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Abstract

Lianas (woody vines) can have profound effects on tree recruitment, growth, survival, and diversity in tropical forests. However, the dynamics of liana colonization soon after land abandonment are poorly understood, and thus it is unknown whether lianas alter tree regeneration early in succession. We examined the liana community in 43 forests that ranged from 1 to 31 yr old in central Panama to determine how fast lianas colonize young forests and how the liana community changes with forest succession. We found that lianas reached high

densities early in succession, commonly exceeding 1000 stems/ha within the first 5 yr of forest regeneration. Lianas also increased rapidly during early succession in terms of basal area but did not show evidence of saturation within the 30 yr of our chronosequence. The relative contribution of lianas to total woody plant community in terms of basal area and density increased rapidly and reached a saturation point within 5 yr (basal area) to 15 yr (density) after land abandonment. Our data demonstrate that lianas recruit early and in high density in tropical forest regeneration, and thus lianas may have a large effect on the way in which secondary forests develop both early and throughout succession.

Mature tropical forests contain more than half of the earth's terrestrial species and contribute nearly a third of global terrestrial carbon stocks and net primary productivity (Field et al. [15] , Körner [22] , Pan et al. [30]). However, these tropical forests are currently being lost at a rapid rate (Laurance & Peres [24] , Aide et al. [1]). Simultaneously, secondary forests are increasing in area as marginal agricultural lands are abandoned and allowed to regenerate as forest in many tropical regions. Secondary forests now comprise up to 60 percent of tropical forests worldwide (Wright & Muller-Landau [48] , Wright et al. [49] , Aide et al. [1]), resulting in a net increase in total tropical forest area in some regions, despite the loss of mature forests (Aide et al. [1]). Consequently, determining the factors that influence the development of secondary forests is essential to predicting the future composition and function of tropical forests.

One of the most notable structural attributes of secondary tropical forests is the high density of lianas (woody vines; Hegarty & Caballé [19] , Schnitzer & Bongers [37] , Letcher [25]). Lianas recruit rapidly into disturbed areas where they have myriad positive and negative effects on tropical forests. Lianas produce a large number of clonal stems and add significantly to plant diversity and forest structural complexity (Putz [34] , DeWalt et al. [12] , Schnitzer et al. [39] , [42] , [43] , Dalling et al. [7]). Lianas provide connectivity and structure to tropical forests for animals (Yanoviak & Schnitzer [51] , Yanoviak [50]) and liana leaves, fruits, and flowers are an important resource for wildlife (Dunn et al. [14] , Arroyo-Rodriguez et al. [2]). Lianas also produce large quantities of leaf litter, contributing significantly to forest nutrient cycles (Putz [33] , Kazda & Salzer [21] , Powers [32]).

Lianas also have negative effects on tree recruitment, growth and survival, which can ultimately reduce tree species diversity and alter community composition. For example, in forest gaps in central Panama, early infestation of lianas reduced tree regeneration and diversity, damaged tree seedlings and saplings, and stalled the formation of a tall canopy (Schnitzer et al. [39] , Schnitzer & Carson [38]). Heavy liana infestation early in succession may limit colonization of trees (Clark & Clark [5] , Schnitzer et al. [39] , Ingwell et al. [20] , Schnitzer & Carson [38]).

Previous studies on successional chronosequences in tropical forests demonstrated that liana density peaks after a few decades (reviewed by Letcher [25]). For example, DeWalt et al. ([12]) found that forests between 20 and 40 yr old in central Panama had the highest density of lianas when compared to older secondary and mature forests. In Costa Rica, Letcher and Chazdon ([26]) found that liana density was highest in 20-yr-old forests, and decreased with forest age. Recent evidence from the Agua Salud watershed in central Panama provides evidence that liana species richness (and other diversity indices) increased rapidly with forest age over the first 32 yr of succession (Van Breugel et al. [47]).

