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A Host–parasite Model Explains Variation in Liana Infestation Among Co-occurring Tree Species

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Abstract

1. Lianas are structural parasites of trees that reduce the growth, survival and reproduction of their hosts. Given that co-occurring tree species differ strongly in the proportion of individuals that are infested by lianas (liana prevalence), lianas could differentially impact tree species and thereby influence tree community composition. Surprisingly, little is known about what governs variation in liana prevalence.

2. Here, we apply an approach inspired by disease ecology to investigate the dynamics of liana prevalence over 11 years on Barro Colorado Island, Panama. We followed the fate of 1,938 individual trees from 21 tree species, recording deaths and change in liana infestation status. With these data, we fit species-specific Markov chain models to estimate four rates: colonization by lianas (analogous to disease transmission), shedding or loss of lianas (analogous to host recovery), baseline mortality of uninfested trees (baseline mortality) and additional mortality of infested trees (parasite lethality).

3. Models explained 58% of variation in liana prevalence among tree species, and revealed that host shedding of lianas and parasite lethality were the most important contributors to interspecific variation in liana prevalence at our site. These rates were also strongly related to shade tolerance, with light-demanding species having greater rates of shedding and lethality, and lower rates of liana prevalence. An indirect path analysis with a structural equation model revealed that both greater rates of liana shedding and liana-induced lethality contribute to the observed lower rates of liana prevalence for light-demanding tree species.

4. *Synthesis*. Our approach revealed that the prevalence of liana infestation among tree species is driven via indirect pathways operating on the rates of shedding and lethality, which relate to the ability (or inability) of trees to shed and/or tolerate lianas. Shade-tolerant trees have greater proportions of trees infested by lianas because they are both less able to shed lianas and more able to tolerate infestation.

1 INTRODUCTION

Lianas—woody climbers—are globally widespread, highly diverse, and play important roles in forest ecosystems (Putz & Mooney, 1991; Schnitzer, Bongers, Burnham, & Putz, 2015). Lianas can be considered structural macroparasites of trees (Stevens, 1987; Stewart & Schnitzer, 2017). They take advantage of tree stems and branches to grow into the canopy where they typically deploy their foliage above their hosts, thus gaining access to light at the expense of their hosts (Avalos, Mulkey, & Kitajima, 1999; Putz, 1984a), while simultaneously competing with hosts for below-ground resources (e.g., Dillenburg, Whigham, Teramura, & Forseth, 1993). As a consequence, liana infestation generally has strong negative effects on tree growth, survival, and reproduction (Clark & Clark, 1990; Ingwell, Wright, Becklund, Hubbell, & Schnitzer, 2010; Schnitzer & Bongers, 2002; Wright, Sun, Pickering, Fletcher, & Chen, 2015). Lianas are also increasing in abundance in many Neotropical forests (reviewed in Schnitzer, 2015; Wright et al., 2015).

A key question is how lianas influence the relative competitive ability—and ultimately the relative abundances—of tree species. In theory, host species that are less impacted by a shared parasite gain an advantage in competition (Holt, Grover, & Tilman, 1994). The net effects of lianas on a given tree species depend on how sensitive each host species is to infestation (liana tolerance) and on the proportion of its population infested (liana prevalence; see Muller-Landau & Pacala, 2018; Visser et al., 2018). A recent study has shown that tree species differ strongly in their tolerance of liana infestation, with especially fast-growing and light-demanding species being least tolerant of liana infestation (Visser et al., 2018). Sympatric tree species also vary considerably in the proportion of individuals infested with lianas, with empirical evidence suggesting that light-demanding species display the lowest levels of liana prevalence (Clark & Clark, 1990; van der Heijden et al., 2008).

Here, we ask whether the negative effect of lianas on host populations is greater for light-demanding or for shade-tolerant species. A key issue is the interpretation of the low liana prevalence in light-demanding species. Are fewer individuals of light-demanding species infested because these species are able to avoid or shed infestation (as hypothesized by Clark & Clark, 1990; Putz, 1984a, 1984b; Schnitzer, Dalling, & Carson, 2000)? Or are lianas less prevalent among light-demanding species simply due to survivor bias, with infested individuals dying rapidly and uninfested individuals surviving, leading to a low proportion of infested live individuals (as hypothesized by Visser et al., 2018)? These two possibilities lead to opposite predictions about the relative impact of liana infestation for light-demanding versus shade-tolerant host species. To distinguish between these two possibilities, the cause of interspecific variation in liana prevalence must be determined (Muller-Landau & Pacala, 2018; Visser et al., 2018).

Many studies assume that variation in liana prevalence among tree species reflects variation in colonization and loss rates (e.g., Clark & Clark, 1990; van der Heijden et al., 2008), which in turn are attributed to varying tree defences against lianas. Hypothesized tree defences include large leaves, flexible trunks, fast monopodial growth, and ant symbionts (Hegarty, 1989; Putz, 1980, 1984a, 1984b), which are all associated with fast-growing and light-demanding species. However, liana prevalence will depend not only on colonization (transmission) and loss (shedding) rates but also on baseline host tree mortality and the effects of lianas on host mortality (lethality), just as for any other parasite or pathogen (Anderson & May, 1982). Variation among tree species in liana prevalence may reflect interspecific variation in any and all of these rates.

