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Disturbance and Clonal Reproduction Determine Liana Distribution and Maintain Liana Diversity in a Tropical Forest

Alicia Ledo
University of Wisconsin - Milwaukee

Stefan A. Schnitzer
Marquette University, stefan.schnitzer@marquette.edu

Disturbance and clonal reproduction determine liana distribution and maintain liana diversity in a tropical forest

ALICIA LEDO[1,3] AND STEFAN A. SCHNITZER[1,2]

[1]*University of Wisconsin-Milwaukee, Department of Biological Sciences, P.O. Box 413, Milwaukee, Wisconsin 53210 USA*
[2]*Smithsonian Tropical Research Institute, Unit 0948, DPO AA 34002-0948 USA*

Abstract. Negative density dependence (NDD) and habitat specialization have received strong empirical support as mechanisms that explain tree species diversity maintenance and distribution in tropical forests. In contrast, disturbance appears to play only a minor role. Previous studies have rarely examined the relative strengths of these diversity maintenance mechanisms concurrently, and few studies have included plant groups other than trees. Here we used a large, spatially explicit data set from Barro Colorado Island, Panama (BCI) to test whether liana and tree species distribution patterns are most consistent with NDD, habitat specialization, or disturbance. We found compelling evidence that trees responded to habitat specialization and NDD; however, only disturbance explained the distribution of the majority of liana species and maintained liana diversity. Lianas appear to respond to disturbance with high vegetative (clonal) reproduction, and liana species' ability to produce clonal stems following disturbance results in a clumped spatial distribution. Thus, clonal reproduction following disturbance explains local liana spatial distribution and diversity maintenance on BCI, whereas negative density dependence and habitat specialization, two prominent mechanisms contributing to tree species diversity and distribution, do not.

Key words: density dependence; disturbance; habitat specialization; point pattern analysis; spatial pattern; species coexistence.

INTRODUCTION

The maintenance of species diversity and the mechanisms that control species' distributions are fundamental questions in ecology. While many mechanisms have been proposed to explain plant diversity maintenance and distribution, negative density dependence (Janzen 1970, Connell 1971) and niche assembly driven by habitat specialization (Grubb 1977, Tilman 1982) have received the most empirical support. For example, negative density dependence has been shown to operate in both temperate grasslands and forests (Schnitzer et al. 2011, Johnson et al. 2012), as well as in diverse tropical forests, where negative density-dependent effects have been found for many tree species (Comita et al. 2010, Mangan et al. 2010).

Niche assembly and differentiation through topographic and edaphic habitat specialization, where plant diversity and distribution is driven by strong habitat preferences, has also been proposed to explain high plant diversity and species distributions in various ecosystems (e.g., Tilman 1982, Clark et al. 1999). In tropical forests, habitat specialization has been reported to explain the distribution and diversity maintenance for many tree species. For example, John et al. (2007) examined the distribution and diversity of trees in three different neotropical forests and demonstrated that up to 51% of tree species had strong associations with particular soil nutrients. Bagchi et al. (2011) reported that habitat characteristics were responsible for the clumped spatial pattern of 84% of the species in four tropical forests in Ecuador, Malaysia, Panama, Sri Lanka. At Yasuní National Park, Ecuador, up to 90% of the seedlings of tree species were significantly associated with a specific habitat type (Metz 2012). In lowland tropical forest in Borneo, 85% of tree species were associated with a particular habitat (Potts et al. 2002).

Disturbance has a rich theoretical history as a community diversity maintenance mechanism in tropical forests (reviewed by Brokaw and Busing 2000); however, it has received little empirical support as a mechanism to explain tree species diversity maintenance and distribution (Hubbell et al. 1999, Schnitzer and Carson 2001). For instance, in a comprehensive test using more than 1200 treefall gaps in a Panamanian forest, tree diversity was equal in disturbed forest areas compared to undisturbed areas, suggesting that disturbance did not maintain tree diversity (Hubbell et al. 1999). Schnitzer and Carson (2001) also found that overall tree species diversity in Panama was not maintained by treefall gaps, except for high-light-demanding species, which constitute a small proportion of the total number of tree species (Schnitzer and Carson 2001, 2010).

Rarely are multiple mechanisms to explain the maintenance of diversity and distribution of tropical

plant species tested simultaneously with the same data set, thus limiting our ability to determine the relative strength of these mechanisms. Furthermore, almost no studies on the maintenance of tropical plant species diversity and distribution have examined species other than trees, thus limiting our ability to conclude that these mechanisms are relevant to plant growth forms beyond trees. For example, liana (woody vine) density and species diversity have been found to be higher in treefall gaps than in non-gap areas, thus supporting the hypothesis that disturbance maintains liana diversity and controls liana distribution in tropical forests (Schnitzer and Carson 2001, Dalling et al. 2012). However, the disturbance hypothesis has rarely been compared simultaneously with alternative explanations for the maintenance of liana diversity, and no study to date has simultaneously compared the relative roles of density dependence, habitat specialization (niche assembly), and disturbance, three processes with the potential to strongly influence woody plant species distribution and maintain woody plant species diversity.

Here, we tested the relative roles of density dependence, edaphic/topographic habitat specialization, and disturbance in controlling the local distribution and diversity maintenance of liana and tree species in a Panamanian tropical forest. We used a comprehensive and spatially explicit data set of nearly 67 500 rooted liana stems collected across a 50-ha area on Barro Colorado Island, Panama (Schnitzer et al. 2008, 2012), where there is strong empirical support for both negative density dependence and edaphic habitat specialization to explain tree species distributions and diversity maintenance (Harms et al. 2001, John et al. 2007, Comita et al. 2010, Mangan et al. 2010).

