



Does soil moisture availability explain liana seedling distribution across a tropical rainfall gradient?

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ABSTRACT

Liana density tends to increase with decreasing rainfall and increasing seasonality. However, the pattern of liana distribution may be due to differences in soil water retention capacity, not rainfall and seasonality *per se*. We tested the effect of rainfall and soil substrate with respect to the distribution of liana seedlings in six sites across a rainfall gradient from the wet Atlantic to the dry Pacific in central Panama. Soils were either limestone, with low water-holding capacity, or laterite, with higher water-holding capacity. We sampled liana seedlings at each site using three 1 × 100 m transect. We found that relative liana seedling density was higher on limestone soils compared to laterite soils regardless of the amount of rainfall. Furthermore, liana community composition on limestone soils was more similar to dry forest sites than to adjacent wet and moist forest sites. Liana seedling species diversity relative to trees was significantly higher in a low-fertility dry forest site compared to a high-fertility forest, but did not differ from the other sites. Thus, liana seedling density and community structure may be driven more by soil type and thus by soil moisture availability than strictly by mean annual rainfall and the seasonality of rainfall.

Abstract in Spanish is available with online material.

Key words: canopy height; diversity; lianas; Panama; rainfall seasonality; soil.

TOTAL ANNUAL RAINFALL, THE SEASONALITY OF RAINFALL, AND SOIL PROPERTIES (WATER RETENTION CAPACITY, TEXTURE, AND CHEMISTRY) ARE IMPORTANT FACTORS THAT influence plant diversity, abundance, and distribution (Gentry 1988, Clinebell *et al.* 1995, Pyke *et al.* 2001). Lianas are one of the most characteristic growth forms of tropical forests (Schnitzer & Bongers 2002, Schnitzer *et al.* 2015), and they have a unique distribution with respect to rainfall compared to competing woody plants. Liana density peaks in tropical seasonal dry forests and decreases with increasing rainfall and decreasing seasonality, a pattern that is opposite from that of trees (Schnitzer 2005, DeWalt *et al.* 2010, 2015); thus, rainfall amount and seasonality are strong predictors of liana density among forests (Schnitzer 2005). One mechanism proposed for this pattern is that lianas have well-developed root systems that allow them to more effectively tap water from deeper soil sources than neighboring trees, giving lianas the chance to outgrow trees during the dry season, a hypothesis that has received some empirical support (Zhu & Cao 2009, Cai *et al.* 2009, Chen *et al.* 2015).

The change in liana density with mean annual rainfall may be driven by the seasonal pattern of rainfall itself, the availability of water in the soil, or some combination of other variables that are related to mean annual rainfall. Liana density does not appear

to be affected by soil chemistry and nutrients (Dalling *et al.* 2012) or habitat type (elevation, slope, and aspect; Nabe-Nielsen 2002, Ledo & Schnitzer 2014, and Molina-Freaner *et al.* 2004). However, soil type with respect to soil water-holding capacity, that is, limestone soil vs. lateritic soil, may influence liana density independently of total annual rainfall and seasonality. If so, the availability of soil moisture may be a better explanation for the pattern pan-tropical of liana density than strictly the amount and seasonality of annual rainfall.

We tested the hypothesis that the distribution of lianas is affected by soil moisture availability, regardless of the annual amount and seasonality of rainfall. We examined the change in liana seedling density, diversity, climbing strategy, and community composition along the strong rainfall gradient across the isthmus of Panama from the wet, relatively non-seasonal Caribbean (>3000 mm rainfall per year) to the drier and highly seasonal Pacific coast (~1300 mm per year) (Condit 1998, Pyke *et al.* 2001, Sautu *et al.* 2006). We focused on liana seedlings, which can constitute up to a quarter of all woody seedlings (Putz 1984), because rainfall and soil water availability will likely have the greatest effect on the mortality of seedlings and consequently on seedling relative densities (Engelbrecht *et al.* 2005, 2007). Dry forests on limestone are uncommon on the Pacific coast of Panama, so we restricted our comparison of limestone and laterite soils to the wet and moist forest sites along the gradient, which allowed us to test whether the amount and seasonality of rainfall (and

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their associated factors) predicted liana density among the wetter forests, or whether soil moisture availability (lower in limestone than in laterite soils in the wet and moist forest sites) was a better predictor of liana density and distribution.

We also hypothesized that liana growth strategy would shift predictably with mean annual rainfall. Specifically, we hypothesized that freestanding liana seedlings, those that do not need a support host immediately after germination and can grow like a small sapling or shrub for months to many years, would be relatively more abundant on the wettest part of the rainfall gradient because they can tolerate the lower-light understory conditions that are found in those forests. By contrast, climbing liana seedlings, those that begin twining and searching for a host immediately after germination, would be in higher abundance in the dry end of the gradient, where there is more light penetration into the forest (Condit *et al.* 2000) and the fast growing liana growth form is advantageous when competing trees are less active (Schnitzer 2005, 2015).