Variation in liana prevalence among tree species could be explained in large part by the demography of the host trees (Muller-Landau & Pacala, 2018). First, tree species with shorter life spans have less time to become infested and hence should have a lower proportion of infested individuals. Second, species that experience higher mortality when infested should also have lower proportions infested, because the infested individuals exit the population faster. Both these mechanism are plausible: it is well known that baseline mortality varies extensively among tree species (Condit et al., 2006), and the effects of lianas on host mortality differs greatly among species (Visser et al., 2018). Yet, the idea that host demography may shape observed interspecific variation in liana infestation has received almost no attention in the literature (Visser et al., 2018). It is not known how variation in liana infestation among host tree species relates to variation in colonization versus shedding versus host demography. Disentangling these rates requires estimation of colonization and loss rates from dynamic data on changes in liana infestation, something no previous study has done.

Here, we apply models from disease ecology to explain the proportion of trees infested by lianas in 21 tropical tree species on Barro Colorado Island, Panama. We estimate rates of liana-free mortality, liana-infested mortality, liana colonization, and liana loss for each species from field data. We then use a host–parasite model to predict liana prevalence (the proportion of individuals infested) for each tree species and evaluate the accuracy of these predictions. We test alternative hypotheses that interspecific variation in liana prevalence is predominantly driven by interspecific variation in colonization and shedding (e.g., Putz, 1980; van der Heijden et al., 2008) or in host demography, specifically baseline host tree mortality and liana-induced lethality (after Muller-Landau & Pacala, 2018; Visser et al., 2018). We quantify the relative contributions of interspecific variation in liana colonization rates, liana shedding rates, and tree demography to interspecific variation in liana infestation. Finally, we test whether any of these rates, and their integration into liana prevalence, relate to measures of shade tolerance across tree species.

2 MATERIALS AND METHODS

2.1 Study site

Barro Colorado Island (9°9′N, 79°51′W), Panama hosts a moist tropical forest. Temperature averages 27°C, and annual rainfall averages 2,650 mm (since 1929), with a dry season between January and April (Leigh, 1999). Liana infestation data are from the 50-ha Forest Dynamics Plot on the centre of the island, and four 4-ha plots.

2.2 Tree and liana data

We assessed the presence of lianas in tree crowns for 1,781 trees ≥20 cm DBH in the 50-ha plot in 1996 and 2007 (Ingwell et al., 2010; Wright et al., 2005) and for all 1,537 trees ≥20 cm DBH in four 4-ha plots located near the 50-ha plot in 2005 and 2015. For each tree, we evaluated crown liana infestation status from the ground using binoculars (details on field methodology given in Ingwell et al., 2010; Visser et al., 2018). We classified each tree as liana-free (F) or liana-infested (I) in the initial census, and as F, I, or dead (D) in the final census. For each species, we then constructed a matrix giving the number of trees observed for each combination of the F, I, and D categories in the two censuses. This matrix, $\boldsymbol{N}_{0\to t}$, has elements n_{ij} denoting the number of individuals initially in state j at time 0, and in state i at time t (years), with states ordered as F, I, and D in the columns and rows. This matrix was the basis for our subsequent model fits. For each species, we also calculated observed liana prevalence (P), defined as the observed proportion of individuals infested in the initial census, as a basis for comparison against model predictions.

2.3 Estimating liana colonization rates, liana loss rates, and tree mortality rates

We used transition matrices to estimate probabilities per time step (defined below) of mortality in liana-free trees (M; hereafter mortality), additional mortality in liana-infested trees (L; lethality, constrained to be ≥0), liana colonization of liana-free trees (C; colonization), and loss of lianas from liana-infested trees (R; shedding, akin to “recovery” in epidemiology). These parameters define the transition probabilities per time step. For example, the probability of transitioning from liana-free to liana-infested is the product of the survival probability of a liana-free individual and liana colonization, C(1 − M) (Figure 1A). The full transition matrix for state changes in a single time step, ***A***, is then defined as

$$A = \begin{pmatrix} (1-C)(1-M) & R(1-(M+L)) & 0 \\ C(1-M) & (1-R)(1-(M+L)) & 0 \\ M & M+L & 1 \end{pmatrix} (1)$$

with states ordered as F, I, and D in columns for time 0 and rows for time *t*. The zeros and one in the final column indicate that death is an absorbing state. Recruitment of new trees to the population is not considered. The estimated transition matrix for 2 time steps is **A*****A** (using matrix multiplication). That is, the probability that an individual that is liana-free in time 0 is dead in time 2 is the sum of the probability it takes paths F0-F1-D2, F0-I1-D2, and F0-D1-D2 (Figure 1B). More generally, the estimated transition matrix A(t) for a total of *t* time steps is defined by A(t) = $\mathbf{A}^t$.