Lianas are exceptionally abundant and diverse in lowland tropical forests, and they play a key role in many aspects of forest dynamics (Schnitzer and Bongers 2002, 2011). For example, lianas on Barro Colorado Island (BCI) constitute 35% of the woody species and 25% of the rooted woody stems (Schnitzer et al. 2012), and lianas compete intensely with trees on BCI (Ingwell et al. 2010) and in other tropical forests (e.g., Grauel and Putz 2004, Toledo-Aceves and Swaine 2008, Schnitzer and Carson 2010). Liana stems and species were recently found to be distributed nonrandomly in the 50-ha BCI plot (Dalling et al. 2012, Schnitzer et al. 2012), a pattern that could be consistent with edaphic/topographic habitat specialization, negative density dependence, or disturbance from treefall gaps. If the mechanisms that maintain tree diversity and control tree distribution are to be accepted as general to vascular plants, then we would expect that they also apply to lianas. Furthermore, liana abundance and biomass are increasing in neotropical forests relative to trees (reviewed by Schnitzer and Bongers 2011), with huge implications for a change in tropical forest dynamics and functioning (e.g., Phillips et al. 2002). Thus, determining the mechanisms responsible for liana distribution and

diversity is central to understanding the causes and consequences of these ongoing large-scale changes in neotropical forests.

METHODS

Study site and liana census

We conducted this study in the 50-ha forest dynamics plot on Barro Colorado Island, Panama (BCI). Mean annual rainfall on BCI is ~2600 mm, with a dry season from December until May (Leigh 1999). The BCI 50-ha forest dynamics plot was established in 1980, when >230 000 trees ≥1 cm in diameter were tagged, mapped, measured, and identified (Condit 1998). In 2007, we tagged, mapped, measured, and identified a total of 67 497 rooted liana stems (≥1 cm diameter) comprising 162 species in the BCI 50-ha plot (Schnitzer et al. 2012), using methods described by Gerwing et al. (2006) and Schnitzer et al. (2008). We included all independently rooted stems, which we call "genets," as well as clonal stems (ramets that were still attached to another stem in the census) if they had their own root system and thus would likely survive on their own when separated from the mother stem (Schnitzer et al. 2012). Stems attached to another stem in the census without a distinct root system were considered branches of the original stem and were not classified as clones. In total, >20 000 (30%) of the 67 497 rooted stems were clones that had their own root system but were still attached to another individual in the study (Schnitzer et al. 2012). We identified lianas to species using a combination of stem, leaf, and flower characteristics, and we were able to identify 98.4% of the individuals to species (Schnitzer et al. 2012). For additional information on the liana census methods and the abundance, diversity, species composition, and distribution of lianas in the BCI 50-ha plot, see Schnitzer et al. (2008, 2012). A more detailed description of BCI and the 50-ha plot can be found in Condit (1998) and Leigh (1999).

Analyses

To test the contributions of density dependence, habitat specialization, and disturbance to explain liana species distribution and diversity maintenance, we analyzed whether and to what extent the spatial patterns of density dependence, edaphic/topographic habitat differentiation, and disturbance explained the distribution of liana saplings (10–11 mm diameter) for each species. We restricted our sample to liana saplings because they survived the vulnerable seedling stage, and thus are likely to have already experienced the potential causes of mortality from NDD, inhospitable conditions due to poor edaphic/topographic habitat, or a lack of disturbance. If one of the three diversity maintenance mechanisms that we are testing is operating, we should be able to detect its signature on the current distribution pattern of liana saplings, rather than seedlings or larger stems. Thus, our analyses differ from previous studies on the factors that control liana distribution on the BCI

50-ha plot (i.e., Schnitzer and Carson 2001, Dalling et al. 2012).

To explicitly test whether the patterns of liana species distribution and diversity were consistent with the negative density-dependence hypothesis (NDD), we examined the spatial relationship between liana saplings in relation to conspecific large stems (>50 mm diameter). If NDD maintains liana diversity and controls species' distributions, then small stems should be overdispersed in relation to larger stems (Janzen 1970, Connell 1971). The use of spatially explicit distribution data for saplings (10–11 mm diameter), rather than seedlings, provides a powerful approach to determine whether the negative density-dependent decrease in seedling growth and survival is sufficiently strong to overcome dispersal limitation (c.f., Comita et al. 2010). We selected 50 mm as the minimum size class for adults because lianas >50 mm are nearly always in the forest canopy and are likely reproductive adults (Kurzel et al. 2006). To avoid spurious results from low sample size, we focused our analyses on the 52 species with a minimum of 65 individuals, of which at least 30 were saplings (including genets). We conducted the analyses both including and excluding clonal stems. The number and proportion of clonal stems for each species are reported in the supplementary material and in Schnitzer et al. (2012).