METHODS

STUDY SITES.—We conducted the study in six separate late-secondary forest sites located across the Panama canal watershed. Two of the sites were on the ever-wet Caribbean side of the isthmus, two were halfway across the gradient in the seasonal center of the Panama isthmus, and two were located on the highly seasonal Pacific coast (Fig. 1). In both the Caribbean and central sites, one forest site was located in a forest growing on an outcrop of limestone (LS-W1 and LS-M2, respectively) and the other site was located in a forest growing on the more common laterite soil (LA-W1 and LA-M2, respectively). On the dry Pacific side of Panama, we placed both sites in forests growing on lateritic soil sites (LA-D1, LA-D2)—one site (LA-D1) had relatively low-fertility soils, and the other site (LA-D2) had relatively high-fertility soils (Turner & Engelbrecht 2011). Limestone soil forest sites do not exist in the dry Pacific area of the isthmus. Nonetheless, the limestone soils provide the strongest contrast and thus the best test of water-holding capacity hypothesis in the wet and moist forest sites, and not the dry forest site.

We collected the environmental variables (rainfall, dry season length, soil substrate, elevation, topography, canopy height, and density of trees ≥ 50 cm dbh) for each of the six study sites (Table 1). Rainfall across the gradient ranged from the wet, relatively a-seasonal Atlantic coast (>3000 mm mean annual rainfall) to the seasonal middle part of the Panama isthmus (2400 mm mean annual rainfall), to the drier and highly seasonal Pacific coast (~ 1300 mm mean annual rainfall) (Pyke *et al.* 2001, Condit *et al.* 2004). The length of the dry season is approximately 106 days on the Atlantic side, 118 days in the middle of the gradient, and 129 days on the Pacific side (Condit 1998, Condit *et al.* 2000). The two limestone sites had higher fertility levels than their paired laterite sites. Of the two dry forest laterite sites, LA-D2 had higher fertility than LA-D1 (Turner & Engelbrecht 2011, B. Turner pers. comm.). Additional information on the sites is available in Turner and Engelbrecht (2011), Condit *et al.* (2013),

and from the Center for Tropical Forest Science Web site: (<http://ctfs.si.edu/Public/Datasets/PanamaTreePlots/PanamaPlotInfo.php>).

FIELD METHODOLOGY.—During the wet season in 2008, between October and November, we established a square 1 ha plot at each site and placed three 1-m-wide and 100-m-long transects within each plot. The first transect was located in the middle of the plot, and the two others were located 40 m to either side of the first. For each transect, we placed a 1-m² PVC frame with marks at 0.5 m on all sides over a rope that indicated the center of the transect in such a way that the 0.5 mark was directly over the rope. We surveyed all liana seedlings (10–300 cm in length) located within the sampling frame along the entire length of each transect. This methodology has been used in several other studies (Harms *et al.* 2000, Comita *et al.* 2010).

For each liana encountered, we identified it to species, categorized it by growth strategy (climbing or freestanding), counted the number of leaves, and measured stem length, stem diameter at 5 cm from the soil (to be used as basal diameter), and stem diameter at 5 centimeters below the apical bud (to be used as the apical diameter). We categorized a seedling as ‘climbing’ if it was actively climbing another plant and as ‘freestanding’ if the seedling was self-supporting and not entwined with (or leaning on) another plant. We placed a uniquely numbered tag on every liana seedling longer than ten centimeters in length. If the stem was longer than 1.3 m, we recorded the stem diameter 1.3 m distance along the stem from the ground (methods follow Gerwing *et al.* 2006, Schnitzer *et al.* 2008). If the liana stem was longer than 3 m, it was considered out of the seedling category and was not included in the census.

At each site, we measured the canopy height and the leaf area index (LAI) of the forest at the time of the seedling census (October–November). The canopy height was measured using a Nikon Pro Staff Laser 440 Rangefinder (Nikon Corporation, Japan) every five meters along each transect. At each five meter point along every transect, we recorded three measurements: one directly above the transect and two more five meters to one side and five meters to the other side of that point. We measured LAI every 5 m along the transects using a PAR/LAI ceptometer LP-80 (Decagon Devices Inc. Pullman, Washington, USA).

We sampled the soil in five of the six sites between March and April 2014 to construct water retention curves to confirm our assumptions that the limestone soils were drier than the laterite soils (Turner & Engelbrecht 2011). We omitted one of the Pacific laterite sites (LA-D2) because it was unreachable at the time of the survey. At each of the five sites that we sampled, we collected a soil core from the top ten centimeters of soil. We selected the bottom 2 centimeters of the sample and saturated it with water and then slowly dried the sample in an airtight container with silica desiccant. We measured soil water potential with a dew point potentiometer (MODEL WP4C, Decagon Devices) every 15 min until soil water potentials were close to or below -10 Megapascals (Mpa)

