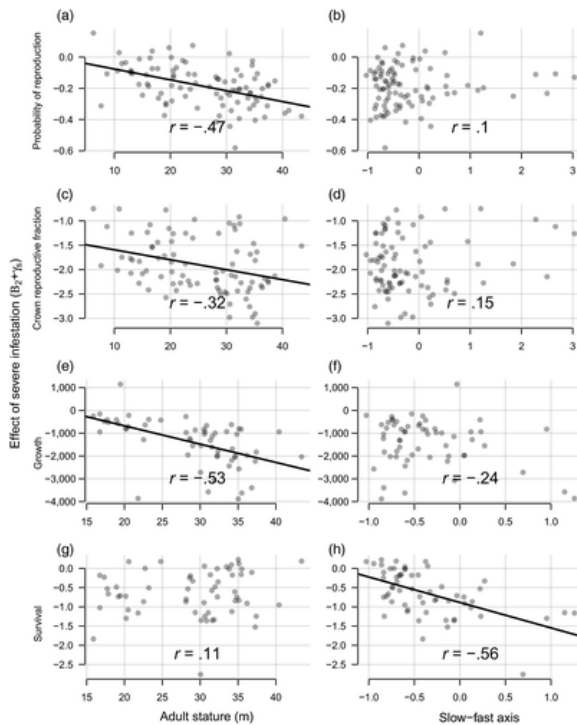
Figure 3 The relationship of interspecific variation in effects of heavy liana infestation to adult stature (a, c, e and g) and to host position on the slow–fast axis (b, d, f and h). Vital rates include reproduction (a, b), fecundity (c, d), growth (e, f) and survival (g, h). The additive species-specific impact of lianas associated with heavy liana infestation, estimated as the species-specific liana load coefficients: $\beta_2 + \gamma_s$, where β_2 represents the fixed effect and γ_s the species-specific random effect (see Equation 1). Black lines indicate a statistically significant relationship (Bonferroni-corrected significance level set at 0.00625) and *r* denotes the Pearson correlation coefficient. Larger values on the slow–fast axis correspond to faster growth and lower survival

3.4 Effects of lianas on tree species population growth rates

Mean population growth rates declined with increasing severity of liana infestation and were significantly lower for heavy liana infestation (L = 3 and 4) compared to liana-free populations (L = 0, Figure 4). The average estimated population growth rates for liana-free populations of the 33 species was −0.4% per year (posterior 95% CI: −2.29, +1.4%). Light to moderately infested populations (liana loads 1 and 2) were projected to decline with −0.37% (CI: −1.60, +1.54) and −0.92% (CI: −3.07, +0.99) per year (Figure 4). The average for populations with liana load 3 (50%–75% of the canopy infested by lianas) was −1.16% annually (CI: −3.2, +0.5%), and with liana load 4 (>75% of the canopy infested) was −2.4% (CI: −4.15, −1.27%; Figure 4). Comparison of models including liana effects on some vital rates and not others revealed that the effects of lianas on tree survival were largely responsible for the reduction in population growth rates (Figure 5).
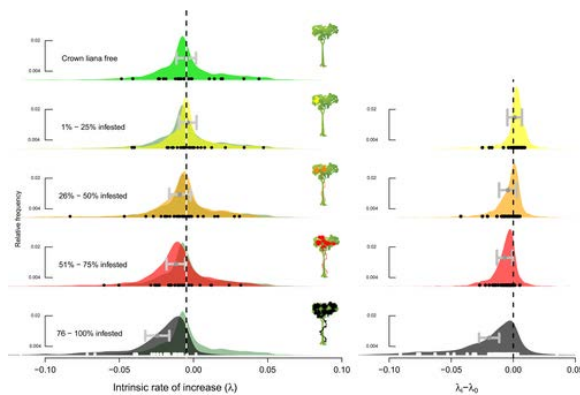
Figure 4 Distributions of projected annual population growth rates for tree populations with different levels of liana infestation (left; $\lambda_{L=0,1,2,3,4}$) and the distributions of the difference between each infested and the liana-free projected population growth rates (right; $\lambda_{L=i} - \lambda_{L=0}$). To aid comparison, the distribution of $\lambda_{L=0}$ is given as a green-shaded background for each of the infested tree populations ($\lambda_{L\neq0}$) on the left. Distributions were generated by sampling from the posterior distributions of all fitted vital rate models and therefore include variation among species as well as uncertainty in the data and models. Mean rates and differences are given by the grey dot, and 95% confidence intervals are given by the grey error bars. The dashed vertical lines give the mean population growth rate of liana-free populations (left) or the point of zero difference (right). Mean population growth rates (left) or mean differences (right) for each species are given by the black dots (white in the bottom row)
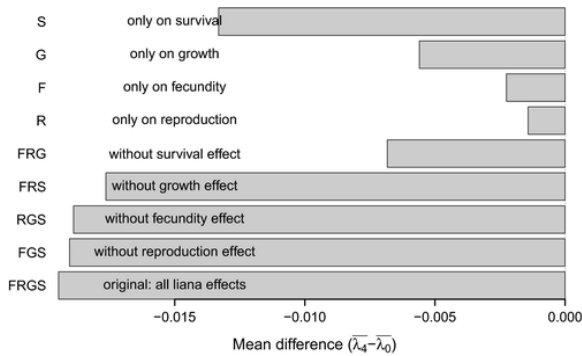