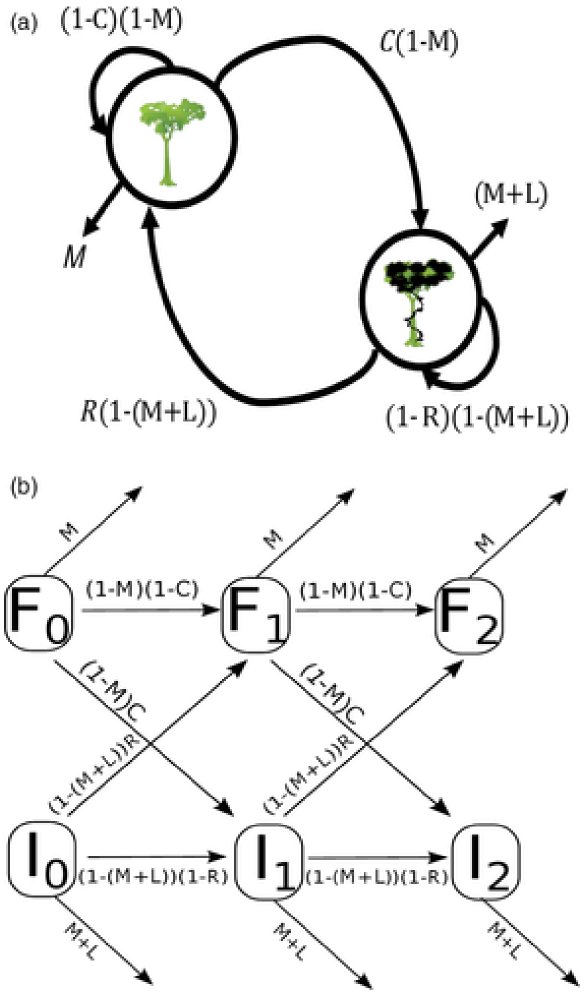

Figure 1 (a) Diagram of the Markov transition model used to explain liana prevalence (the proportion of trees infested with lianas). Each tree population is divided into uninfested individuals (left) and liana-infested individuals (right). Trees can leave the population through mortality: uninfested individuals die with probability M per time step, and infested individuals die with probability M + L. Uninfested individuals are colonized with probability C, and thus transition to liana-infested in

one time step if they survive and are colonized (C(1 − M)). Liana-infested individuals shed their lianas (i.e., recover from infestation) with probability R, and thus transition to liana-free in one time step if they survive and lose their lianas (R(1 − M − L). (B) To estimate these rates from data for multiyear intervals, we need to account for multiple transitions between the liana-free (F) and the liana-infested (I) state. The total transition probability from one state at time 0 to another state at time 2 is obtained by summing over different possible paths, with the rate of any given path being the product of the rates along the path. For example, the probability of a tree that was liana-free at time zero (in F0) being liana-infested at time 2 (in I2) is (C*(1 − M)*(1 − R)*(1 − M − L) + (1 − C)*(1 − M)*C*(1 − M). Failure to account for multiple transitions will yield biased estimates of rates (Figure S1) [Colour figure can be viewed at wileyonlinelibrary.com]

The choice of time step determines the potential number of transitions that occur in a given time. The time interval between our censuses (10–11 years) is long enough for individual trees to make multiple transitions among states (Figure 1B), and failure to account for this biases estimates (Figure **S1**). We tested a variety of time steps, and found that parameter estimates converged as the duration of the time step decreased, with little change for time steps smaller than 1–2 years (Figure **S1**). Thus, we chose to use annual time steps, with 10 or 11 time steps between the two census points depending on the plot.

We restricted our analyses to species for which we had data for at least 49 individuals in the combined datasets, because preliminary analyses showed this to be the minimum sample size providing credible estimates for all transition probabilities (defined conservatively as having confidence intervals less than the full range of possible values from 0 to 1; that is, there are sufficient data to at least somewhat reduce the range of possible values). For each species, we obtained maximum likelihood estimates of all rates (C, R, M, L) by searching for the parameter combinations that maximized the multinomial likelihood of the observed combinations of initial and final states (**N**) given the expected transition probabilities ($A(t) = \mathbf{A}^t$) under the parameter values. The parameter space was searched using generalized simulated annealing (Xiang, Gubian, Suomela, & Hoeng, **2013**). We estimated standard errors for each model parameter through numerical approximation of the second partial derivative matrix of the log-likelihood function at the maximum likelihood estimate (Bolker, **2008**). Our data and the R-script used to fit the models are given in the supplemental material (Text **S1**, Table **S1**).

2.4 Predicting the proportion of trees infested with lianas

We calculated the equilibrium liana prevalence (proportion infested; $\widetilde{\mathbf{P}}$) under the Markov model (**A**) for each species given its estimated colonization, shedding, mortality and lethality. We calculated $\widetilde{\mathbf{P}}$ as the asymptotic stable state distribution (i.e., the dominant right eigenvector; Caswell, **2001**) using the first two rows and columns of **A**. Model predictions ($\widetilde{\mathbf{P}}$) should be close to observed P if the population is close to a stable state and if new recruits (into the population of trees ≥20 cm DBH) have similar prevalence as those already in the population (the second assumption is required because our model includes no recruitment). Model performance was evaluated by comparing observed (in the initial census) with predicted proportions of liana-infested individuals across species (P with $\widetilde{\mathbf{P}}$). We quantified performance using (a) the coefficient of determination (r^2), a measure of variance explained; (b) the root mean squared error (RMSE), a measure of the typical deviation between predicted and observed; (c) the difference between the predicted and observed means (Bias), a measure of systematic error; and (d) the difference between predicted and observed standard deviations, a measure of ability to capture interspecific variation (Δσ). We also evaluated interspecific Pearson correlations between P and each of the four rates.

2.5 Investigating the importance of different factors for interspecific variation in liana prevalence

We investigated the relative importance of interspecific variation in colonization, shedding, and lethality for explaining variation in $\widetilde{\mathbf{P}}$ among species. To do this, we compared predictions under models in which different combinations of parameters were set either to species-specific or to species-averaged values. Species-averaged values were arithmetic means over all species. We calculated the above metrics of model fit (r^2, RMSE, Bias, $\Delta\sigma$) for all combinations of species-specific and species-averaged rates, but are especially interested in the following combinations:

1. Full model, including species-specific rates of all parameters (M_s, L_s, R_s, C_s);
2. Tree demography only model—species-specific mortality and lethality rates and species-averaged colonization and shedding (M_s, L_s, $\bar{\mathbf{C}}$, $\bar{\mathbf{R}}$);
3. Colonization and shedding only model—species-specific colonization and shedding rates and species-averaged mortality and lethality rates ($\bar{\mathbf{M}}$, $\bar{\mathbf{L}}$, C_s, R_s);
4. Species-specific values of one parameter and species-averaged values of the other three;
5. Species-specific values of three parameters and species-averaged values of the final parameter.