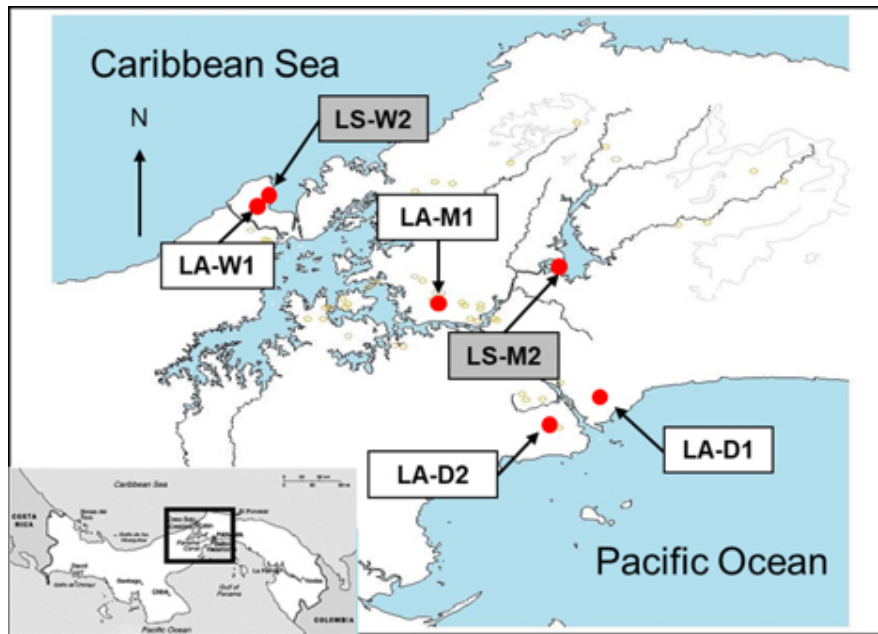


FIGURE 1. Locations of CTFS plots, small circles, and the study sites, red circles, across the Panama isthmus. Insert shows Panama with the square indicating the location of the large map. The names LA and LS corresponded to laterite or limestone soil, respectively, W, M, and D to the position across the rainfall gradient: wet, mid and dry, finally the number is to separate sites in the same part of the gradient.

TABLE 1. Environmental characteristics for the six study sites used in this study. UTM coordinates correspond to zone 17. The mean canopy height was measured parallel to the census transects and is given as a mean \pm 1 SD, $n = 190$ for all study sites. Significance symbols (a and b) indicate that those means followed by the same letter do not differ using Tukey's HSD pairwise comparisons. All significant differences are at $P < 0.001$ (ANOVA $F_{5, 1062} = 24.8$, $P < 0.001$).

CTFS site code	Atlantic Wet Side		Middle		Pacific Dry Side	
	LS-W2 P01	LA-W1 P02	LS-M2 Campo Chagres	LA-M1 P15	LA-D2 Cerro Galera	LA-D1 PNM
Environmental characteristic						
Precipitation (mm/year) ^{1,2}	3140 ¹	3140 ¹	2378 ²	2130 ²	1866 ¹	1797 ²
Soil type ¹	Limestone	Laterite	Limestone	Laterite	Laterite	Laterite
Dry season length (Days) ³	106	106	118	118	129	129
Elevation (mamsl) ⁴	20	100	109	70	300	64
Easting coordinates (UTM) ⁴	-79°57'14.76"	-79°57'43.56"	-79°35'59.28"	79°44'43.08"	-79°37'41.26"	-79°32'34.8"
Northing coordinates (UTM) ⁴	9°19'57.11"	9°19'22.66"	9°12'41.26"	9°9'42.34"	8°55'36.12"	8°59'40.52"
Site topography ⁴	Irregular	Level	Level	Level	Sloped	Irregular
Canopy height (m)	15.79 \pm 7.43 ^b	22.02 \pm 7.33 ^a	15.92 \pm 8.55 ^b	21.32 \pm 7.57 ^a	21.93 \pm 8.07 ^a	20.49 \pm 6.28 ^a
Stand age ⁴	Secondary	Primary	Mature Secondary	Mature Secondary	Mature Secondary	Secondary
Stems \geq 50 mm per Ha ⁴	605	570	585	663	358	412

Sources: ¹Smithsonian Tropical Research Institute, Environmental Science Program. ²Panama Canal Authority, Meteorology and Hydrology Branch. ³Pyke *et al.* (2001). ⁴Center for Tropical Forest Science.

(Gubiani *et al.* 2013). This measure of soil retention is robust to the conditions and season of sampling.