However, little information exists on the rate at which lianas colonize early in forest succession in terms of density and basal area, two factors that largely determine lianas' effect on the community (Schnitzer et al. [39] , Letcher [25]). The combination of liana density and basal area is a good predictor of the potential for liana competition with trees, as well as the effect of lianas on the faunal community (e.g., Grauel & Putz [17] , Schnitzer et al. [44] , Yanoviak [50]). High liana abundance positively affects tropical forest fauna by connecting forest canopies and providing copious resources for arboreal species (Dunn et al. [14] , Yanoviak & Schnitzer [51]

). Liana density and basal area are strongly linked to reduced tree performance and survival (Ingwell et al. [20]). The more severe a liana infestation (indicated by higher number of stems and larger total basal area), the higher the likelihood that liana infestation will have a negative outcome for the host tree (Phillips et al. [31] , Ingwell et al. [20] , Schnitzer & Carson [38]). Furthermore, liana competition may be particularly severe for saplings, which may be especially sensitive to liana colonization (Schnitzer et al. [41]).

Determining the rate of liana colonization in young secondary forests is important because lianas have the potential to alter the successional trajectory of tropical forests when regenerating trees are small and presumably most vulnerable to liana infestation. Therefore, we used a chronosequence approach with 43 forests to investigate the rate at which liana density and basal area increased with stand age, as well as the proportion of the woody plant community (lianas, shrubs, and trees) that lianas comprised over the course of liana succession. The forests ranged from very young (1 yr old) to early/mid-successional (31 yr old) and were located in the Agua Salud watershed in central Panama.

We addressed two main questions: (1) how does liana abundance change throughout succession in terms of absolute numbers and relative to other woody stems (i.e., the rate at which lianas colonize early successional forests)? and (2) what is the shape of the liana successional trajectory during the first three decades of succession? We tested among three theoretical growth trajectories of liana abundance in early successional forests. First, lianas may increase in abundance (stem number and basal area) steadily throughout succession in a linear fashion. Alternatively, liana abundance may increase asymptotically, saturating within the first 31 yr. A third possibility is that lianas peak in abundance early in succession and then decrease later in succession, as suggested by DeWalt et al. ([12]) and Letcher and Chazdon ([26]). We also examined how the most common liana species changed with forest age, and between 5-yr age classes, to gain insight into whether the species that contributed to liana density and basal area early in liana succession were also dominant later in succession, or whether the contribution of species to liana stem number and basal area changed with succession.

Methods

Study site

We conducted this study at the Agua Salud research site in central Panama. The Smithsonian Tropical Research Institute in collaboration with the Panama Canal Authority (ACP) and the National Environmental Authority (ANAM) established the Agua Salud Project to study the effects of different land-use types on ecosystem function in the provision of targeted ecosystem services in the Panama Canal watershed (Stallard et al. [46]). We used data from a permanent secondary forest dynamics plot network that was established at Agua Salud in 2008 to understand landscape scale processes driving early secondary forest development in terms of forest dynamics and ecosystem function (Hassler et al. [18] , Neumann-Cosel et al. [28] , van Breugel et al. [4] , Battermann et al. [3] , Van Breugel et al. [47] , Zimmermann et al. [53]). Agua Salud is located adjacent to Soberania National Park in the central part of the Panama Canal Watershed (9°13' N, 79°47'W; Fig. [NaN]). The mean annual precipitation at Agua Salud is 2700 mm with a dry season from mid-December until early May (Ogden et al. [29] , Van Breugel et al. [47]). Historically, land in this area was used for cattle pasture and small-scale agriculture (Van Breugel et al. [47]). The site covers 700 hectares and contains a mixture of secondary forest, mature forest, cattle pasture, fallowed farmland, cultivated fields, and plantations. Within this forest matrix, we identified an early successional chronosequence with forests ranging from recently abandoned pastures (1 yr old) to 31 yr old. Forest plot ages were determined using landowner interviews that established the time of abandonment from agriculture (Van Breugel et al. [47]).
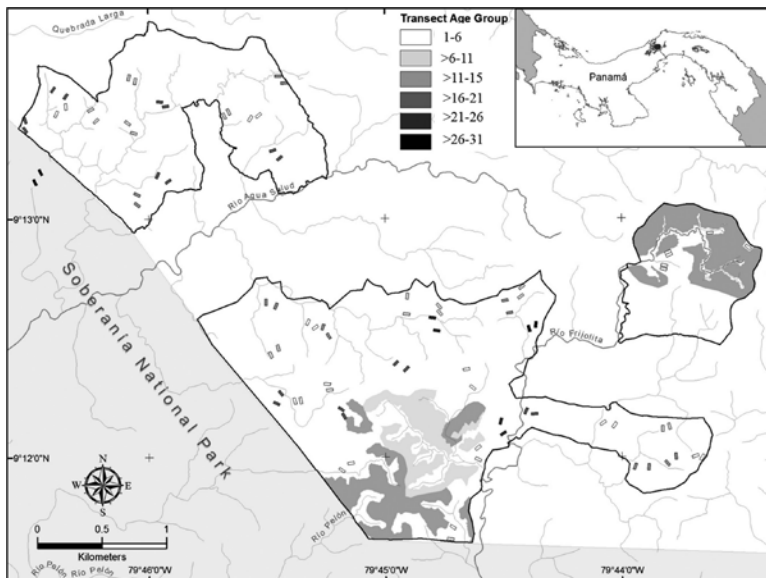
Figure 1 Map of the Agua Salud Project in central Panama bordering Soberania National Park. The Agua Salud project consists of a matrix of secondary forests, pastures, and cultivated fields managed by the Smithsonian Tropical Research Institute. Dark gray regions are comprised of a mixed-species reforestation experiment, light gray represents teak plantation. Rectangles represent each of our 43 study sites, which are color coded by age group. Each site consists of two plots, one upslope and one downslope. For the purposes of our analyses, we considered each site as a single replicate, as upslope and downslope plots did not differ significantly for any variable.