We also numerically calculated the sensitivity of $\widetilde{\mathbf{P}}$ to small changes (1%) in each underlying rate. The contribution of each rate to interspecific variation in equilibrium liana prevalence should be proportional to the product of this sensitivity and the observed interspecific variance of the rate if the model appropriately captures interspecific variation in prevalence. It is important to note that our model includes no recruitment, and hence the importance of the tree demography parameters may change in a model with recruitment.

2.6 Relating shade tolerance and liana infestation

We evaluated how interspecific variation in colonization, shedding, liana-free mortality, lethality, and overall prevalence were related to measures of shade tolerance. As shade tolerance is not directly observable, previous studies have used various proxies including growth and mortality rates of juvenile and larger trees or wood density (van der Heijden et al., 2008; Visser et al., 2018; Wright et al., 2010). Here, we used two separate approaches to combine all these measures into metrics of shade tolerance. The first was to test for bivariate correlations of a shade intolerance index with R, C, L, or P (we excluded M from this analysis, because the shade tolerance index is derived in part from mortality). The shade intolerance index was defined as the first factor score of a principal components analysis including wood density (data from Wright et al., 2010), mortality and mean relative growth rates of saplings (1–4 cm DBH) and larger trees (>10 cm DBH; data from Condit et al., 2006). The first PCA axis explained 60% of the variation (eigenvalue 2.8 among 21 species), with greater values indicating increasing light requirements (as in Visser et al., 2018). Significance levels were Bonferroni corrected.

The second approach was a multivariate latent variable analysis using structural equation models (SEMs). Structural equation models are useful for modelling unobservable constructs such as shade tolerance, for representing hypotheses of casual relationships, and for quantifying the relative strengths of direct and indirect effects in systems where multiple processes operate (Grace, Anderson, Olff, & Scheiner, 2010). Here, we constructed multiple SEMs to: (a) estimate a latent construct resembling “shade (in)tolerance,” using multiple imperfect indicators, (b) test for relationships between C, R, M, and L and the latent shade tolerance variable, and (c) quantify the relative influences of indirect effects of host shade tolerance on liana prevalence operating via the pathways of C, R, M, and L. In each SEM, we represented the hypothesized causal direct and indirect relationship between observed values, shade intolerance, and its indicators. Here, paths were constructed as follows: wood density, mortality and mean relative growth rates of saplings and trees informed a latent variable (hereafter latent SI), which was related to C, R, M, and L, which then predicted P. Covariance between latent SI and the P was also estimated. The full model is presented in Figure S2, all other evaluated models were simpler subsets of the full model. We included M here as SEMs generally do not require the error structures to be independent of one another (Fox, 2006). We evaluated 15 different models, each including different combinations of wood density, relative growth rates, and mortality to inform the latent SI variable. The fit of each SEM was evaluated based on χ^2 scores and the goodness-of-fit index (GFI; West, Taylor, & Wu, 2012). To assess robustness of the results when different variables inform the latent SI, we evaluated agreement among all models with respect to our three SEM objectives (above). We conducted a Monte Carlo simulation for each fitted SEM to evaluate power and bias and to determine reliability of predictions at our sample size (following Muthén & Muthén, 2002; code given in Text S2). SEMs were fit with the *lavaan* package (Rosseel, 2012).

3 RESULTS

A total of 21 species met our minimum sample size criteria ($N \geq 49$). Among-species means (ranges) of estimated annual rates were 0.040 (0.01–0.12) for colonization (C), 0.031 (0.003–0.21) for shedding (R), 0.016 (0.003–0.055) for tree mortality (M), and 0.021 (0.001–0.07) for lethality (L; Table S2). The observed liana prevalence (P, proportion of individuals infested) at the initial census ranged from 0.06 to 0.92 among these 21 species. Liana prevalence was negatively related to shedding and lethality, weakly positively related to colonization, and unrelated to tree mortality (Figure 2). The rate parameters were not significantly correlated with each other (Figure S3). The sample sizes for different states and plots for all 21 species are given in Tables S3 and S4.

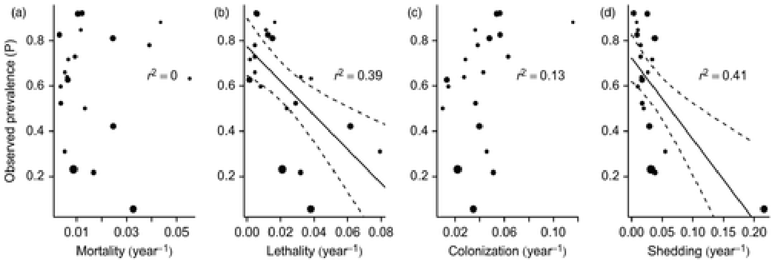

Figure 2 Observed variation among 21 co-occurring tropical tree species in liana prevalence (the proportion of individuals infested with lianas) is unrelated to interspecific variation in baseline tree mortality (a), negatively related to lethality—the additional mortality when infested (b), unrelated to the rate of colonization by lianas (c), and negatively related to the rate at which lianas are lost (d). The size of each circle is proportional to the species sample size. Significant linear relationships are indicated by solid lines (showing ordinary linear regressions), with confidence intervals (95%) given by the dashed lines. The negative relationship between shedding and prevalence (d) remained significant ($p = 0.023$) after removal of the rightmost outlier (*Cecropia insignis*), with r^2 reduced to 0.36. The Bonferroni corrected significance level was set to 0.05/4 = 0.0125