STATISTICAL ANALYSIS.—For each 1 ha plot per site, we calculated the mean liana seedling number, species diversity, species evenness, growth strategy, and community composition using the

three 100 m² transects. We also calculated the number of liana seedlings relative to tree density (stems >10 mm diameter) at each site using data from these plots (Condit *et al.* 2013). A relative measure of liana seedling recruitment allowed us to account for the variation in plant density across plots. To determine how liana communities changed along the rainfall gradient, we

compared the mean species richness and evenness using a one-way ANOVA (means were based on the three 100 m² transects). Species evenness was defined as $(e^H/\ln(S))$, where e = evenness, H = Shannon diversity index, and $\ln(S)$ = the natural log of the number of species in the sample. We compared similarities in species composition of the plots across the gradient using the Bray–Curtis similarity index, which included both species presence and abundance. We analyzed the difference in forest canopy height among the plots using a one-way ANOVA followed by a Tukey HSD *post hoc* test. We compared liana seedling density and diversity (both in absolute values and relative to trees) among the plots using a two-way analysis of variance (ANOVA), with plot type (wet, mid, dry) and soil type (laterite or limestone) as the factors. Because the limestone soils were present only in the mid and wet range of rainfall gradient, and one of our main goals was to decouple rainfall from soil moisture-holding capacity, we restricted our comparisons to those two sets of plots for this latter test. All analyses were conducted in PAST (Paleontological Statistics) software ver. 2.06 (Hammer *et al.* 2001), which is available online: <http://folk.uio.no/ohammer/past/>.

We used a log-linear analysis of the distributions of the freestanding and climbing liana species across the study sites using R v. 2.9.2 software (R Development Core Team, 2010, Oksanen *et al.* 2013). We compared the distribution of the freestanding and climbing seedlings across the rainfall gradient, as well as tested the effect of the interaction between rainfall and soil on the distributions of the two liana seedling categories. We also compared the mid and wet sites that have both limestone and laterite soils to assess the effect of soil substrate independently of the rainfall pattern.

RESULTS

We found a total of 1455 seedlings comprising 74 species in the six sites. Eleven species ‘morphotypes’ were identified only to the family level and consequently were removed from the final species count, reducing the total number of species to 63 in 43 genera and 19 families. The final number of identified liana seedlings was 1397. The most diverse families with respect to the number of species were the Sapindaceae (11 species in three genera), Bignoniaceae (nine species in nine genera), and Fabaceae (nine species in four genera), which is consistent with other sites in central Panama (*e.g.*, Schnitzer *et al.* 2012).

Absolute seedling density was significantly higher in the limestone plots than in the laterite plots ($F_{\text{soil},1,12} = 9.32$, $P = 0.009$), regardless of location along the rainfall gradient (Fig. 2A). The plot with the highest number of seedlings was LS-W2 (limestone soil) at the wettest part of the rainfall gradient, with 479 individuals, followed by 388 individuals in the more seasonal limestone soil plot located in the middle of the rainfall gradient (LS-M1). The laterite plots had far fewer liana seedlings, ranging from 131 to 190 seedlings per site (Table 2).

The relative number of liana seedlings (with respect to tree density) was highest in the two limestone sites and one of the

dry forest sites ($F_{5,12} = 6.87$, $P = 0.003$; Fig. 2B). In terms of soil fertility, both absolute and relative liana densities were highest in the two limestone plots. However, relative liana density was significantly higher in the infertile dry forest than in the fertile dry forest. Absolute liana density did not differ between the infertile and fertile dry forest plots.

Species richness did not differ significantly among the plots ($F_{5,12} = 1.18$, $P = 0.3724$; Fig. 2C). The highest species richness was at plot LA-M1, with 31 species, followed by LS-M2 with 30, LA-W2 (29), LA-D2 (27), LS-W2 (26), and LA-D1 (26) (Table 2, Fig. 2C). However, relative species richness was two times more in infertile dry forest site (LA-D1) than in the other sites (Fig. 2D).

There were substantially fewer climbing lianas than freestanding lianas in all of the plots (Fig. 2E). However, the relative abundance of climbing liana seedlings was significantly higher on the dry side of the rainfall gradient than in the middle or wet ($df = 2$, $G^2 = 99.49$, $P < 0.001$). There was a slightly higher proportion of climbing liana seedlings in the limestone sites compared to the laterite sites ($df = 1$, $G^2 = 5.31$, $P = 0.02$) (Fig. 2E).

The laterite plots had relatively high species evenness, with the limestone plots having very low species evenness (Table 2, Fig. 3). In the limestone plots, only a few species were dominant, and thus, the species dominance curves showed a rapid decrease in common species (Fig. 3). In LS-W2, we found 26 species, with the two most abundant species, *Connarus turkestaninowi* and *Hippocratea volubilis*, accounting for 58 percent of the total number of seedlings. In LS-M2, we found 30 species, with only one species, *Anthodon panamense*, accounting for 50 percent of all the individuals.

Liana species in our study seem to be generalists with respect to the rainfall gradient, and 45 of 63 species were present in all plots across the gradient. Only nine species (14%) were restricted to the wet side of the gradient, while seven species (11%) were restricted to the dry side of the gradient (Table 3). Nearly half of the species (26 of 56) were present on both soil substrates (Table 3), while 13 and 17 species were found only in limestone or laterite soils, respectively (Table 3). The Bray–Curtis similarity analysis revealed that the two limestone (LS-W2, LS-M2) and laterite plots (LA-W1, LA-M2) at the high and middle rainfall locations (LS-W2, LS-M2) were very different (they clustered together on their own separate branches), leaving the two dry forest plots (LA-D1, LA-D2) in between (Fig. 4).

