

ECOLOGY OF LIANAS

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BIOGEOGRAPHICAL PATTERNS OF LIANA ABUNDANCE AND DIVERSITY

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OVERVIEW

Liana abundance and species diversity are higher in tropical than temperate forests, but substantial variation exists in liana community structure within tropical forests, particularly among biogeographical

regions and along gradients in altitude, precipitation, and edaphic characteristics. We used liana surveys from across the world, which we compiled into the Global Liana Database (GLD), to examine patterns

in liana abundance and diversity among continents, between islands and continental regions, and along climatic gradients. We focused particularly on the change in tropical liana abundance and diversity with mean annual precipitation and dry season length, both of which appear to be strong predictors of liana community structure.

Tropical sites in the GLD provide a wide environmental gradient, spanning gradients in mean annual rainfall of 850–7000 mm and seasonality (dry season length) of 0–7 months. The GLD presents a higher resolution alternative to the global dataset of 0.1 ha transects that Alwyn Gentry compiled in the 1980s and 1990s because the replication at each site is much greater, thus yielding a better estimate of liana abundance and diversity per site.

Using the GLD, we found that neotropical and African forests have almost twofold greater liana density than forests in Asia, and that African liana diversity is 50% greater than sites in South America and 140% greater than sites in Central America and Asia, after accounting for climatic conditions. Within each biogeographical region, liana density declines with increasing mean annual precipitation and increases with seasonality in precipitation. Liana diversity, in contrast, shows a tendency for a hump-shaped relationship with mean annual precipitation but no relationship with dry season length. Differences in liana density and diversity among biogeographical regions in the GLD mirror those found in Gentry's global dataset, but patterns of abundance and diversity in relation to mean annual precipitation and dry season length did not. Documentation of pantropical biogeographical patterns in liana abundance and diversity is a leap forward in the study of liana ecology because it provides the basis for the generation of hypotheses about pantropical drivers of liana proliferation and speciation.

INTRODUCTION

Tropical forests are well known for their high liana abundance and diversity relative to temperate forests (Gentry 1982; 1991). Lianas in mature lowland tropical forests are particularly abundant and diverse, but substantial variation exists in the structural importance and diversity of lianas among these forests (Gentry 1991; DeWalt & Chave 2004; Schnitzer 2005; DeWalt et al. 2010). For example, lianas compose

2–32% of woody stems and 9–35% of woody species, when comparing similarly sized stems (DeWalt & Chave 2004; van der Heijden & Phillips 2008, 2009; Schnitzer et al. 2012; Schnitzer et al., Chapter 7 in this volume). The abundance and diversity of lianas, like other plant growth forms, are affected by numerous processes, which lead to biogeographical differences among continents and islands, as well as variation along altitudinal, climatic, and edaphic gradients. Understanding the processes responsible for the abundance and distribution of organisms is a central goal in ecology. In this chapter, we examine pantropical patterns of liana abundance and species diversity and their correlates with climatic characteristics to gain insight into which processes are important for the distribution of tropical lianas.

Our analyses follow from the standard sampling protocol of liana diversity and abundance used by Alwyn Gentry in the 1980s and 1990s, which allowed for the first direct comparisons in these metrics for forests around the world (Gentry 1988; 1991). Specifically, this protocol enabled the first assessments of how liana abundance and species richness change with soil fertility and precipitation on regional and global scales (Gentry 1988; Clinebell et al. 1995; Schnitzer 2005; van der Heijden & Phillips 2008, 2009). Although the magnitude of Gentry's tremendous contributions should not be diminished, his transects were narrow (2 m × 50 m), and greater liana density and species richness are typically found in narrower rather than wider rectangles or in square plots, particularly for small plots (Schnitzer et al. 2006, unpublished data). In addition, Gentry used a fairly large size cutoff for lianas (2.5 cm diameter), and his transects encompassed small areas (10 transects each of 0.01 ha, equaling 0.1 ha at each site). Because lianas are typically clumped and most liana stems are in smaller size classes (Putz 1984; Campbell & Newbery 1993; Ibarra-Manríquez & Martínez-Ramos 2002; Dalling et al. 2012; Schnitzer et al. 2012), variance in liana density and species diversity is high among small plots. Not surprisingly, large differences have been found in liana abundance between the Gentry data and those gathered from larger plots, as well as wider plots with the same total sampled area as the Gentry transects (DeWalt & Chave 2004). Therefore, to test the correlates and possibly drivers of liana abundance and distributions, it is essential to use surveys from much larger sampling plots than those represented in the original Gentry datasets.