Figure 5 Difference in average population growth rates between severely infested and uninfested tree populations ($\bar{\lambda}_{L=4} - \bar{\lambda}_{L=0}$). The letters indicate the vital rates for which liana effects were included (S = survival, G = growth, F = fraction of crown reproductive and R = probability of reproduction)

The negative effect of liana infestation on population growth rates was related to shade tolerance, but not to adult stature (Figure **6**). Liana-free population growth rates, λ_0, tended to increase with species positions on the slow–fast axis, although this correlation was not significant after Bonferroni correction (Figure **6**d, $r = .38$, $\alpha = 0.0083$). Population growth rates when heavily infested decreased significantly with species position on the slow–fast axis (Figure **6**e, $r = -.616$, $p = .002$). The sensitivity of population growth rate to liana infestation ($\lambda_4 - \lambda_0$) also decreased significantly with species position on the slow–fast axis (Figure **6**f, $r = -.783$, $p < .00001$). That is, shade tolerance correlates with tolerance of liana infestation. Analysis of the other infestation classes confirmed this trend (Figure **S6.14–16**).
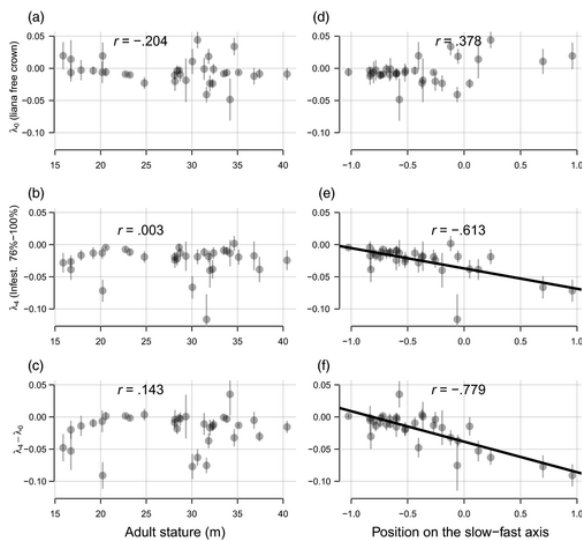