The Agua Salud forest network contains 52 distinct forest sites, which represent regional forest composition and structure. In each site, we established two replicate 20 m × 50 m plots, one at or near the top of the slope and one at or near the bottom of the slope to account for within-forest changes in elevation. We excluded nine sites for which we did not have reliable information on age and forest use as abandonment and sites where the upslope and downslope plots were not within 1 yr of age of each other. In total, we selected 43 sites, which ranged in age from 1 yr old to 31 yr old. Plot size in two of the sites was 2500 m², and thus we scaled liana density and basal area in all forests to the hectare level to control for sampling area.

Vegetation sampling

We used plot data from 2010. All lianas ≥1 cm that were rooted in the plot were identified and their diameter was measured (methods follow Gerwing et al. [16] , Schnitzer et al. [45] for lianas). We did not attempt to distinguish clonal stems from 'apparent genets' (cf., Schnitzer et al. [40] , [42]) and thus included all rooted stems ≥1 cm. We identified and measured the diameter of all trees ≥5 cm diameter in each plot. In addition, we measured trees ≥1 cm diameter in half of each plot to give an estimate of the density and basal area of smaller stems. Over 98 percent of individuals were identified to species. Voucher specimens were collected and stored at the herbarium of the Smithsonian Tropical Research Institute (Index Herbariorum code: SCZ). For more details about the site and sampling at Agua Salud SFD network, see Van Breugel et al. ([47]).

Data analysis

We scaled the plot data to per hectare scale assuming a linear increase in liana and total stem number per area. We used an ANOVA to compare upslope and downslope plots, which did not differ significantly for total stem density ($F_{1,103}$ = 2.521, P = 0.115) or total basal area ($F_{1,103}$ = 0.443, P = 0.507). Thus, we used the sum of the two plots per forest for all regression analyses and refer to this combination of two plots (upslope and downslope) as a site.

Some of the sites varied in distance from each other, which may lead to similarities among sites that are attributable to the site's location rather than to ecological factors (spatial autocorrelation). To test for this spatial autocorrelation, we calculated the Euclidean distance between each site and all other sites (using the 'dist' function in R) and performed a Mantel test (mantel.rtest in package 'ade4' v. 1.6-2; Dray & Dufour [13]) for each of our four variables with 1000 permutations (all reported P values for Mantel tests are simulated P values). We found significant spatial autocorrelation for liana density (P = 0.015, Pearson's r = 0.169), and no significant spatial autocorrelation in liana basal area (P = 0.053, Pearson's r = 0.101), relative liana density (P = 0.081, Pearson's r = 0.084), and relative liana basal area (P = 0.27, Pearson's r = 0.039). To examine the extent of the autocorrelation between location and liana density, we regressed Euclidean distance between sites with the difference in liana densities between those sites and found that while the model was significant (P < 0.001), the amount of variation it explained was very low ($F_{1,593}$ = 17.35, r^2 = 0.027), and thus we did not use location or site as a random effect in our analyses.