We compared our spatially explicit tests of NDD for lianas with those of trees on BCI, which have been shown to exhibit lower growth and survival of seedlings in close proximity to conspecific adults (Comita et al. 2010, Mangan et al. 2010). We used tree distribution data from the 2005 BCI tree census, excluding dead trees and those of unknown diameter. We selected tree species represented by >65 individuals, of which at least 30 were saplings. We considered adult trees those >50 cm in diameter, and sapling trees as individuals 10–15 mm in diameter, which provides a robust sample size for saplings. If both liana and tree saplings have repelled (overdispersed) recruitment in relation to conspecific adults, we accept the hypothesis that NDD is contributing to the maintenance of liana and tree diversity.

We assessed the spatial dependence between rooted liana and tree saplings and large conspecifics for each species through point-pattern analysis using the bivariate K_{rs} function (Dale 1999). The bivariate K_{rs} function is a symmetric version of the bivariate K_{12} (Lotwick and Silverman 1982), derived from the univariate Ripley's K function (Ripley 1977). The Ripley's K function describes the second-order moment properties of the distribution of the point layer as a function of the inter-point distance, which allows for the detection of the observed spatial pattern of the objective point layer at different scales. The bivariate K_{rs} function identifies the spatial attraction or repulsion produced by the individuals of one type over the individuals of another type at different distances. Point pattern analysis has been employed previously to compare the observed point

pattern distribution with a known distribution function that reflects the null hypothesis, such as the Poisson function for a random process (Illian et al. 2008). In our current analysis, we used the K_{rs} function to provide a species-specific estimate of the spatial relationship of the saplings centered around large (adult) conspecific stems at different distances (Dale 1999).

We compared our empirically derived density-dependent patterns against a null hypothesis of spatial independence between saplings and adult conspecific stems at different distances (d) for species of both lianas and trees. We calculated 999 simulations of the toroidal shift null model (Goreaud and Pélissier 2003) to obtain a boundary of acceptance of the null hypothesis of spatial independence between saplings and adult stems. The toroidal shift model creates a null model comparison by maintaining the position of the points of one class (either sapling or adult) unchanged and shifts all the points of the other class by the same random vector (Goreaud and Pélissier 2003, Ledo et al. 2011). We compared the empirical $\hat{K}_{rs}(d)$ function (the spatial relationship between saplings and large conspecific adults) with the 95% quantiles of the upper and lower interval values of the toroidal shift null model. If the empirical $\hat{K}_{rs}(d)$ function is above the quantile bounds generated by the toroidal shift null model, the two sets of points show spatial attraction at the observed scale. If the empirical $\hat{K}_{rs}(d)$ function is below the quantile bounds generated by the toroidal shift null model, the two sets of points are overdispersed at this scale. If the empirical $\hat{K}_{rs}(d)$ function is within the quantile bounds generated by the toroidal shift null model, the two sets of points are spatially independent from each other and the null hypothesis of spatial independence is accepted.

We quantified the strength of density dependence as the maximum (for a clumped, positive density-dependent distribution) or minimum (for an overdispersed negative density dependence) value reached by the $\hat{K}_{rs}(d)$ empirical function, above the upper or below the lower limit, respectively, of the band of acceptance of the null hypothesis weighted by the distance interval between the upper and lower curves of the band of acceptance at that exact point. The distance of density dependence is the largest distance value at which the $\hat{K}_{rs}(d)$ empirical function is out of the band of acceptance of the null hypothesis. We regressed linearly the strength of density dependence (both positive and negative) onto the abundance of each species. To determine whether the production of clonal stems predicted density-dependent patterns, we regressed linearly the strength and distance of density dependence onto the proportion of clonal stems of each species, both including and excluding clonal stems.

To test the contributions of disturbance and edaphic/topographic habitat specialization on liana distribution, we focused our analyses on the spatial distribution of rooted liana saplings in relation to disturbance rate and habitat conditions. For habitat specialization, we used a

set of topographical variables: elevation, slope, curvature, and aspect per 20×20 m quadrats throughout the plot. These are the same basic variables used by other studies that reported compelling effects of habitat characteristics on tree species' distributions (Harms et al. 2001, Bohlman et al. 2008, Bagchi et al. 2011, Brown et al. 2013, Ledo et al. 2013). While there are other, nonlinear combinations that can be used for habitat variables (Bagchi et al. 2011), we used a linear combination so that we would have a tractable number of parameters, but still a complex enough set of variable combinations to reflect distinct habitat conditions, as demonstrated by previous studies (Harms et al. 2001, Bohlman et al. 2008, Brown et al. 2013, Ledo et al. 2013). Because topography influences soil conditions (Hook and Burke 2000, John et al. 2007), we considered habitat specialization to be the combination of topographic and edaphic specialization.

We determined the degree of disturbance using the tree mortality rate data from the six previous BCI 50-ha plot tree censuses (1981–1983, 1985, 1990, 1995, 2000, 2005 [Condit 1998]). We quantified tree mortality rate every five years in a 20×20 m grid in the BCI plot, quantifying disturbance severity as the proportion of dead trees and accounting for the time since tree mortality. We refined our disturbance index by considering the presence of large trees (dbh ≥ 80 cm) in each 20×20 m quadrat as indicative of no recent high disturbance. Hence, we calculated a disturbance index for each 20×20 m quadrat as the sum of the severity of disturbance (measured as a proportion of tree mortality of the stems present in the previous census) in subsequent censuses multiplied by the census number (to weigh the more recent disturbances more heavily) minus the number of large trees in 2005 (census 6). The equation for the disturbance index is

$$\text{DIST} = \left(\sum_{i=2}^{6} i(D_i - D_{i-1})/N_i \right) - B_6,$$

where i represents each of the six BCI censuses, from $i = 1$ (1981–1983) to $i = 6$ (2005); D represents the number of dead standing trees (considering all diameter classes); N represents the number of standing live trees; and B represents the number of large trees (dbh ≥ 80 cm).