Soil from the limestone plots dried faster and reached lower water potential faster than soil from the laterite plots (Fig. 5), confirming that the limestone soils indeed had lower water-holding capacity than the laterite soils (Turner & Engelbrecht 2011, Condit *et al.* 2013). Forest canopy height was lower in the limestone forests than in the lateritic sites, but did not differ between the lateritic sites across rainfall gradient (Table 1). Forest leaf area index (LAI) was slightly but not significantly lower in the limestone plots than in the laterite plots (Fig. S2). Thus, the limestone plots had lower soil water capacity and a lower canopy than the laterite plots, but leaf area index (and thus light penetration into

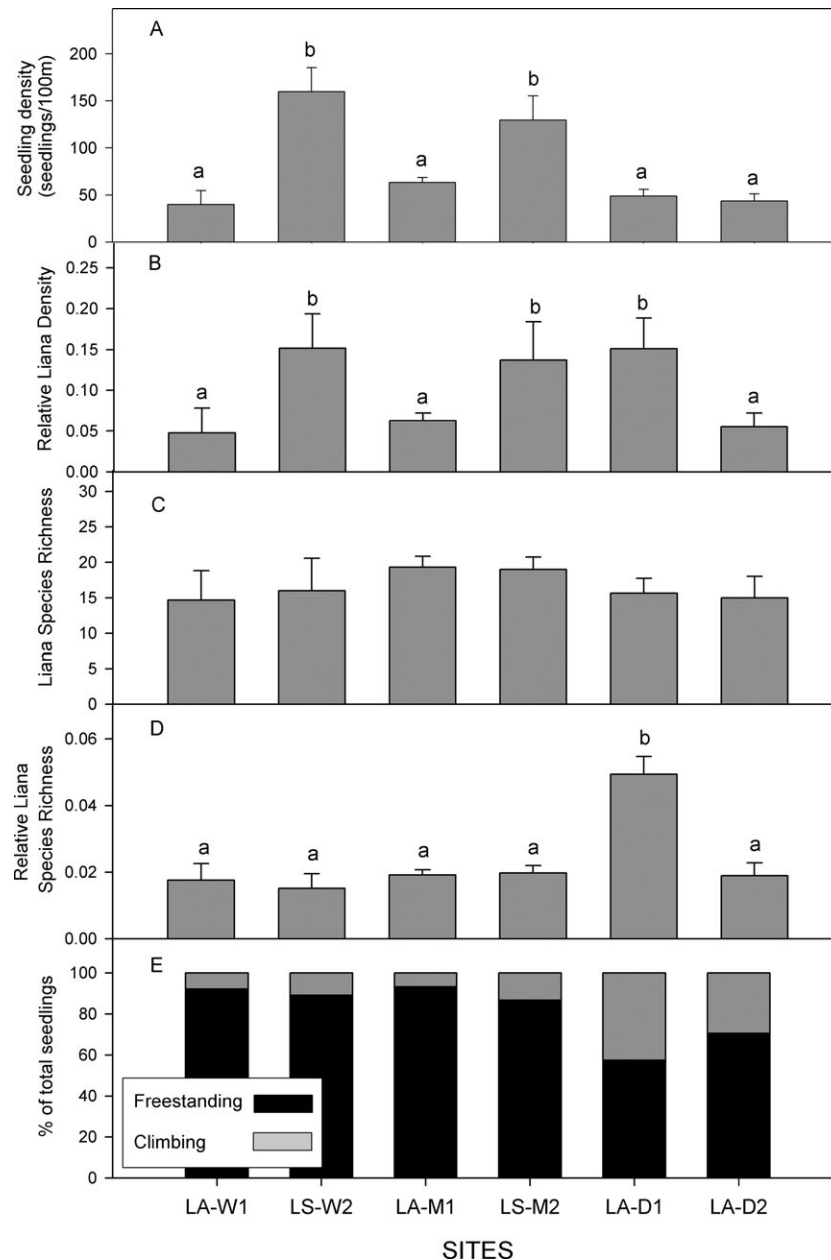


FIGURE 2. (A) Mean liana seedling density using three one hundred meters transects, (B) Mean relative liana density (relative to tree stems >10 mm dbh), (C) Mean liana species richness by site, (D) Mean relative liana richness (relative to tree stems >10 mm dbh), (E) percentage of liana seedlings that were climbing (light bars) or freestanding (dark bars). Plot means and standard errors were calculated using three 100 × 1 m transects per site. Different letters indicate significant differences ($P < 0.05$).

the forest understory) did not differ significantly between the plots.

DISCUSSION

The ability to predict liana density in Neotropical forests based on mean annual rainfall and seasonality has been examined in a variety of papers. Several authors found adult lianas to be more abundant and diverse in tropical dry forest than in tropical wet

forest (Schnitzer 2005, Swaine & Grace 2007, DeWalt *et al.* 2010, 2015) For example, using the same rainfall gradient in Panama, the abundance of lianas was higher in the dry forest than in the wet forest. These findings have led to the hypothesis that the general pattern of adult liana abundance is controlled by the seasonality and amount of rainfall, with highest liana abundance in seasonally dry tropical forests (Schnitzer 2005, 2015)

Our findings differed from those of previous studies in interesting ways and may provide evidence for the causal factors

TABLE 2. Biodiversity indices, density of liana seedlings, relative liana seedling density (per tree stems >10 mm), relative liana seedlings richness over tree stems (per tree stems >10 mm), number of freestanding and climbing seedlings, and diversity indices for each of the study sites.