We used regression analyses to examine the relationship of the following variables with forest age: (1) liana density (stems/ha); (2) liana basal area (m^2/ha); (3) relative liana density (total number of liana stems/ha/total number of woody stems/ha); (4) relative liana basal area (liana basal area/ha/total woody plant basal area/ha); and (5) mean liana basal area per stem (m^2). For each variable, we hypothesized that liana abundance in terms of each of the above-mentioned variables could increase along one of three possible trajectories: (1) A linear increase (y = mx + b); (2) A saturating increase using the Monod enzyme kinetics model (y = (a * x) / (b + x)); or (3) An increase that peaked with subsequent decrease using a polynomial model (y = x + x^2). For the first two possible trajectories, we performed the analysis using the linear model (lm) function in R statistical software. However, the saturating model cannot easily be linearized and thus we used the non-linear least squares (nls) function. We used 95% confidence intervals to determine model significance for the Monod model because P values and R^2 are not good metrics of significance for non-linear models. We used Akaike information criterion (AIC) to test the goodness of fit for each of our possible trajectories to each variable. The AIC also weights models in terms of their complexity, penalizing models that have higher numbers of parameters, thus favoring more parsimonious models over models that are more complex (Crawley [6]). All analyses were done using R statistical software (v. 2.3.0).

Results

There were a total of 13,628 rooted lianas and 44,827 rooted trees ≥ 1 cm in diameter in the 43 sites across the chronosequence. Mean liana density was 1576 stems/ha and basal area was 0.48 m^2/ha. On average (across all sites), liana stems constituted 13.7 percent of all woody stems and 1.8 percent of basal area. At their maximum density, in an 11-yr-old plot, there were 3975 lianas/ha and lianas represented 30.3 percent of the total number of woody stems. A 25-yr-old forest with 3140 lianas/ha had the highest proportion of total woody plant basal area: 1.27 m^2/ha, with lianas contributing 31 percent of the total woody basal area (Table 1).

Table 1. Mean values of liana density and basal area for 43 forested sites in the Agua Salud watershed in central Panama. At each site we sampled two 20 × 50 m plots with the exception of the two 3-yr-old forests which were divided into two 25 × 100 m plots. Age represents forest age

Age	# of sites	Mean liana density (stems/ha)	S.E. (Liana density)	Mean liana basal area (m^2/ha)	S.E. (Basal area)
1	2	40	0	0.007	0.002
2	3	191.67	76.61	0.025	0.014
4	2	128	40	0.016	0.004
5	3	1461.67	238.93	0.359	0.055
6	4	1118.75	182.16	0.332	0.053

7	4	1038.75	159.16	0.228	0.013
8	4	2022.50	310.60	0.556	0.071
11	1	1860.00	0	0.377	0
12	2	3197.50	777.50	0.744	0.049
13	3	1720.00	210.18	0.547	0.041
14	1	1785.00	0	0.324	0
15	1	1170.00	0	0.393	0
16	1	2235.00	0	0.824	0
17	1	2540.00	0	0.665	0
18	1	1745.00	0	0.642	0
19	3	1880.00	260.24	0.633	0.059
21	3	2421.67	187.22	0.853	0.060
25	1	1795.00	0	0.683	0
26	1	3140.00	0	0.254	0
29	1	2285.00	0	0.241	0
30	1	2725.00	0	0.202	0
Total	43	1575.72	138.60	0.480	0.050