To this end, we have created the Global Liana Database (GLD) (<http://www.LianaEcologyProject.com/global-liana-metadata>). The GLD includes plot, species, and individual-level information for lianas surveyed in more than 30 tropical, subtropical, and temperate forest locations. Most of the sites include plots greater than 0.1 ha. In the GLD, we include only liana-centered studies designed to document liana abundance or diversity in fixed areas; excluded are tree-focused studies that primarily document liana loads and associations between liana abundance and tree demographics. An earlier version of the GLD, which included 24 sites, was used to examine relationships among density and basal area of lianas and a variety of abiotic, edaphic, and geographic factors (DeWalt et al. 2010).

To examine how climatic conditions are associated with liana density and diversity, we focus our analyses on old-growth continental forests (including continental-fragment islands such as Borneo) at <1050 m in elevation and with mean annual precipitation >850 mm yr⁻¹. These sites therefore include tropical dry broadleaf forest and tropical moist broadleaf forest. As of May 2013, the GLD included 29 such sites for which we can examine patterns of liana density. Species identifications are available for 20 of the 29 sites (4 in Central America and Mexico, 5 in South America, 2 in Africa, and 9 in Asia), which allow us to examine patterns of diversity (Fig. 11.1). We compare patterns generated by the GLD with those generated by the global Gentry dataset (Phillips & Miller 2002), which includes 11 sites in Africa including Madagascar, 65 in the neotropics (mostly in South America), 13 in Asia (including Taiwan, New Guinea, and Borneo), 1 in Australia, and 1 in New Caledonia. These liana surveys were previously reported in several publications (Gentry 1991; Clinebell et al. 1995; van der Heijden & Phillips 2008, 2009). To broaden the discussion of determinants of liana density and diversity beyond climatic factors, we also comment on differences between temperate and tropical forests and between continental and island regions. To this end, we discuss sites in the GLD from temperate forests in Australia, subtropical forest in Argentina, and an island in the Caribbean, and also review the available literature.

STANDARDIZATION OF LIANA SAMPLING

Without standardized sampling methods, it is difficult to compare liana species richness, composition, or even abundance across studies. Measuring liana diameter at different locations along the stem, treatment of the ramet-genet issue, plot shape, and inclusion or exclusion of hemi-epiphytes and rattans can all affect estimates of liana abundance and diversity (Schnitzer et al. 2006, 2012; Schnitzer et al., Chapter 7 in this volume). To standardize across studies, we followed the methods of DeWalt et al. (2010), who used the allometric equations from Schnitzer et al. (2006) to adjust diameter measurements made at points other than 130 cm along the stem from the last substantial roots. This point of measurement is the suggested point of measurement for liana surveys (Gerwing et al. 2006; Schnitzer et al. 2008). To include the most sites in the GLD, we used 2.5 cm as the minimum liana diameter. For studies that noted when single lianas had multiple rooted stems, we included only the largest diameter stem of each genet or "principal stem" for the density and diversity analyses (Gerwing et al. 2006; Schnitzer et al. 2008). We excluded species in the Araceae, Arecaceae, Marcgraviaceae, Poaceae, and all ferns. Members of the Araceae and Marcgraviaceae tend to be hemi-epiphytes but are sometimes included in liana studies (Gentry 1991; Rice et al. 2004; Gerwing et al. 2006). Arecaceae (e.g., rattans) and Poaceae (e.g., climbing bamboo) are monocots, do not have secondary thickening, and often have leaf sheaths around the stem that increase the apparent diameter. We included, however, the monocot families Smilacaceae and Dioscoreaceae, which are often included in liana studies because of their persistent fibrous stem and their presumed ecological equivalence to many liana species (Gerwing et al. 2006; Schnitzer et al. 2008).

It was not possible to standardize plot shape across the disparate studies. Liana individuals meeting the above criteria were simply counted and summed for each plot. For the estimate of liana diversity (see below), we included only individuals positively identified to species or morphospecies.