We determined the spatial distribution of rooted liana saplings for each liana species by fitting an Inhomogeneous Poisson Process Model (IPPM) of point–liana distribution using an independently estimated spatial density function (Illian et al. 2008). For each species, we fitted three different IPPM models, taking into consideration three different covariates: (1) a pure spatial model; (2) habitat distribution; and (3) degree of disturbance. The IPPM requires estimating the parameter $\lambda(u)$, the intensity function of the point process at location u, and the spatial locations. In the pure spatial mode, u_i depended on the Cartesian coordinates of the plot surface. The habitat and disturbance models depended on a linear combination of the value of a set of spatial covariates at point u_i. We defined $\lambda(u)$ as a linear combination of either the topographical parameters or the disturbance parameters as covariates, $\lambda_\theta(u) = \exp(\theta_0 + \theta_1 Z_1(u_1) + \ldots + \theta_n Z_n(u_n))$, where $Z_i(u_i)$ was the value of each covariate at spatial location u_i from a total of n covariates. We estimated the λ parameters using the Huang-Ogata approximate maximum likelihood method (Huang and Ogata 1999) using 999 simulated realizations to parameter estimation. We used the translate method for the edge correction (Baddeley and Turner 2000), and calculated the quadrat count test using a goodness-of-fit (GoF) χ^2 test (Baddeley 2010).

We accepted as significant the models that had a P value >0.01 in the GoF quadrat count test, suggesting that the model deviated significantly from the null. We selected the most explanatory and parsimonious model on the basis of the Akaike Information Criterion (AIC), which measured the quality of a model and is commonly used to compare nested models (Burnham and Anderson 2004). The AIC is calculated as: $\text{AIC} = 2k - 2\ln(L)$, where k is the number of parameters included in the model and L is the likelihood function for the estimated model. The spatial covariate, either habitat specialization or disturbance, that produced the most accurate IPPM model (the model with the lower AIC among the existing models) was accepted as the predominant process controlling liana distribution within the forest. If the pure spatial model was the most accurate model, then neither disturbance nor edaphic/topographic habitat specialization satisfactorily explains liana diversity and distribution. To test the effect of disturbance acting simultaneously with density dependence, we included density dependence in the spatial modeling just described. We added the density of largest stems (>50 mm diameter) of each species as linear covariates in the density estimation function $\lambda(u)$ of liana sapling distribution in the disturbance IPPMs.

We tested whether liana species' response to disturbance was enhanced by clonal stem production, by comparing the production of clones in high- and low-disturbance areas using an F test. We classified the high- and low-disturbance areas as the ones with the highest and lowest one-quarter disturbance index values, respectively. We tested whether disturbance maintained liana species diversity by comparing liana richness in high- and low-disturbance areas while correcting for differences in stem density among areas using rarefaction (Gotelli and Colwell 2001). The rarefaction function we used is based on Hurlbert's (1971) formulation, and the standard errors on Heck et al. (1975). For these two analyses, we did not restrict our sampling to saplings, but we included all liana individuals of the 52 species.

All computations were done in R (R Development Core Team 2011). We used the *ppm* function for the model fitting and *Kcross* and *envelope* functions for the bivariate analysis, from the spatstat 1.25-3 package
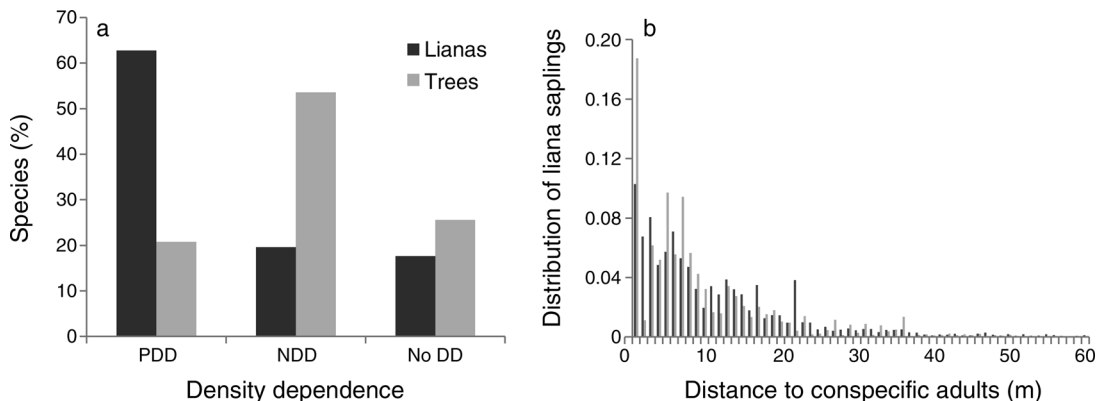
FIG. 1.　(a) The percentage of lianas including clonal stems (dark gray) and trees (light gray) with clumped distribution (positive density dependence, PDD), overdispersed distribution (negative density dependence, NDD), and no spatial dependence (no DD). (b) Proportion of the distribution of distances of liana saplings to the nearest conspecific adult for species with positive density dependence. The dark gray bars represent all rooted lianas, including clonal stems, whereas the light gray bars exclude clonal stems and thus represent only the main genets.