	Atlantic Wet Side		Middle		Pacific Dry Side	
	LA-W1	LS-W2	LA-M1	LS-M2	LA-D1	LA-D2
Individuals	141	479	190	388	147	131
Species	29	26	31	30	26	27
Genera	21	20	24	25	22	23
Families	14	13	12	14	11	11
Seedlings/m ²	0.47	1.6	0.63	1.29	0.49	0.44
Relative liana seedling density/m ²	0.045	0.15	0.062	0.14	0.15	0.055
Relative liana seedling richness/m ²	0.02	0.013	0.019	0.021	0.052	0.021
Freestanding	132	429	178	341	85	93
Climbing	9	50	12	47	62	38
Dominance D	0.1	0.2	0.09	0.3	0.09	0.07
Shannon H	2.82	2.07	2.88	1.85	2.71	2.88
exp(H)	16.73	7.96	17.76	6.33	15	17.89
Simpson 1-D	0.9	0.8	0.91	0.7	0.91	0.93
1/D	10.27	5.11	10.82	3.36	10.65	13.39
Evenness (H/lnS)	0.58	0.31	0.57	0.21	0.58	0.66
Equitability J	0.84	0.64	0.84	0.54	0.83	0.88
Fisher alpha	13.16	5.96	10.54	7.67	9.37	10.54

of liana distribution. We found that absolute liana seedling density was influenced more by soil water-holding capacity in the moist and wet forests than by mean annual rainfall or the seasonality of rainfall. Liana seedling density, using both absolute values and relative values, was more than two times higher in the limestone sites than in laterite sites with the same amount of rainfall. These findings suggest that the water-holding capacity of the soil, more than the amount and seasonality of rainfall, is an important predictor of liana abundance. That is, in relatively wet regions, forests on soils with low water-holding capacity have many more lianas than in adjacent forest on the more common clayey soils. In a study at Xishuangbanna, China, Chen *et al.* (2015) found that lianas in a karst forest with low water-holding capacity relied on a greater amount of deep water and performed better than trees in terms of predawn leaf water potential, sap flow, and leaf water status during the dry season than in forests with higher water-holding capacities. Likewise, in this same forest, (Cai *et al.* 2009) reported that, compared to trees, lianas suffered less reduction in photosynthesis and carbon assimilation during the dry season than in the wet season. Thus, our findings, along with those of others, support the hypothesis that lianas perform well when water availability is low, and our comparison of forests with vastly different soil types while holding rainfall constant is a compelling test of this hypothesis.

The two limestone soil sites in the wet and moist forests had a different species composition than the adjacent laterite sites, and the limestone sites were more similar to the dry sites in terms of the liana seedling community. This finding indicates that liana species are adapted to different conditions and are adapted to forest type, even though the vast majority of the liana species

in this study were present across the isthmus of Panama. Tree species composition in the wet limestone sites was also more similar to that of dry forests in Panama than to wet forests on laterite soils (Pyke *et al.* 2001), indicating that the limestone forest provides a habitat more similar to dry laterite forests than to nearby wet laterite forests. The low evenness measure for lianas in the limestone sites suggests that some liana species thrive in dry sites, where they can become particularly dominant.

Liana seedling density (in absolute terms) did not peak in the dry forests, as we had expected. This finding was somewhat inconsistent with previously reported findings for adult lianas, which increased in density in dry forests (*e.g.*, Schnitzer 2005, DeWalt *et al.* 2010, 2015). Nonetheless, relative liana density was high in one of the dry forest sites, with a density similar to that of the limestone forests. The relative measure of liana density accounts for the variation in plant density among plots, and thus, we are able to better compare the change in liana density relative to tree density across the gradient. Furthermore, the relative measure is more consistent with the initial hypothesis to explain the negative correlation between liana density and rainfall, which was that lianas had the ability to outperform co-occurring trees in drier forests compared to wet forests (Schnitzer 2005).