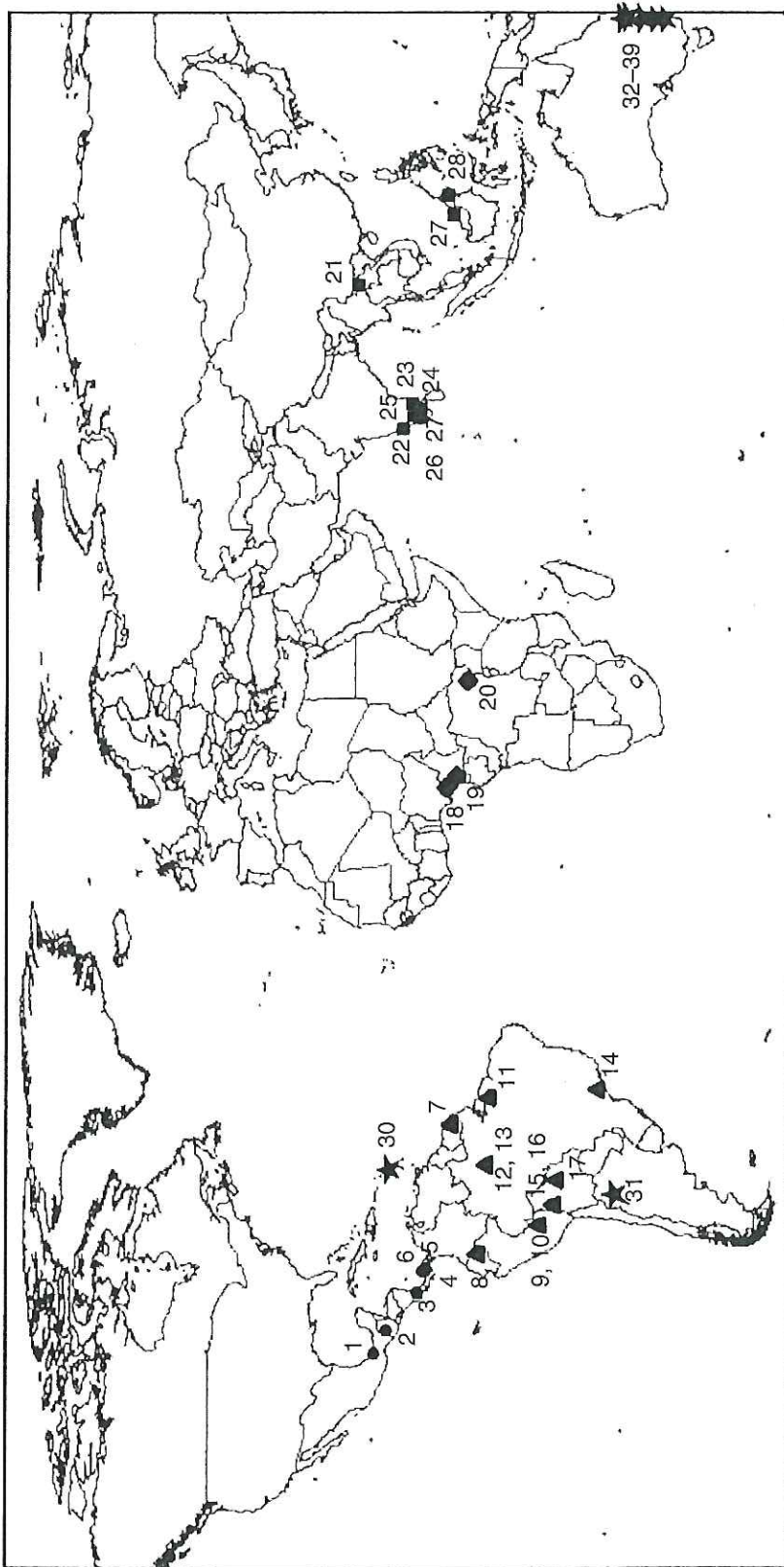


Fig. 11.1 Sites currently in the Global Liana Database and used in this study. Numbers correspond to site codes in Table 11.1. Sites are labeled with circles for Mexico and Central America, triangles for South America, diamonds in Africa, and squares in Asia. Shapes correspond to those used in the other figures. Stars denote sites not included in analyses but mentioned in the text.

Table 11.1 Density and diversity of lianas ≥ 2.5 cm diameter in sites included in the Global Liana Database. Density is mean number of lianas per ha at a site. Diversity is presented as Fisher's α . MAP is mean annual precipitation (mm yr^{-1}). DSL is the mean number of months per year with ≤ 100 mm/mo. Altitude is mean altitude (m above sea level) of plots within each site. Area is the total number of ha sampled across studies at each site. Means computed for each biogeographical region are not adjusted for differences in climate, as they are in Fig. 11.2. Source denotes the citation(s) for each study.