Absolute liana density and basal area were lowest in the youngest forests (1 yr old) but increased rapidly with forest age (Fig. [NaN] A and B). The saturating model of liana colonization with forest age was the best-fit model for all variables (Table [NaN]). The fit was significantly better than both the linear and polynomial models for all variables except basal area (Table [NaN]). Absolute liana basal area also increased quickly, reaching high levels of basal area within the first 5 yr of succession, and continued to increase steadily up to 31 yr of forest development showing no indication of saturation (Fig. [NaN] B). The increase in liana density, both in absolute values (Fig. [NaN] A) and relative to the total woody plant density (Fig. [NaN] C) began to level off within 7 yr of forest abandonment. However, liana basal area relative to total basal area increased very quickly within the first 2.5 yr of succession and attained near saturation within the first 5 yr of forest regeneration (Fig. [NaN] D). Mean liana basal area per stem increased quickly within the first 5 yr of succession at which point the rate of increase in per stem basal area decreased (Fig. 2 E).
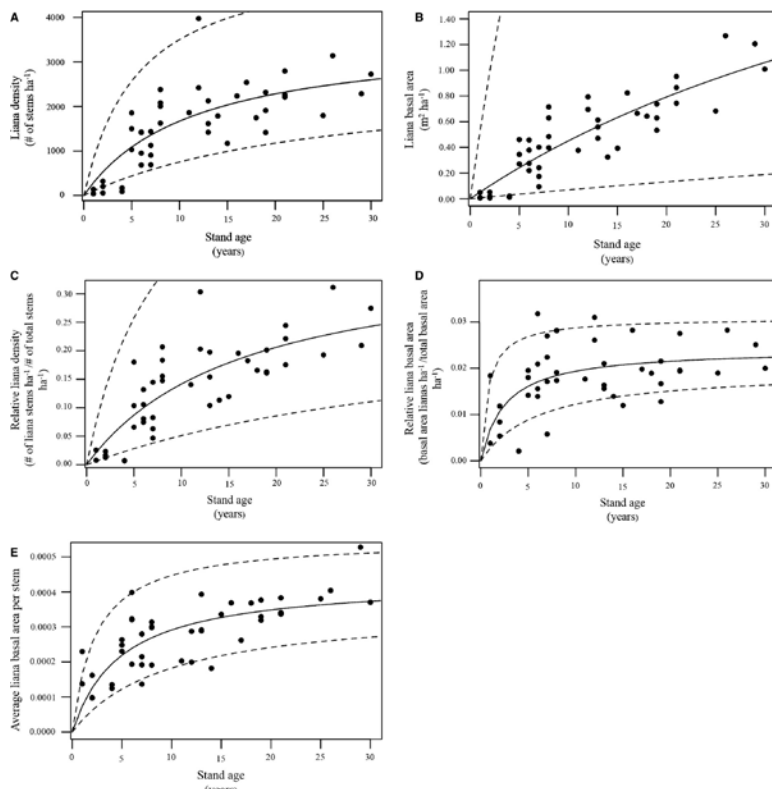
Figure 2 Change in liana density and basal area over forest age at Agua Salud. Liana density (A), liana basal area (B), relative liana density (# of liana stems/ha/# of total stems/ha) (C), relative liana basal area (liana basal area/ha/total basal area/ha) (D), and per stem basal area (liana basal area/ha/# of liana stems/ha) (E). All figures are for all lianas ≥1 cm diameter. All liana metrics saturated by the time forests reached 30 yr of age, except for liana basal area (C). Solid lines represent best-fit models (Akaike information criterion Table 2) and dashed lines represent 95% confidence intervals.

Table 2. Results of Akaike information criterion analysis for liana density, basal area, and species richness along the 30-yr chronosequence at Agua Salud. The lowest value for each variable is considered the best fit. Goodness of fit is considered significant if the difference is ≥2. Significant differences are shown in bold

Variable	Linear model	Monod model	Polynomial model
Liana density	697.13	670.58	675.13
Relative liana density	−116.31	−136.00	−131.50
Liana basal area	−26.53	−31.58	−30.25
Relative liana basal area	−263.70	−301.86	−286.78
Liana basal area per stem	−648.74	−687.68	−669.39

Table 3. The five most common species in each 5-yr age group of the 30-yr chronosequence at Agua Salud in central Panama. Davilla nitida and Connarus panamensis were the most common two species in every age class; the other three most common species were highly variable. The five most common species represented more than 50 percent of all stems at Agua Salud in each age class. Climbing habit was classified as S (stem twiner) or T (tendril climber)

Age class (years)	# of sites	Top five most common species in order from most common to	Family	Climbing habit	Proportion of total stem density comprised of the most	Proportion of total stem density comprised of top five most