Figure 6 Relationship of tree species' adult stature (a–c) and position on the slow–fast axis (d–f) to projected population growth rates of host trees when liana-free (a, d; $\lambda_{L=0}$) and when heavily infested by lianas (b, e; $\lambda_{L=4}$), and to the difference

between the two (c, f; $\lambda_{L=4} - \lambda_{L=0}$). Larger values on the slow–fast axis correspond to faster growth and lower survival, and species with larger scores on this axis tended to be more sensitive to liana infestation. Solid lines indicate a statistically significant relationship (Bonferroni-corrected significance level set to 0:0083) and *r* is the Pearson correlation coefficient. Vertical lines are standard deviations estimated by sampling from model posterior distributions

4 DISCUSSION

This is the first study to systematically quantify the net effects of liana infestation on population growth rates of host tree species. We found that lianas strongly influenced individual vital rates (Figures **2** and **3**), and when integrating all lower level effects on vital rates, heavy liana infestation severely decreased population growth rates (Figure **4**), particularly for fast-growing tree species (Figure **6**). This strong differential effect of lianas demonstrates that lianas have the potential to alter tree species functional composition.

The finding that liana infestation is more harmful to fast-growing tree species (Figure **6**e,f) appears to be at odds with the general expectations in the literature (Clark & Clark, **1990**; Putz, **1984**; Schnitzer & Carson, **2010**; Schnitzer, Dalling, & Carson, **2000**; van der Heijden & Phillips, **2009**; van der Heijden et al., **2008**). Previous studies proposed that shade-tolerant tree species should be disproportionately negatively affected by lianas because shade-tolerant species have higher levels of liana infestation than light-demanding species (Schnitzer & Bongers, **2002**). Higher levels of infestation have been interpreted as evidence that shade-tolerant species are more vulnerable to becoming infested (Clark & Clark, **1990**; van der Heijden et al., **2008**; but see Ingwell et al., **2010**). Our results suggest an alternative interpretation. Liana infestation greatly decreases survival in fast-growing, light-demanding species (Figure **3**h), such that surviving individuals are disproportionately liana-free (shown in Appendix **S7**). This survivorship bias is much weaker in slow-growing, shade-tolerant species, leaving higher proportions of individuals infested. Static levels of liana infestation integrate initial colonization by lianas and subsequent tolerance of infestation and do not reflect the net impact of lianas on their host demographic rates.

4.1 Potential mechanisms determining liana tolerance and intolerance

When they reach the canopy, most liana species in central Panama form a single layer of leaves on top of their host crowns (Avalos, Mulkey, & Kitajima, **1999**). Liana leaves are placed immediately above host leaves and intercept a large proportion of the light that would otherwise reach the host (Avalos et al., **1999**; Stevens, **1987**). Liana leaves displace host tree leaves on a 1-to-1 mass basis (Kira & Ogawa **1971**). This reduction in light availability and loss of leaf area deals a severe blow to fast-growing, light-demanding and gap specialist trees that tend to have leaves with high light compensation points (Kitajima, **1994**) and shallow crowns with low leaf area indices (leaf area per ground area or LAI; Kitajima, Mulkey, & Wright, **2005**). By contrast, later-successional and more shade-tolerant tree species tend to have lower light compensation points for individual leaves (Kitajima, **1994**) and deep crowns (Kohyama et al., **2003**) and larger leaf area indices (Kitajima et al., **2005**); thus, they are expected to be less affected by the loss of light and leaf area due to liana infestation.

More generally, shade-tolerant tree species are adapted to tolerate stress and low light in many ways beyond leaf and crown traits. Liana infestation may just be a special case that leads to the low-light levels to which shade-tolerant species can easily adjust. Below-ground competition between lianas and trees for water and nutrients may also be important (Dillenburg, Whigham, Teramura, & Forseth, **1993**; Schnitzer et al., **2005**). Tree species with high potential growth rates tend to require more water than slower growing tree species, and lianas are strong competitors for water (Álvarez-Cansino et al., **2015**; Cai, Schnitzer, & Bongers, **2009**). Fast-growing tree species and lianas also require high concentrations of nitrogen, phosphorus and potassium per unit leaf area to maintain photosynthesis in high light (Asner & Martin, **2012**). For these reasons, slow-growing tree

species with conservative nutrient and water use should also be better able to tolerate below-ground competition from lianas than are fast-growing tree species.