Site	Location	Density (ind./ha)	Fisher's α	MAP (mm yr^{-1})	DSL (mo)	Altitude (m)	Area (ha)	Source
<i>Central America</i>								
1	Los Tuxtlas	Mexico	221	6.5	4725	1	100	1.00 3;22
2	Chajul	Mexico	622	14.9	3000	4	111	1.20 15
3	La Selva	Costa Rica	218	11.0	4000	0	103	1.48 7;16;23
4	Cocoli	Panama	463	—	1750	5	25	0.08 35
5	Barro Colorado Island	Panama	283	16.0	2600	4	79	47.00 7;9;37;38;40
6	Fort Sherman	Panama	300	—	3000	0	50	0.09 35
<i>Central America mean</i>		351	12.1	3179	2	78		
<i>South America</i>								
7	Nouragues	French Guiana	417	—	3000	3	100	0.24 36
8	Yasuní	Ecuador	379	21.2	3000	0	243	4.00 4;17;34
9	Cocha Cashu	Peru	277	—	2099	3	357	1.40 5;7
10	Los Amigos	Peru	266	21.8	2800	3	303	1.00 5
11	Fazenda Sete	Brazil	1414	—	1700	6	100	0.29 14
12	Km41	Brazil	105	—	2650	2	75	0.60 7
13	Ducke	Brazil	220	—	2400	2	70	14.00 27
14	Ubatuba	Brazil	180	17.3	2200	3	375	1.00 1
15	Madidi	Bolivia	262	9.8	2335	3	620	1.30 18;19
16	NW Bolivia	Bolivia	275	—	2550	4	235	0.20 10
17	Oquiriquia	Bolivia	1283	7.6	1500	6	200	1.08 30
<i>South America mean</i>		462	15.5	2385	3	243		
<i>Africa</i>								
18	Ebom	Cameroon	339	—	2035	5	409	26.00 29
19	Korup	Cameroon	320	35.7	5272	3	160	10.00 41
20	Ituri	D. R. Congo	464	16.3	1785	5	750	20.00 2;12;20
<i>Africa mean</i>		374	26.0	3031	4	440		
<i>Asia</i>								
21	Baka	China	524	7.7	1050	7	750	0.50 6
22	Agumbe	India	121	4.8	7250	5	425	2.00 28
23	Coromandel Coast (Coastal)	India	353	5.5	1292	5	10	4.00 32
24	Coromandel Coast (Inland)	India	304	4.3	854	6	119	4.00 33
25	Eastern Ghats	India	210	4.2	1058	5	645	55.00 24
26	Valparai	India	113	10.4	3497	4	1048	4.40 25
27	Varagalaia	India	126	9.1	1845	4	600	30.00 26
28	Lambir Hills	Borneo	122	—	2980	0	133	0.65 31;39
29	Sepilok	Borneo	136	7.1	2929	0	100	2.00 8
<i>Asia mean</i>		223	6.6	2528	4	426		

Table 11.1 (continued).

Site	Location	Density (ind./ha)	Fisher's α	MAP (mm yr ⁻¹)	DSL (mo)	Altitude (m)	Area (ha)	Source
Island								
30	Dominica	Caribbean	76	1.7	–	–	492	3.50 11
Subtropical								
31	Tucumán	Argentina	323	2.1	1100	5	1000	6.00 21
32	Wooyung	Australia	333	–	1811	–	11	0.03 13
33	Iluka*	Australia	767	2.2	1522	–	20	0.03 13
Temperate								
34	Bongil Bongil*	Australia	1000	1.1	1679	–	15	0.03 13
35	Sea Acres*	Australia	967	1.2	1590	–	55	0.03 13
36	Myall Lakes*	Australia	800	1.2	1366	–	30	0.03 13
37	Bass Point	Australia	800	–	1407	–	23	0.03 13
38	Beecroft	Australia	867	–	1394	–	14	0.03 13
39	Mimosa	Australia	367	–	959	–	29	0.03 13

Note: * Fisher's α is calculated for lianas ≥ 1.0 cm diameter.