		least common			common species	common species
1–6	14	Davilla nitida	Dilleniaceae	S	0.40	0.61
Connarus panamensis	Connaraceae	S				
Doliocarpus major	Dilleniaceae	S				
Doliocarpus multiflorus	Dilleniaceae	S				
Doliocarpus dentatus	Dilleniaceae	S				
>6–11	9	Davilla nitida	Dilleniaceae	S	0.55	0.59
Connarus panamensis	Connaraceae	S				
Davilla kunthii	Dilleniaceae	S				
Cnestidium rufescens	Connaraceae	S				
Sabicea panamensis	Rubiaceae	S				
>11–16	8	Davilla nitida	Dilleniaceae	S	0.45	0.64
Connarus panamensis	Connaraceae	S				
Doliocarpus multiflorus	Dilleniaceae	S				
Doliocarpus major	Dilleniaceae	S				
Doliocarpus dentatus	Dilleniaceae	S				
>16–21	8	Davilla nitida	Dilleniaceae	S	0.43	0.59
Connarus panamensis	Connaraceae	S				
Bignonia corymbosa	Bignoniaceae	T				
Maripa panamensis	Convolvulaceae	S				
Doliocarpus major	Dilleniaceae	S				
>21–26	2	Davilla nitida	Dilleniaceae	S	0.37	0.62
Doliocarpus multiflorus	Dilleniaceae	S				
Connarus panamensis	Connaraceae	S				
Doliocarpus dentatus	Dilleniaceae	S				
Odontadenia puncticulosa	Apocynaceae	T				
>26–31	2	Davilla nitida	Dilleniaceae	S	0.36	0.55

Connarus panamensis	Connaraceae	S					
Doliocarpus multiflorus	Dilleniaceae	S					
Bignonia corymbosa	Bignoniaceae	T					
Maripa panamensis	Convolvulaceae	S					

The two most common species of liana in all but one age class were Davilla nitida (Dilleniaceae) and Connarus panamensis (Connaraceae), respectively (Table [NaN]). Davilla nitida alone represented 35 percent or more of the total stem number in all age classes and the five most common species represented more than 50 percent of total stem number in all age classes (Table [NaN]). Doliocarpus multiflorus (Dilleniaceae) was among the most common species in four of six age groups. All but five of the 36 most common species were represented in the five most abundant species in more than one age group (Table [NaN]). The Dilleniaceae was by far the most dominant liana family at Agua Salud, representing 54.6 percent of the total stem number in all of the sites combined (Table 3).

Discussion

This is the first study to quantify the exceptional rate at which lianas colonize and accumulate in tropical forests during early succession. At Agua Salud, forests as young as 5 yr old commonly had more than 1000 lianas/ha (≥1 cm diameter), which is nearly the density of lianas in the nearby old growth forest on Barro Colorado Island (BCI; Schnitzer et al. [42]). By the time a forest at Agua Salud reached 10 yr in age, mean liana density was 2194/ha—more than 60 percent higher than liana density in the old growth forest on BCI (Schnitzer et al. [42] , [43]). As these forests continue to age, they will likely accumulate more liana stems, although liana stem density eventually begins to decline after 40–50 yr (DeWalt et al. [12] , Letcher & Chazdon [26]). Nonetheless, the relative abundance of lianas (as a proportion of all woody stems) at Agua Salud may continue to increase over time, leveling off at around 25 percent of the woody stem density, which is consistent with nearby old growth forests (e.g., Schnitzer & Bongers [37] , Schnitzer et al. [42]). Lianas at Agua Salud consistently represented more than 5 percent of the total woody stems in 5-yr-old forests and, in more than a quarter of the forests, lianas represented more than 15 percent of the woody stem density.

Relative liana basal area also increased rapidly with forest age, with lianas representing more than half of the relative basal area of nearby old growth forest on BCI within 5 yr of forest regeneration (0.015 m^2/ha lianas for every 1 m^2/ha total basal area in Agua Salud vs. 0.0293 m^2/ha lianas for every 1 m^2/ha total basal area on BCI). Mean relative liana basal area comprised 1.8 percent of the total woody basal area within 5 yr of forest regeneration and remained relatively constant afterwards. These data demonstrate the rapid rate at which lianas colonize in young secondary forests, which now represent more than 60 percent of global tropical forests (Aide et al. [1]). Several different factors may contribute to high relative liana abundance, including rapid recruitment of new stems, growth of existing stems, or relatively low tree basal area. Despite their clear prominence in secondary tropical forests, we understand relatively little of how liana presence in high abundance early in succession affects forest development, and whether lianas in high density will redirect forest succession toward a liana- and pioneer tree-dominated ecosystem, as hypothesized by Schnitzer et al. ([39]).