Lianas also exert strong mechanical stress and torque on tree limbs (Putz, **1984**). Species with high potential growth rates tend to have low-density wood (Wright et al., **2010**). Wood rupture strength is proportional to the product of wood density and basal area (Larjavaara & Muller-Landau, **2010**). Hence, at similar basal areas, we would expect fast-growing species to be at greater risk of stem breakage or limb loss, factors that increase tree mortality (Paciorek, Condit, Hubbell, & Foster, **2000**). Competition for light, water and nutrients and resistance to breakage might all favour tolerance of liana infestation among slow-growing tree species and sensitivity among fast-growing species.

4.2 Predicting the effects of liana increases on tree communities

Theory and empirical evidence indicate that generalist parasites with different levels of virulence (lethality) on different hosts affect the outcome of competitive interactions among their host species (Borer, Hosseini, Seabloom, & Dobson, **2007**; Holt & Dobson, **2007**; Holt & Pickering, **1985**; Packer & Clay, **2000**). In such systems, host species that can better tolerate the parasite gain an advantage (Holt, Grover, & Tilman, **1994**). We show that liana infestation has clear negative impacts on tree population dynamics (Figure **4**) and affects some species more severely than others (Figure **6**). In addition, liana prevalence is high, in particular, 73.6% of BCI trees (≥20 cm DBH) are infested by lianas (with *L* ≥3 for 39.2%; data from Ingwell et al., **2010**). Hence, the basic requirements for liana-mediated (co-) regulation of host abundance are present. The percentage of BCI tree crowns infested by lianas increased from 32% in 1968 to 73.6% in 2007 (Ingwell et al., **2010**; Schnitzer et al., **2012**). Similar, dramatic increases in the importance of lianas have been documented in many Neotropical forests (reviewed by Schnitzer, **2015**, Wright, Sun, et al., **2015**). The increasing prevalence of lianas presents the possibility that differential effects on host fitness might alter tree species composition.

A complete quantification of the effects of lianas on tree species relative performance requires integrating the differential effects of liana infestation on host demography that are quantified here (Figures **2**-**6**) with a mechanistic understanding of the determinants of variation in liana infestation prevalence and its variation across tree species (Figure **1**). Variation in liana prevalence among tree species (e.g. Clark & Clark, **1990**; van der Heijden et al., **2008**) reflects the combined influences of liana colonization, liana loss and host tolerance (Figure **1**). Furthermore, lianas are dependent on their hosts for success (see e.g. Balcázar-Vargas, Salguero-Gómez, & Zuidema, **2015**), and variation in liana prevalence may feedback on the relative success of different liana strategies varying in virulence (Ichihashi & Tateno, **2011**). Hence, there exists a complex interplay where lianas affect their hosts who in turn affect the lianas (Figure **1**).

Previous work has assumed that variation in the proportion of individuals infested with lianas reflects variation in the ability to avoid colonization by lianas (Clark & Clark, **1990**; Putz, **1984**; van der Heijden et al., **2008**). The host traits associated with low proportions of infested individuals include rapid growth, monopodial stems, few branches and large leaves (Putz, **1984**). These same traits characterize many gap-dependent tree species. We observed that gap-dependent species die rapidly when infested by lianas (Figure **3**h). All else being equal, different levels of tolerance to lianas will cause differences in the proportion of trees infested (as we show in Appendix **S7**). Thus, survivorship bias—where the observable sample is biased towards those that survived (e.g. Zens & Peart, **2003**)—compromises inferences of colonization sensitivity from observations of proportions of individuals infested. Future research should obtain unbiased estimates of interspecific variation in the ability to evade liana colonization and shed lianas when infested. Interspecific variation in tolerance of liana infestation (Figures **3** and **6**) could be balanced at least in part by variation in ability to avoid initial colonization because species that are less tolerant of infestation will experience stronger selection to avoid colonization. This question could be addressed by studies that quantify species differences in liana infestation rates while controlling for

both survivorship bias caused by different rates of liana induced mortality and spatial location relative to areas of high liana density such as gaps (Ledo & Schnitzer, **2014**; Schnitzer et al., **2012**).