(Baddeley and Turner 2005). For the rarefaction analysis we used the *specaccum* and *rarefy* functions of the vegan package (Oksanen et al. 2011).

RESULTS

Liana species exhibited strong density-dependent patterns, with 42 of the 52 species (81%) showing a pattern consistent with density dependence at small spatial distances (Fig. 1a). Contrary to our expectation that an overdispersed (negative density-dependent) pattern would be prevalent in lianas, the $\hat{K}_{rs}(d)$ analyses indicated that liana saplings were nonrandomly clumped around larger conspecific stems, a pattern consistent with positive density dependence. Specifically, 63% of liana species exhibited a pattern of saplings clumped around large conspecific stems, whereas only 19% had an overdispersed (negative density-dependent) pattern. The remaining 18% of liana species had no significant spatial pattern with respect to the location of saplings in relation to adults (Fig. 1a). Excluding clonal stems decreased the number of liana species exhibiting a clumped distribution to 46% and increased the number of species exhibiting an overdispersed distribution to 46%, with 8% not showing any density-dependent pattern. In contrast, saplings of most tree species were overdispersed in relation to adults, and only 20% of tree saplings were clumped around adults (Fig. 1a), consistent with previous studies documenting negative density dependence in trees at this same site (e.g., Comita et al. 2010, Mangan et al. 2010), and confirming the reliability of our test of density dependence using spatially explicit data.

Saplings of most liana species were positively associated with adults at very small distances (<1 m) and up to 20 m, following a J-shaped distribution (Fig. 1b). There was a strong positive relationship between the strength of the positive density-dependent (clumped) pattern and the capacity of a liana species to reproduce clonally (Fig. 2a). That is, the species with the highest percentage of clonal stems demonstrated the strongest positive density dependence, a pattern that was present both when excluding and including clonal stems in the analyses (Fig. 2b).

Disturbance was the most important correlate of liana distribution in the BCI 50-ha plot, explaining the distribution of ~50% of the liana species (Figs. 3 and 4). The majority of liana species (54%) produced significantly more clones in high-disturbance areas than in low-disturbance areas ($P < 0.05$). Thus, clonal reproduction appears to enhance the ability of lianas to colonize nearby disturbed areas. In contrast to disturbance, habitat specialization was not a strong cause of liana species distribution, explaining the spatial pattern of only a small percentage of liana species (Figs. 3 and 4). The addition of density dependence to the disturbance model increased the explanatory power, while at the same time, it further decreased the explanatory power of the habitat specialization and pure spatial models (Fig. 3; Appendix). The distribution of 75% (79% including clonal stems) of the liana species in the BCI plot was explained by a combination of both disturbance and positive density dependence (Fig. 3). The inclusion of clonal stems increased the role of habitat in explaining liana species distribution. However, even with clonal stems, habitat had only limited explanatory power compared to disturbance or the pure spatial model representing an unknown mechanism (Fig. 3; Appendix).

Liana density and diversity (after controlling for density using rarefaction) were significantly higher in the areas with the highest disturbance than in low-disturbance areas (F test density, $P < 0.0001$; F test rarefied diversity, $P < 0.005$; Fig. 5). The finding that disturbance contributes to the maintenance of liana density and species diversity was the same when we included rooted clonal stems in the analysis.
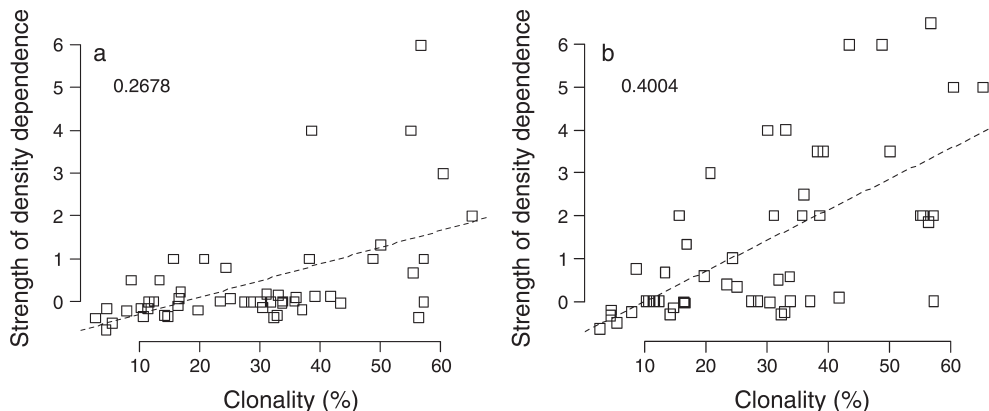
FIG. 2. The linear correlation between the percentage of clonality on the *x*-axis and strength of density dependence of the species on the *y*-axis. The percentage of clonality per species is from Schnitzer et al. (2012). Panel (a) excludes clonal stems; panel (b) includes clonal stems. The negative *y*-axis values (below the axis numbers) correspond to negative density dependence. The values shown in the upper left corners of the graphs are the R^2 linear correlation adjusted value for each analysis.