The full model, incorporating all four rates, explained 58% of interspecific variation in P, had an RMSE of 0.16 (Table 1, Figure 3A), and tended to underestimate the prevalence of liana infestation by 0.08 (see "Bias" in Table 1). It captured the magnitude of interspecific variation in P well ($\Delta\sigma = 0.01$), as can be seen by comparing the distributions of the observed and predicted P values (see inset in Figure 3A). Models that included or omitted species-specific variation in particular rates varied greatly in explanatory power (Table 1, Figure 3b,c). Models incorporating species-specific shedding and colonization while omitting interspecific variation in host demography did better than those incorporating species-specific demography and omitting interspecific variation in shedding and colonization (compare Figure 3b,c). The single most influential rate was the rate at which trees shed their lianas, as evidenced by the performance of models that included or omitted only this parameter (shedding rate R, Table 1). The second most influential parameter influencing host tree abundance was lethality (L), the liana-associated additional mortality rate. The rate of colonization was the third most influential parameter; however, models incorporating species-specific shedding and colonization actually did worse than those including only species-specific shedding (Table 1). The least influential parameter was the mortality of uninfested individuals. Overall, variation in expected liana prevalence in this model among our focal species appears to be driven primarily by shedding and lethality.

Table 1. Summary statistics for alternative models for interspecific variation in liana prevalence (the proportion of individuals infested with lianas). Models differed in whether particular rates took species-averaged or species-specific values (e.g., C for species-averaged or C_s for species-specific colonization rates). Statistics are based on comparing observed (in the initial census) with predicted liana prevalence across species. Models are compared in their coefficient of determination (r^2), root mean squared error (RMSE), difference between the predicted mean and observed mean prevalence (bias), and difference between predicted standard deviation and observed standard deviation ($\Delta\sigma$). The predicted range of prevalence (range) is also shown, as is the number of species-specific parameters (N). The observed mean prevalence was 0.61, the observed standard deviation was 0.25, and the observed range was 0.06–0.92. Table S5 presents the predicted species-specific estimates of prevalence for each model

Scenario	r^2	**RMSE**	**Bias**	**Δσ**	**Range**	***N***
Full model (M_S, L_S, R_S, C_S)	0.58	0.16	0.08	0.01	[0.13–0.92]	4
All except mortality ($\bar{\mathbf{M}}$, L_S, R_S, C_S)	0.58	0.16	0.08	0.01	[0.13–0.94]	3
All except colonization (M_S, L_S, R_S, $\bar{\mathbf{C}}$)	0.58	0.15	0.02	0.06	[0.14–0.92]	3
Shedding and lethality ($\bar{\mathbf{M}}$, L_s, R_S, $\bar{\mathbf{C}}$)	0.58	0.15	0.02	0.06	[0.14–0.92]	2
Only shedding ($\bar{\mathbf{M}}$, $\bar{\mathbf{L}}$, R_S, $\bar{\mathbf{C}}$)	0.54	0.17	0.03	0.09	[0.15–0.87]	1
Shedding and mortality (M_S, $\bar{\mathbf{L}}$, R_s, $\bar{\mathbf{C}}$)	0.54	0.17	0.03	0.09	[0.15–0.87]	2
Shedding and colonization ($\bar{\mathbf{M}}$, $\bar{\mathbf{L}}$, R_S, C_S)	0.47	0.18	0.09	0.03	[0.13–0.92]	2
All except lethality (M_S, $\bar{\mathbf{L}}$, R_S, C_S)	0.47	0.18	0.09	0.03	[0.13–0.92]	3
Only liana lethality ($\bar{\mathbf{M}}$, L_s, $\bar{\mathbf{R}}$, $\bar{\mathbf{C}}$)	0.41	0.19	0.11	0.18	[0.33–0.56]	1
Mortality and lethality (M_s, L_s, $\bar{\mathbf{R}}$, $\bar{\mathbf{C}}$)	0.41	0.19	0.11	0.18	[0.33–0.56]	2
Colonization and lethality ($\bar{\mathbf{M}}$, L_S, $\bar{\mathbf{R}}$, C_s)	0.28	0.22	0.15	0.08	[0.16–0.77]	2
All except shedding (M_S, L_S, $\bar{\mathbf{R}}$, C_S)	0.28	0.22	0.15	0.08	[0.16–0.77]	3
Colonization and mortality (M_S, $\bar{\mathbf{L}}$, $\bar{\mathbf{R}}$, C_s)	0.10	0.24	0.15	0.09	[0.17–0.77]	2
Only colonization ($\bar{\mathbf{M}}$, $\bar{\mathbf{L}}$, $\bar{\mathbf{R}}$, C_s)	0.10	0.24	0.15	0.09	[0.17–0.77]	1
Only mortality (M_S, $\bar{\mathbf{L}}$, $\bar{\mathbf{R}}$, $\bar{\mathbf{C}}$)	0.00	0.25	0.12	0.25	[0.49–0.5]	1