Lianas also alter tree environments. One possibility is that the increasing abundance of lianas will increase tree mortality rates (Figures **2**d and **3**h) and therefore the rate of gap creation. At BCI, 80% of gap-making trees carry lianas (Ingwell et al., **2010**), and these trees frequently pull down neighbouring trees connected by shared lianas (on average 2.6 trees >10 cm; Putz, **1984**). Greater liana abundance may therefore result in increased gap formation rates and increased gap sizes. More gaps, in turn, might favour both lianas and fast-growing tree species (Ledo & Schnitzer, **2014**; Schnitzer & Carson, **2010**; Schnitzer et al., **2000**). Trees growing near liana-infested trees are also far more likely to become infested with lianas (van der Heijden et al., **2008**). Hence, liana-infested individuals of slow-growing tree species that survive despite heavy liana loads may facilitate the infestation of fast-growing neighbours. Thus, it is unclear whether increasing liana abundance will favour slow-growing species that tolerate liana infestation (Figure **6**e,f) or fast-growing species that benefit from intensified gap creation.

5 CONCLUSIONS

We confirm that lianas reduce growth, survival and reproductive rates of their host trees (Figure **2**), and provide the first quantification of total liana effects on host population growth rates (Figure **4**). We show that the negative effects of lianas on host population growth rates are largely caused by reductions in host survival (Figure **5**), and that tree species differ widely and predictably in their ability to survive liana infestation. In particular, light-demanding tree species characterized by rapid growth and low survival rates are most severely impacted by lianas when infested (Figures **3**h and **6**e,f).

The observed interspecific variation in survival when infested would lead to differences in observed proportions of trees infested even if all tree species were infested at the same rate. Thus, our finding casts doubt on previous inferences of species-specific abilities to avoid liana colonization based on static observations of species-specific proportions of liana-infested individuals. Future research should use repeated censuses to evaluate species-specific abilities to avoid initial colonization and to shed lianas after infestation. Lianas have additional effects on gap dynamics in forests that might indirectly influence tree species composition and also require quantification. The net effect on host tree species composition of documented increases in liana abundance will require combining the impacts of lianas on host tree population growth rates documented here with species-specific information on rates of colonization and of loss of lianas and additional understanding of the indirect effects of lianas via changes in forest structure and dynamics.

AUTHORS' CONTRIBUTIONS

M.D.V., S.A.S., S.J.W. and H.C.M. designed the study; M.D.V., H.C.M., E.J. and S.J.W. analysed the data; M.D.V. did the modelling; M.D.V., S.A.S. and S.J.W. wrote the first draft; M.D.V., S.A.S., S.J.W., H.C.M., E.J., H.K., L.S.C. and S.P.H. contributed substantial revisions.

DATA ACCESSIBILITY

Dataset 1: **https://doi.org/10.5479/data.bci.20130603** (Condit et al., **2012**); Dataset 2: **https://doi.org/10.5479/si.data.201511251100** (Wright, Bruijning, Brassfield, Cerezo, & Visser, **2015**); Dataset 3: **https://doi.org/10.5479/data_stri/10088/32270** (Wright, **2015**); Dataset 4: **https://doi.org/10.5479/si.data.201511251137** (Wright & Calderon, **2015**); Dataset 5: **https://doi.org/10.5479/si.data.201511251134** (Wright, Calderon, & Hernandez, **2015**); Dataset 6: **https://doi.org/10.5061/dryad.fm654** (Visser et al., **2016a**, **2016b**).

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