It is possible that differences in soil nutrient levels may have contributed to the pattern of relatively high liana density in the limestone forest. Indeed, soil fertility was higher in the two limestone forests compared to their paired laterite forest sites (Turner & Engelbrecht 2011). However, in the dry forest sites, liana density in absolute terms did not differ between the high and low-fertility sites. Furthermore, relative liana density was more than two times higher in the low-fertility dry forest plots than in the

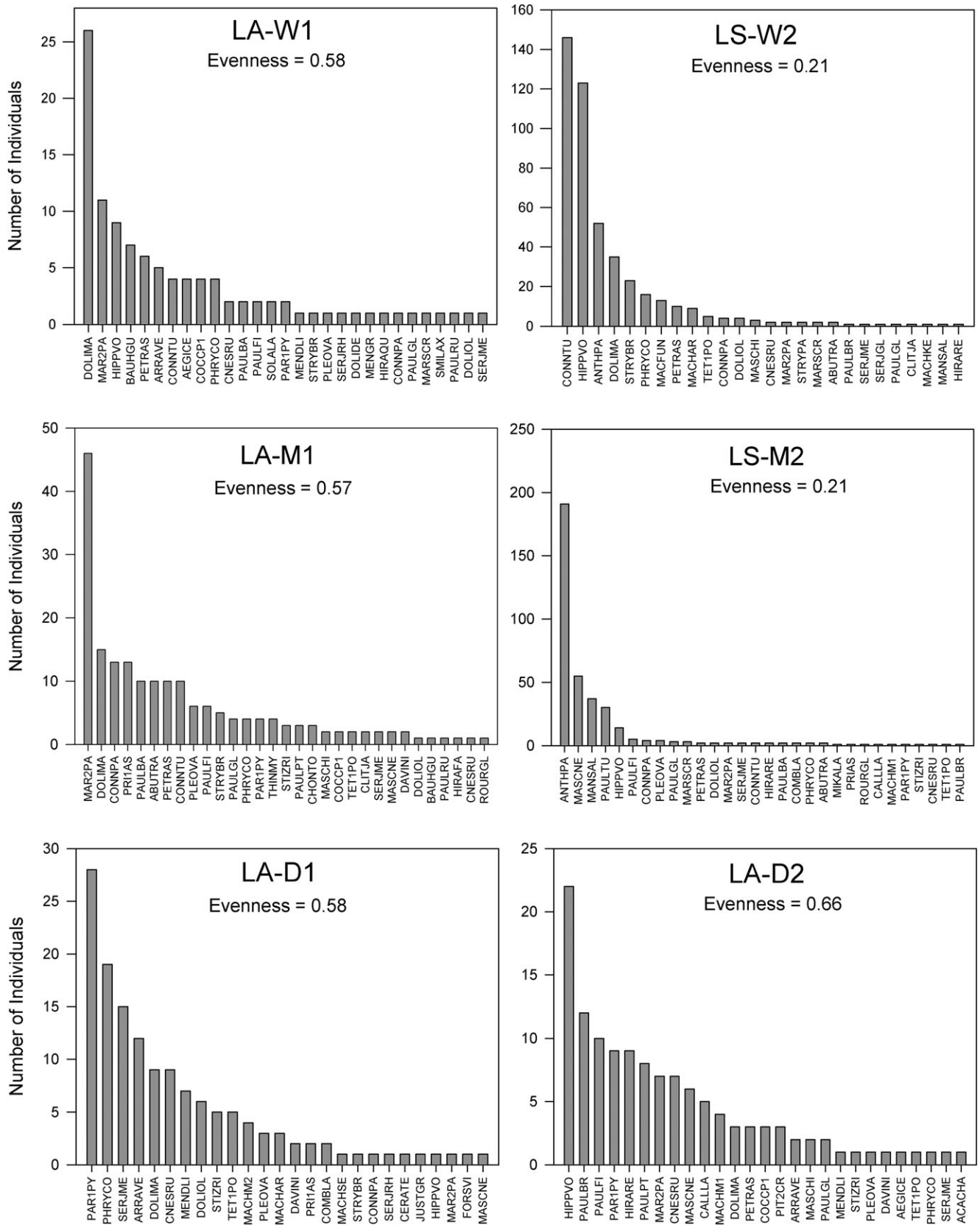


FIGURE 3. Number of seedlings by species in each study site and the evenness ($E = H/\ln(S)$) value for each site. Total number of seedlings per species is shown on the y-axis and species name, using the appropriate CTF species code (Table 3).

TABLE 3. Mean canopy height, measured every five meters along the 100 meters transects and leaf area index (LAI) measured in the same points as the canopy height in the six study sites.

	LA-W1	LS-W2	LA-M1	LS-M2	LA-D1	LA-D2
Mean canopy height	36.02	15.80	33.32	15.92	26.49	27.93
Mean LAI	4.23	3.48	4.72	3.17	3.83	3.50

high-fertility dry forest plots, suggesting that soil fertility was not responsible for liana density—at least in dry forests, where lianas are typically in peak abundance (Schnitzer 2005).