DISCUSSION

Nearly all tests of the maintenance of diversity and the mechanisms that control tropical plant species distributions used trees as the representative plant group, and thus it was previously unknown whether these mechanisms are generalizable beyond trees. Lianas constitute ~25% of the rooted woody stems and species in many tropical forests (Schnitzer and Bongers 2002), and on the BCI 50-ha plot, lianas constitute 25% of the rooted woody stems and 35% of the woody species (for individuals ≥1 cm diameter [Schnitzer et al. 2012]). Therefore, determining whether the mechanisms responsible for tree diversity maintenance and distribution also apply to lianas is essential for a general understanding of the maintenance of plant species diversity in tropical forests.

Comparing multiple putative mechanisms for the maintenance and distribution of liana species diversity revealed that disturbance strongly influenced the majority of liana species in this forest. The positive spatial association between saplings and large conspecific stems at short distances further explained the distribution of lianas species, and combined, these two mechanisms explained the distribution of >75% of the 52 liana species examined. By contrast, patterns consistent with negative density dependence and habitation specialization, the two major putative mechanisms to explain tree distribution on the BCI plot (John et al. 2007, Comita et al. 2010, Mangan et al. 2010, Feeley et al. 2011), explained only a small proportion of liana species distribution. Consequently, our findings indicate that the mechanisms that maintain liana diversity and control liana distribution differ markedly from those of trees, and thus previous studies of the maintenance of species diversity that focused on trees cannot necessarily be extended to the broader plant community.
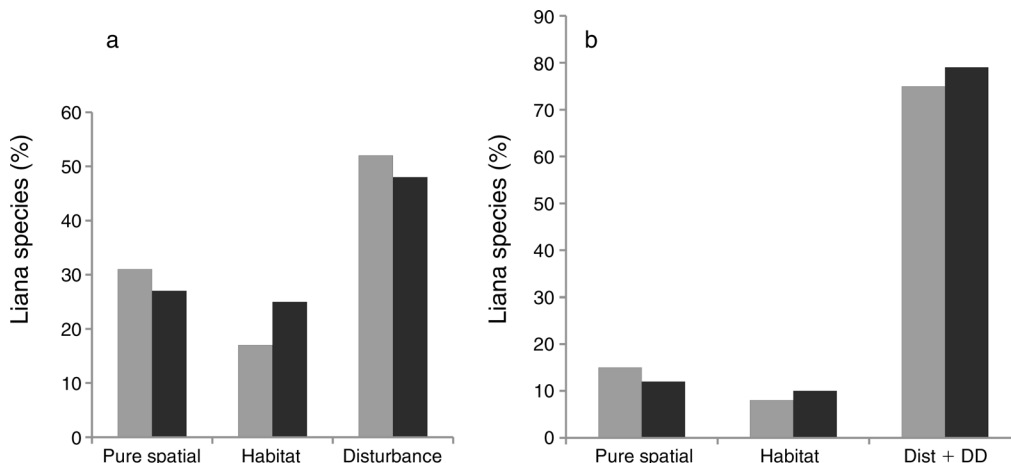

FIG. 3. Data from fitted Inhomogeneous Poisson Process Models (IPPM) showing (a) the percentage of liana species that exhibit a pure spatial (unexplained) pattern, habitat specificity, or are associated with disturbance. (b) Similar IPPMs, but density dependence (DD) was included as an additional explanatory variable in the disturbance model. The dark gray bars represent all rooted lianas, including clonal stems; the light gray bars exclude clonal stems and thus represent only the main genets.
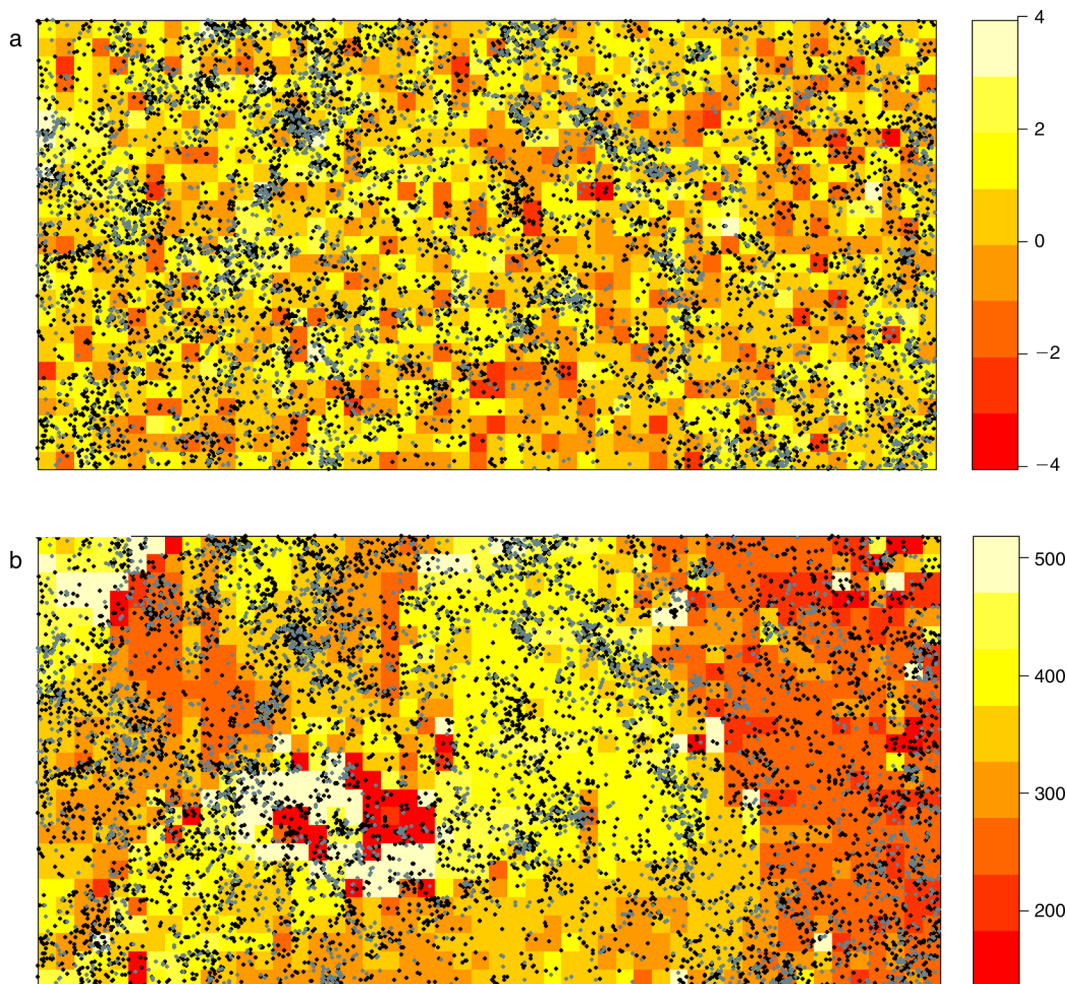
FIG. 4.   (a) Spatial map of all rooted liana stems ($\geq$1 cm diameter) superimposed on the spatial pattern of disturbance. Lighter-colored quadrats represent high disturbance; darker (red) quadrats represent lower disturbance (ranging from 4 to −4). (b) Spatial map of all rooted liana stems ($\geq$1 cm diameter) superimposed on the spatial pattern of habitat differences per 20 × 20 m quadrat. The different colors represent different habitat types, as a combination of the topographic variables. For both panels, the black circles represent the genet stems and the gray circles represent the clonal stems.