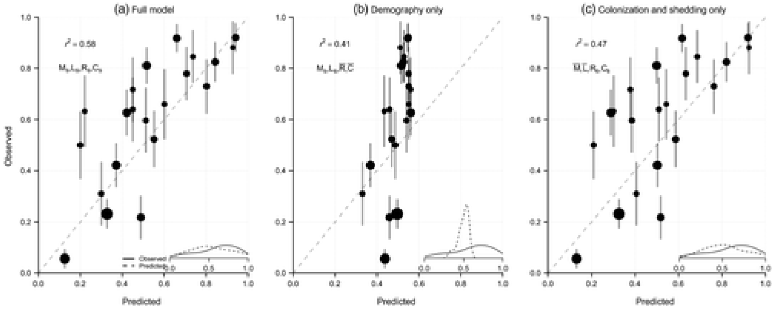

Figure 3 The full model including species-specific rates of baseline mortality (M), lethality (L), shedding a infestation (R), and colonization by lianas (C) did well at predicting observed interspecific variation in liana prevalence among 21 co-occurring tropical tree species (a). In contrast, a model incorporating interspecific variation only in mortality and lethality did very poorly (b), while a model incorporating interspecific variation only in shedding and colonization did fairly well (c). Point size reflects sample sizes for individual species; vertical grey lines represent 95% confidence intervals of observed proportions. The dashed grey line represents the 1:1 line. The inset figures display the distributions of the observed (solid) and predicted (dashed) values of liana prevalence

In our simple model, liana prevalence is most sensitive to the rates of colonization and shedding, and somewhat sensitive to lethality, with background tree mortality having no influence (Figures S4 and S5). At the same time, mortality and lethality varied considerably more among tree species than did colonization and shedding (Figure S4b). The product of the sensitivity of liana prevalence to each rate and interspecific variation in the rate predicted the relative importance of the rate in explaining interspecific variation in observed P, as expected if the model captures this variation well (Figure S4c,d).

Host tree shade intolerance was negatively related to liana prevalence, positively with shedding and lethality, and unrelated to colonization (Figure 4). Liana prevalence was strongly related to shade intolerance, with light-demanding species showing lower prevalence (Figure 4a, $r^2 = 0.49$, $p = 0.0003$). Shade intolerance was also significantly positively related to shedding rates (Figure 4b, $r^2 = 0.37$, $p = 0.0034$) and lethality rates (Figure 4c, $r^2 = 0.30$, $p = 0.01$), with more shade-tolerant species showing lower shedding and lethality. Colonization was unrelated to the shade intolerance index (Figure 4d, $r^2 = 0.002$, $p = 0.83$).

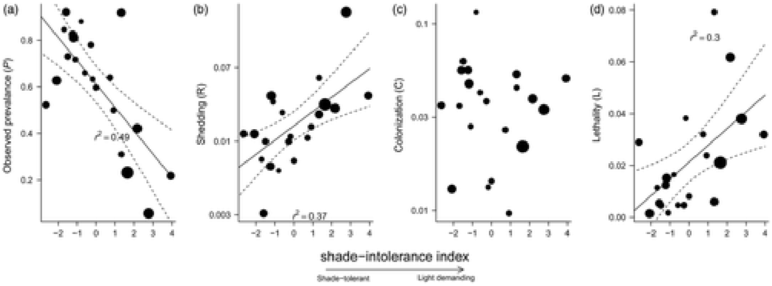

Figure 4 Relationships of shade intolerance with liana prevalence (a), shedding (b), colonization (c), and lethality (d) among our 21 focal tree species. Solid lines indicate significant relationships based on a Bonferroni corrected significance level of 0.0125 (0.05/4). Dashed lines represent 99% confidence intervals. Symbol size is proportional to sample size or number of individual trees assessed for each species

All 15 structural equation models indicated a strong and significantly negative relationship of prevalence with latent shade intolerance (i.e., positive with shade tolerance), and a significant negative relationship of prevalence with shedding and lethality. However, not all models were unbiased. Simulations showed that the top five models (as ranked by the GFI) had low bias in parameter estimates (<5%) and high power (>88%; Table S6). Bias was much greater for the remaining 10 SEMs (Table S6), indicating that we had too few samples to credibly estimate these models.

The best fitting structural equation model explained 64% of interspecific variation in liana prevalence ($r^2 = 0.643$, GFI = 0.97, $\chi^2_{df=6} = 1.5$, $p = 0.958$, Figure 5, Table S7). This model included only one shade tolerance indicator—the relative growth rates of trees larger than 10 cm DBH. The SEM predicted that shade-tolerant trees have greater levels of liana infestation because they have lower shedding and lethality rates. An indirect pathway analysis showed that this was primarily due to shedding, with the indirect effect of the latent shade intolerance on liana prevalence via shedding 44% larger than the pathway via lethality (−0.221 vs. −0.153). The top five unbiased SEM models all agreed in the relative ranking of the (indirect) pathways, with shedding ranked first and lethality second. Shedding and lethality were also significantly related to shade tolerance in all five of the top ranked models. The SEM path coefficient estimated for the relationship between shade intolerance and colonization is just 0.21 (Figure 5) consistent with the lack of a pairwise relationship (Figure 4c).