While many tropical tree species respond to soil nutrients (e.g., Baribault *et al.* 2012, Condit *et al.* 2013), previous studies do not support a meaningful relationship between soil fertility and liana density. For example, using a census of the lianas (stems ≥ 1 cm diameter) of the BCI 50-ha plot, Dalling *et al.* (2012) found no support for the hypothesis that liana species had strong affinities to soil nutrients and chemistry, even though liana density at the community level (*i.e.*, including all liana stems) was slightly higher in the drier parts of the plot (see also Ledo & Schnitzer 2014). DeWalt and Chave (2004) did not find differences in abundance of lianas across a soil fertility gradient, which included four biological stations: La Selva, Costa Rica; Barro Colorado Island, Panama (BCI); Coshacashu, Peru; and a field station north of Manaus, Brazil. In a series of sites in the Peruvian Amazon, (Phillips *et al.* 2002) found no evidence for an effect of soil fertility on the abundance of lianas. In Borneo, DeWalt *et al.* (2006) also did not detect a relationship

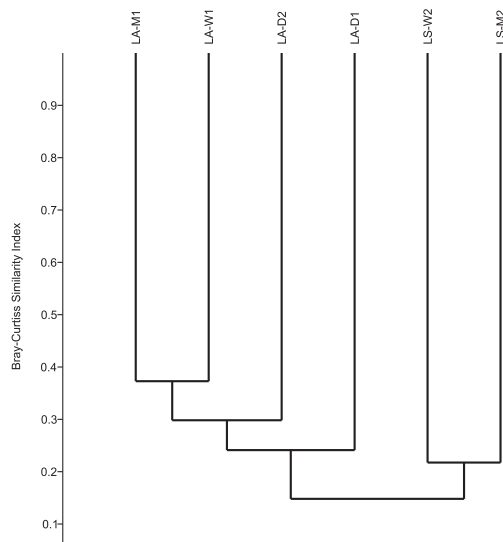


FIGURE 4. Results of a similarity analysis using Bray–Curtiss coefficient for the six study sites indicating that the limestone soil sites share more species between them than with the adjacent laterite soil sites. The dry forest laterite sites were between the wet forest limestone and laterite soils in terms of species similarity.

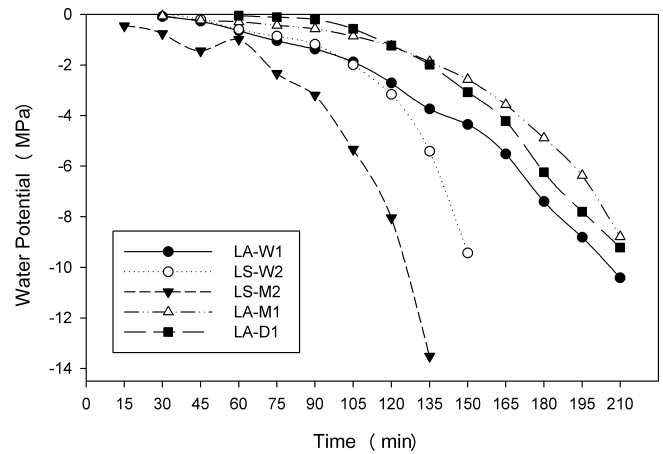


FIGURE 5. Water potential of five of the six study sites as they dried over time.

between the density of small lianas and soil fertility; however, they did find that there were more large lianas in fertile alluvial soil. In sum, the evidence for soil moisture appears to outweigh the evidence for soil fertility.

Forest leaf area index and understory light penetration are also a possible explanation for the pattern of liana distribution. However, LAI differed only slightly and not significantly between the sites. The lower canopy height in the limestone sites coupled with slightly lower LAI may have allowed slightly more light to reach the understory, which could have contributed to a higher liana seedling density in the limestone forest. However, additional data are necessary to make firm conclusions about the relative roles of soil water availability and light as drivers of liana seedling density.

The proportion of climbing lianas was slightly higher in the limestone soil sites than in the laterite forest sites; however, these differences were rather small compared to the far higher proportion of climbing liana seedlings in the dry forest sites. There may be more climbing lianas in the drier sites because there is more available light in those sites due to less cloud cover during most of the year. Higher light penetration into the dry forest sites, especially during the dry season, may facilitate high growth rates of liana species that climb immediately after germination (Kurzel *et al.* 2006). Alternatively, higher dry season light availability may act as a trigger for lianas to begin to climb, and the greater proportion of climbing liana seedlings may be attributable directly to higher light in the understory. By contrast, in wetter forests, liana species that are freestanding as seedlings may be adapted to low light conditions in the understory until they find a suitable host or when a gap in the canopy is created, similar to the strategy used by shade-tolerant tree species.

In conclusion, soil water-holding capacity is a strong predictor of liana density and distribution, perhaps even stronger than total annual rainfall or the seasonal distribution of rainfall. We cannot rule out the role of soil fertility in explaining the pattern of liana density; however, evidence for the role of soil fertility is not as compelling as evidence for soil moisture. Our findings more firmly narrow the explanation for among-

forest liana distribution: the ability of lianas to perform well in sites where soil water availability is limited—not merely in sites that are highly seasonal and receive low mean annual rainfall.

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DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.113v0> (Manzané-Pinzón *et al.* 2017).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

TABLE S1. *Species name, species and family code, and abundance in each of the study sites.*

TABLE S2. *Table of species abundances the gradient.*

TABLE S3. *Table of species abundances on the two soils surveyed.*

FIGURE S1. Water potential of five of the six study sites as they dried over time (A) and plotted against the relative water content (B).

FIGURE S2. Relationship between leaf area index and mean canopy height across the six study sites.

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