Our findings that disturbance largely maintained liana species diversity and controlled liana distribution on BCI are consistent with smaller-scale studies from the same area. For example, Schnitzer and Carson (2001) compared liana and tree density and diversity in gap and non-gap sites on BCI and found that disturbance maintained liana diversity but not tree diversity. One theoretical explanation for disturbance as a stable diversity-maintaining mechanism is that plant species, in this case lianas, partition the unique combination of resources that are available following a disturbance (e.g., Brokaw and Busing 2000). This niche-based explanation would allow liana species to coexist stably over time. However, the weak effect of edaphic/topographic habitat specialization found in this study (apart from disturbed habitat) in contrast to trees (e.g., John et al. 2007) does not support a niche-based explanation (see also Dalling et al. 2012). It is possible that higher liana

species diversity is maintained in gaps because different liana species specialize on different levels of light or soil moisture and thus partition these resources (Schnitzer and Carson 2001); however, there is no direct evidence for this hypothesis.

An alternative explanation is that disturbance maintains liana species diversity by providing a regeneration niche (Grubb 1977), which increases recruitment and regeneration and keeps liana density high. The potential for disturbance to increase liana regeneration may act to equalize the number of offspring among liana species. This equalizing explanation (sensu Chesson 2000) could maintain liana diversity by increasing the density of disturbance-adapted species and allowing many liana individuals to persist until the next disturbance, thus reducing the probability that the local population of any given species goes extinct. If increased recruitment and regeneration in gaps equalizes the reproductive output
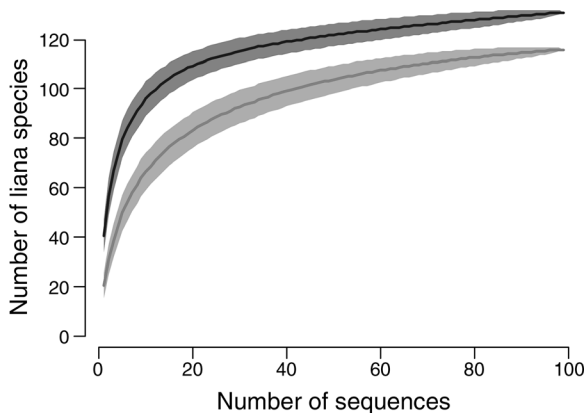
FIG. 5. Rarefaction curves and standard errors in high-disturbance areas (dark gray) and low-disturbance areas (light gray). The solid line represents the rarefaction curve and the lighter color around the curve represents the standard error. This figure excludes clonal stems; however, we found nearly identical patterns when we included clonal stems.

among species (including clonal stem production), then liana species diversity could theoretically be maintained for exceptionally long periods of time (Chesson 2000, Hubbell 2001). The regeneration niche explanation could also be a stabilizing explanation if liana species differ in their ability to respond to disturbance, and these differences are linked to varying liana regeneration strategies.

A regeneration niche explanation may be particularly appropriate for the liana growth form, which is suited to colonize gaps as adults (Putz 1984, Schnitzer et al. 2012, Yorke et al. 2013) and produce copious clonal stems that can capitalize on the high-resource habitat following disturbance. Indeed, the stem anatomy of most liana species allows them to survive falling from the canopy, often with their host tree (Rowe and Speck 1996), whereupon these fallen lianas produce many clonal stems (Putz 1984). The positive correlation between the response of liana species to disturbance and the ability of species to produce clonal stems (Fig. 2) supports the hypothesis that liana species respond to disturbance by clonal reproduction, which explains the clumped, positive density-dependent distribution for most liana species within forests, as well as contributing to the maintenance of liana species diversity.