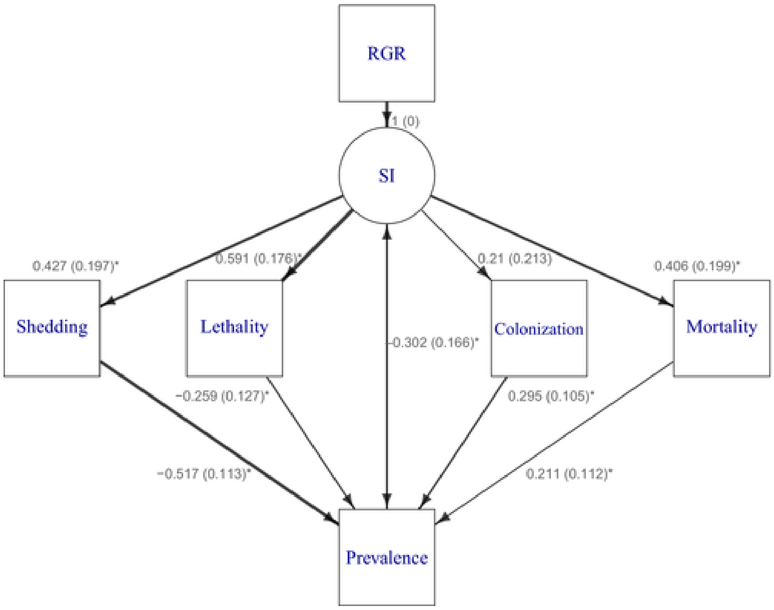

Figure 5 The best fitting structural equation model (SEM), among 15 candidate models using different indicator variables for shade tolerance (full model shown in Figure S2). The SEM shows the hypothesized paths through which the degree of shade in tolerance (SI) influences liana prevalence via shedding, colonization, lethality, and mortality. Squares indicate observed (measured) variables and the circle identifies the one latent variable. The colour, thickness, and shading indicate the direction, size, and significance of each path loading. Respective estimates of loading size are given next to each connecting line, with standard errors in parentheses, and asterisks indicate significance (95% CI do not overlap with zero). The double-headed arrow between SI and prevalence indicates that no direct relationship was hypothesized or fit, but rather only the covariance between variables was estimated [Colour figure can be viewed at wileyonlinelibrary.com]

4 DISCUSSION

The overall effect of lianas on a tree population depends on both the proportion of trees infested with lianas and the magnitude of negative effects experienced by infested individuals, both of which vary greatly among tree species (Clark & Clark, 1990; Toledo-Aceves, 2014; van der Heijden et al., 2008; Visser et al., 2018). This study is the first to explain variation in liana prevalence among co-occurring tree species by integrating species-specific rates of colonization, shedding, baseline host mortality, and lethality (i.e., additional host mortality associated with liana infestation). We found that 21 tropical tree species vary widely in the proportion of individuals infested by lianas (0.06–0.93), and 58% of this variation can be explained by just two parameters: the rates of shedding (R) and lethality (L). Of the four rates, shedding was the most important, then lethality and colonization, whereas uninfested tree mortality was unimportant. The same ranking of parameters was confirmed by four separate analyses: (a) Pearson correlation between estimated rates and observed proportion infested (P, Figure 2), (b) predictive power (r^2) when only one variable was included (Table 1), (c) the loss in r^2 when only one variable was excluded (Table 1), and (d) strength of indirect effects in a multivariate structural equation model (Figure 5).

Our results lead us to reject both of our original hypotheses. Neither interspecific variation in host demography alone nor colonization and shedding alone explain most of the variation among tree species in liana prevalence (Figure 3, Table 1). Rather, the rates of shedding, in combination with lethality, explain interspecific variation in the prevalence of liana infestation in trees in this forest. Furthermore, we show that shade intolerance correlates strongly with shedding and lethality: light-demanding tree species tend to have higher rates of both shedding and lethality (Figures 4 and 5), and this jointly leads them to have lower proportions of individuals infested by lianas (Figure 5).

4.1 The mechanisms underlying interspecific variation in liana prevalence

Traits such as flaky bark (bark shedding), the ability to drop branches (self-pruning), trunk/branch flexibility, and long leaves, are hypothesized to influence the ability of tree species to resist colonization or shed lianas, and thus their liana prevalence (e.g., Putz, 1984b). Consistent with this hypothesis, previous studies reported that liana prevalence is negatively correlated with several host tree architectural traits: branch-free bole-height, smooth bark, longer leaves, and low wood density (Balfour & Bond, 1993; Campbell & Newbery, 1993; Putz, 1980; van der Heijden et al., 2008). These correlations alone, however, do not reveal whether the traits influence the prevalence of liana infestation via colonization, shedding, and/or other rates. A more mechanistic understanding could be gained by evaluating how dynamically estimated rates (i.e., R, C, L, and M) relate to traits.

The two most influential rates here—shedding and lethality—were both associated with shade tolerance, and this may help narrow down which traits influence liana prevalence. Light-demanding tree species have long been known to have rapid leaf turnover times and high levels of self-pruning of shaded leaves and branches (Zon & Graves, 1911). These traits are all likely to increase rates of liana shedding (e.g., Putz, 1980). Furthermore, Visser et al. (2018) hypothesized that fast-growing tree species are less tolerant of liana infestation as they tend to have shallower crowns (vertically) with lower leaf area indices, causing a greater proportional displacement of total leaf area due to infestation. These two observations are linked. Greater rates of branch shedding lead to shallower crowns and lower leaf area indices. Hence, the very traits that increase shedding may simultaneously increase lethality. We did not find a significant correlation between shedding and lethality (Figure S3) but both factors are significantly related to shade tolerance (Figures 4 and 5). The strong positive links of shade intolerance with shedding and lethality also hint that the above traits may not be adaptations specifically for interactions with lianas: light is a principle limiting resource in tropical forests, and these traits may be shaped simply by shade tolerance strategy.