Colonization of forests by lianas appeared to be dominated by a small number of aggressively colonizing species, which recruited early and in high density, and were able to persist in high abundance throughout the 30-yr chronosequence. These early colonizing species (Table [NaN]) represented more than 35 percent of the liana

community in the different aged forests. Our data may document a transition in the relative abundance of some apparently early successional species, to later successional species. The high persistent abundance of D. nitida and C. panamensis in all age groups and the consistently high abundance of several other common species suggest that some liana species recruit early during forest succession and remain persistent for the first 31 yr or longer. However, neither of these species were particularly dominant in the old growth forest of the BCI 50-ha plot, with D. nitida and C. panamensis representing <1 percent and 0.01 percent of the 67,447 rooted stems, respectively (Schnitzer et al. [42]). In contrast, D. major, one the five most common liana species at Agua Salud, represented more than 3 percent of the liana stems in the BCI 50-ha plot, indicating that this species is able to achieve and maintain high stem densities throughout forest succession. Furthermore, Maripa panamensis, one of the most common species in the older forests (>15 yr) at Agua Salud, representing 2.5 percent of the stems in these forests, also represented a substantial proportion of the liana community in the BCI 50-ha plot (4.39 percent of the 67,447 rooted stems). If deterministic processes control liana abundance throughout succession (sensu Clements 1916), the relative abundance of M. panamensis should continue to increase at Agua Salud.

Our findings are consistent with those of previous studies by DeWalt et al. ([12]), Kuzee and Bongers ([23]), and Letcher and Chazdon ([26] ; see also Letcher [25]). DeWalt et al. ([12]) studied an older chronosequence of seasonal forests at the Barro Colorado Nature Monument (BCNM) in central Panama (20 yr old to mature) and found that liana density was highest in forests that were 20 and 40 yr old and decreased sharply in density in forests 70 yr and older. We compared the 20-yr-old forests at Agua Salud with the 20-yr-old forests of DeWalt et al. ([12]) (after controlling for sampling differences) using Welch's two sample t-test and found no significant difference in mean liana density, basal area, or mean basal area per stem (Table [NaN]). Older forests at BCNM tended to have fewer but larger lianas, which is consistent with normal thinning found during succession. For example, the mean basal area per stem was nearly three times higher in the older forests at BCNM than the younger forests at Agua Salud (>30 yr old, 0.00072 m^2 per liana, DeWalt et al. [12]).

Table 4. Results of Welch's t -test comparing data from the 20-yr forests at the Agua Salud 30-yr chronosequence to those of nearby Barro Colorado Island (sampled by DeWalt et al. 12) both in central Panama. We found no significant differences between the liana density and basal area/ha and mean basal area per stem between the 20-yr-old forests at Agua Salud (N = 3) and Barro Colorado Island (N = 2)

Variable	Agua Salud (mean)	DeWalt et al. (mean)	P-value	T-statistic	Degrees of freedom
Liana density/ha	2421.67	2081.25	0.83	0.270	1.046
Total liana basal area/ha	0.853	1.1700	0.77	−0.371	1.010
Mean basal area per stem	0.00035	0.00049	0.44	−1.187	1.032

In a series of different aged wet forests in Costa Rica, Letcher and Chazdon ([26]) reported that liana density (in both absolute terms and relative to trees) was highest in 20-yr-old forest, and decreased linearly thereafter. Liana density was two times higher at Agua Salud than in the relatively aseasonal tropical wet forests in Costa Rica sampled by Letcher and Chazdon ([26]). This stark contrast in liana density may be explained by differences in mean annual precipitation and dry season length. Liana density is inversely correlated with mean annual precipitation and positively correlated with the length of the dry season (Schnitzer [36] , DeWalt et al. [11] , [10]). Mature wet tropical forests in Costa Rica are less than half as liana dense as mature forests in Panama (DeWalt & Chave [9] , Mascaro et al. [27] , Schnitzer et al. [42] , [43] , Yorke et al. [52]). Therefore, lianas may play a much larger role in succession in forests with longer dry seasons and lower mean annual precipitation.

Our findings demonstrate that lianas can recruit rapidly during forest development, and that forests as young as 5 yr old can have liana densities that approach or exceed those of nearby old growth forests. After 10 yr of forest development, mean liana density can be more than 60 percent higher than that of nearby old growth forests. The rapid rate of liana colonization appears to be led by a subset of liana species that colonize early in high abundance and appear to be able to persist well beyond the 30-yr duration of our chronosequence. By rapidly colonizing regenerating forests, lianas may redirect forest successional trajectories, a hypothesis that remains be tested.

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