The clumped, positive density-dependent pattern in lianas was not driven by habitat association, and it was far more spatially concentrated than the aggregation of tree saplings around adult species. Clumping of liana saplings around conspecific adults peaked at exceedingly short distances (<1 m), and decreased with distance in a J-shaped pattern (Fig. 1b). In contrast, the location of tree saplings around adult trees had a humped distribution with a maximum of 10–20 m (Terborgh et al. 2002, Wiegand et al. 2007), which may be the result of the interaction between dispersal limitation and negative density dependence. The majority of seeds fall

very close to the parent tree, with far fewer seeds reaching >20 m away from the parent (dispersal limitation). However, the inability of most tree seedlings to regenerate successfully near their parents (or other conspecifics) due to species-specific enemies (e.g., Comita et al. 2010, Mangan et al. 2010) results in few saplings surviving directly underneath a conspecific tree, but much higher survival of seedlings and saplings located 10–20 m away, which arrived in relatively high numbers but escaped damage from enemies. Thus, the contrasting dispersal patterns between lianas and trees demonstrate that lianas do not respond strongly to negative density dependence, whereas trees do.

Negative density dependence may fail to maintain liana species diversity because a significant proportion of regeneration is through clonal reproduction. Negative density dependence (Janzen-Connell) theory assumes that the parent plants can host disease or enemies without dying because parent plants are strong enough to resist the effects of their natural enemies (e.g., Janzen 1970). In contrast, tree seedlings do not have the size and reserves to resist the effects of these natural enemies, and those growing near the parent plant eventually succumb. In the BCI 50-ha plot, >30% of the 67 497 rooted lianas ≥1 cm were clones (Schnitzer et al. 2012). Clonal stems differ from seedlings in that clonal stems can be supplied with resources from the parent until they are well established, likely allowing them to resist species-specific enemies. Thus, small-stemmed lianas can reach a size refuge from such natural enemies as soil-borne pathogens or vertebrate or invertebrate herbivores. Some liana species, however, do not readily produce clonal stems (Schnitzer et al. 2012), and these liana species appear to have distributions more consistent with a negative density-dependent pattern (Fig. 2).

Liana abundance, productivity, and biomass are increasing relative to trees in neotropical forests, and thus determining the mechanisms responsible for the diversity and distribution of lianas will help determine the most likely mechanisms causing liana increases. Currently, 12 studies document liana increases in neotropical forests (reviewed by Schnitzer and Bongers 2011). On BCI, the increase in lianas over the past 30 years is now indisputable, with four different metrics of liana increase (productivity, flower production, the proportion of trees infested by lianas, and the density of lianas) all showing positive trends in favor of lianas over trees (Wright et al. 2004, Ingwell et al. 2010, Schnitzer et al. 2012). Our finding that disturbance drives liana abundance and diversity within the BCI 50-ha plot is consistent with the hypothesis that increasing rates of disturbance explain the change in liana abundance in neotropical forests (Schnitzer and Bongers 2011). Indeed, tree mortality has increased significantly and tree growth has decreased significantly over the past 30 years on the BCI plot (Feeley et al. 2007), presumably due to the effect of climate change (Feeley et al. 2011). Greater tree mortality would increase the frequency of

disturbance, which would provide more favorable habitat for liana regeneration and survival.

Another potential mechanism for increasing liana abundance and biomass is decreasing rainfall and increasing seasonality. Rainfall on BCI has decreased from 1930 to 1990 (data averaged over a 10-year period; Meteorology and Hydrology Branch, Panama Canal Authority, Republic of Panama) and the tree community has shifted toward more drought-adapted tree species (Condit et al. 1995, Feeley et al. 2011). Lianas are more abundant (in terms of total stem density) in seasonal habitats (Schnitzer 2005, DeWalt et al. 2010), as well as drier areas of the BCI 50-ha plot (Dalling et al. 2012), and thus stronger seasonal droughts would likely benefit lianas, resulting in greater stem proliferation. The observed ability of some liana species to consistently tap into deeper sources of water than trees (Andrade et al. 2005) may also explain the positive response of lianas to the hot, dry environment immediately following disturbance (i.e., treefall gaps [Schnitzer 2005]). Deeply rooted lianas may be able to capitalize on the high light but relatively arid environment of a treefall gap better than more shallowly rooted trees. In addition, the decrease in rainfall may also increase tree mortality, which would increase liana abundance, and disturbance and drought may be operating synergistically (Schnitzer and Bongers 2011). Thus, the importance of disturbance as a determinant of liana diversity and distribution, coupled with decreasing rainfall and increasing disturbance on the BCI 50-ha plot, support the hypothesis that the increase in lianas in this forest is driven by these two putative mechanisms.

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SUPPLEMENTAL MATERIAL

Appendix

List of liana species found in the 50-ha plot on Barro Colorado Island (BCI). The list specifies the number of stems (N), percentage of stems that are not clonal stems (% genets), and the Akaike information criteria (AIC) obtained in the Inhomogeneous Poisson process spatial modeling when included as spatial covariates: (a) X,Y coordinates (Spatial); (b) habitat conditions (Habitat); (c) grade of disturbance (Disturb); and (d) grade and disturbance along with distance to conspecific adults (Dist+DD) (*Ecological Archives* E095-192-A1).