Our model shows that the prevalence of liana infestation is highly sensitive to the rate of host colonization (Figures S4a and S5). However, estimated colonization varied little among species (Figure S4b), and thus played a small role in explaining interspecific variation in prevalence (Figure S4d). The relatively low variance in colonization rates observed among tree species might indicate that colonization is largely a chance occurrence and is mostly unrelated to host tree traits. Lianas infest trees either from the ground up or laterally growing from an infested neighbour (van der Heijden et al., 2008), which means that the rate of colonization may be largely dependent on local liana abundance. Individual canopy lianas infest an average of 1.6 trees on BCI (Putz, 1984a), and instances of lateral (crown to crown) infestation depend on how many adjacent trees carry lianas (van der Heijden et al., 2008). Colonization will also likely depend on the life-history strategies of the lianas present. For example, liana species differ in many traits, including the average number of host trees an individual infests (Ichihashi & Tateno, 2011). We expect that the rate of colonization will depend more on the density of lianas in the forest, the presence of infested neighbours, and on the aggregate traits of local liana species than on host species identity and traits. This hypothesis may explain the relative low variability and predictive power of liana colonization among tree species. It may also introduce error into our estimates of colonization rates for individual tree species. Better species-specific estimates that may correlate with species-specific traits could emerge from models that also include effects of neighbourhood liana density.

Tropical tree species vary continuously along an axis from low mortality and slow growth towards fast growth and high mortality (Gilbert, Wright, Muller-Landau, Kitajima, & Hernandéz, 2006; Wright et al., 2010). We initially expected that because longer lived hosts have a longer time period during which they can become infested, they would have higher prevalence. Yet, the baseline (uninfested) tree mortality rate was the least influential parameter in explaining liana prevalence. The lack of influence of baseline mortality in our Markov chain model at its current parameterization could change if tree recruitment is included into the model. In such a model, baseline mortality can be expected to negatively affect equilibrium prevalence in a model with a constant influx of liana-free individuals in which colonization exceeds shedding. Surprisingly, however, our empirical analyses also showed that baseline mortality was uncorrelated with prevalence across species, and that mortality had the weakest influence of any rate in our path analyses. Moreover, the path analysis estimated a *positive* relationship between mortality and prevalence, which is the opposite of what is expected mechanistically when colonization rates exceed shedding rates (as they do for 14 of our 21 species). We hypothesize that shedding may mask the effect of tree longevity (the inverse of mortality). Shedding rates are independent of tree mortality (Figure S3), and large enough to render any accumulation effect undetectable.

5 CONCLUSIONS AND FUTURE DIRECTIONS

Lianas are a globally widespread and diverse plant group that are vital components of forest ecosystems (Schnitzer & Bongers, 2002), with profound impacts on tree population dynamics (Visser et al., 2018), ecosystem processes including carbon sequestration (van der Heijden, Powers, & Schnitzer, 2015), and animal diversity (Yanoviak, 2015). Yet, we know little about the mechanisms that govern the prevalence of liana infestation at any given site (Muller-Landau & Pacala, 2018). Here, we applied a modelling approach based on simple principles of disease ecology that explained the majority of variation in the proportion of trees infested with lianas among co-occurring tropical tree species. The prevalence of liana infestation was predicted by asymptotic stable stage distributions calculated from observed, species-specific transition rates (Figures 2 and 3). Of the four transition rates, shedding and lethality were the most important in explaining interspecific variation in liana infestation prevalence. We show that the prevalence of liana infestation is positively related to shade tolerance via indirect pathways operating on the rates of shedding and lethality (Figures 4 and 5). Our work demonstrates that an epidemiological approach provides many insights and a sound basis for further exploration of the factors that regulate liana populations.

Future work should investigate how functional traits of both lianas and trees influence their interactions. Our work suggest that this should include traits that influence the likelihood of shedding a liana such as bark flaking and branch abscission, as well as their interaction with liana climb and growth strategies (e.g., tendril, twining, or root climbing; Ichihashi & Tateno, 2011). Which liana traits mediate the impact lianas have on their hosts is also of interest. A seminal study in temperate forests showed that co-occurring liana species can vary greatly in their interactions with host trees and thus in their impacts on host growth and survival (Ichihashi & Tateno, 2011), and there is every reason to expect that similar variation exists among the 162 co-occurring liana species at our study site (Schnitzer et al., 2012). It would be useful to investigate which traits of lianas are associated with this strategic variation in “virulence.” For instance, gap-dependent or light-demanding lianas may be inclined to grow more vigorously, exploiting hosts more intensely and causing greater lethality rates. Indeed, some lianas thrive despite the loss of a tree host, suppressing tree recruitment and regeneration in gaps for decades (Schnitzer et al., 2000; Tymen et al., 2016). Therefore, future work that focuses on liana traits (sensu Ichihashi & Tateno, 2011) in addition to tree traits, while correcting for habitat and spatial neighbourhoods, is needed to generate a mechanistic understanding of how liana traits interact with tree traits to shape the abundance of lianas and trees across a landscape. We conclude that the theoretical and empirical aspects of liana population, community, and evolutionary dynamics are severely underdeveloped and provide fertile ground for further study.

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AUTHORS’ CONTRIBUTIONS

M.D.V., H.C.M.-L., and S.J.W. designed the study, analysed the data, and built the models; M.D.V., H.C.M.-L., and S.J.W. wrote the first draft; M.D.V., H.C.M.-L., S.A.S., S.J.W., E.J., and H.deK. all contributed substantial revisions. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Smithsonian DSpace Repository: **https://0-doi-org.libus.csd.mu.edu/10.25570/stri/10088/35383** (Visser & Wright, 2018) and in the supporting material (Text S1 and S2, Table S1) or were published previously.

Supporting Information

Filename	Description
jec12997-sup-0001-SupInfo.pdfPDF document, 274.1 KB	
jec12997-sup-0002-TextS1.Rtext/r-script, 8.2 KB	
jec12997-sup-0003-TextS2.Rtext/r-script, 9.6 KB	

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