Sources:

1	Alves et al. (2012)	22	Martínez-Ramos unpublished data
2	Bongers and Ewango (Chapter 3 in this volume)	23	Mascaro et al. (2004)
3	Bongers et al. (1988)	24	Muthumperumal and Parthasarathy (2010)
4	Burnham (2002)	25	Muthuramkumar et al. (2006)
5	Burnham unpublished data	26	Muthuramkumar and Parthasarathy (2000)
6	Cai et al. (2009)	27	Nogueira et al. (2011)
7	DeWalt and Chave (2004)	28	Padaki and Parathasarathy (2000)
8	DeWalt et al. (2006)	29	Parren (2003)
9	DeWalt et al. (2000)	30	Pérez-Salicrup et al. (2001)
10	DeWalt unpublished data	31	Putz and Chai (1987)
11	DeWalt and Ickes unpublished data	32	Reddy and Parthasarathy (2003)
12	Ewango (2010)	33	Reddy and Parthasarathy (2006)
13	Gallagher and Leishman (2012)	34	Romero-Saltos et al. (2001)
14	Gerwing unpublished data	35	Schnitzer (2005)
15	Ibarra-Manríquez and Martínez-Ramos (2002)	36	Schnitzer et al. (2006)
16	Letcher and Chazdon (2009)	37	Schnitzer et al. (2012)
17	Macía (2008)	38	Schnitzer et al. (Chapter 7 in this volume)
18	Macía (2011)	39	Schnitzer unpublished data
19	Macía et al. (2007)	40	Schnitzer and Carson unpublished data
20	Makana et al. (1998)	41	Thomas et al. (Chapter 2 in this volume)
21	Malizia et al. (2010)		

CALCULATING LIANA DIVERSITY

Sites may have greater species richness because of a greater underlying diversity of the species pool, greater abundance of individuals, or a combination of the two (Gotelli & Colwell 2011). It is not possible to standardize among sites by dividing observed species richness by the area sampled or the number of individuals sampled because of the non-linearity of species accumulation

curves. Using the ratio of species richness to area in a small area will lead to substantial over-estimates of the number of species expected in large areas (Gotelli & Colwell 2001, 2011).

To examine broad patterns of liana species diversity with data from sites with different liana densities and areas sampled, we calculated Fisher's α , a commonly used diversity metric that is relatively unaffected by sample size (Magurran 2004). It is equal to the

number of species expected to be represented by a single individual in a community; therefore, communities with many rare species are indicated by larger values of Fisher's α (Magurran 2004). Fisher's α was calculated only for plots with ≥ 25 individuals.

ANALYSES OF PATTERNS ASSOCIATED WITH CLIMATE AND BIOGEOGRAPHICAL REGION

We tested whether liana density and diversity differ among biogeographical regions (Central America, including Mexico, South America, Africa, and Asia) and if they vary with mean annual precipitation (MAP) or dry season length (DSL). Individual research groups provided the values for MAP and DSL. DSL was defined as the mean number of months per year with ≤ 100 mm of precipitation. Liana density was scaled to 1 ha for each plot/subplot. To control for sampling area, we computed Fisher's α and density for each 1-ha subplot in plots where ≥ 1 ha had been surveyed and then averaged the values. In addition, to avoid pseudoreplication, we calculated average Fisher's α and density among plots separated by < 100 km if the climate and elevation were similar. In some cases, this meant averaging among several plots/studies conducted at a single site. We natural-log transformed the response variable of liana density to normalize residuals.

We first examined bivariate relationships between liana density or diversity and each of the two climatic variables (MAP and DSL) for each biogeographical region. For this purpose, we compared models that used the untransformed or natural-log transformed variables and fitted linear or quadratic polynomial regressions (i.e., $a \times \text{DSL}$ and $b \times \text{DSL}^2$ or $c \times \text{MAP}$ and $d \times \text{MAP}^2$, where a , b , c , and d are coefficients). We did not include interaction terms between biogeographical region and MAP or DSL because of the relatively low sample sizes for each region, particularly Africa. We selected the best-fitting bivariate model for each of MAP and DSL as the model with the lowest AIC value (data not shown). We then compared these bivariate models with ones containing both climatic variables (MAP and DSL) to determine the best-fitting overall model. All tests were conducted in R v. 3.0.1 (R Development Core Team 2009) using the "glm" function to obtain AIC values and the "lm" function for the F -statistics and multiple R^2 values.

BIOGEOGRAPHIC PATTERNS

Among tropical sites, the density of lianas ≥ 2.5 cm in diameter varied more than 10 times (range: 105–1414 lianas ha^{-1} ; Table 11.1). African, Central American, and South American forests had more than twice the average liana density of Asian forests when calculated at mean values for MAP and DSL (Fig. 11.2A). Asian

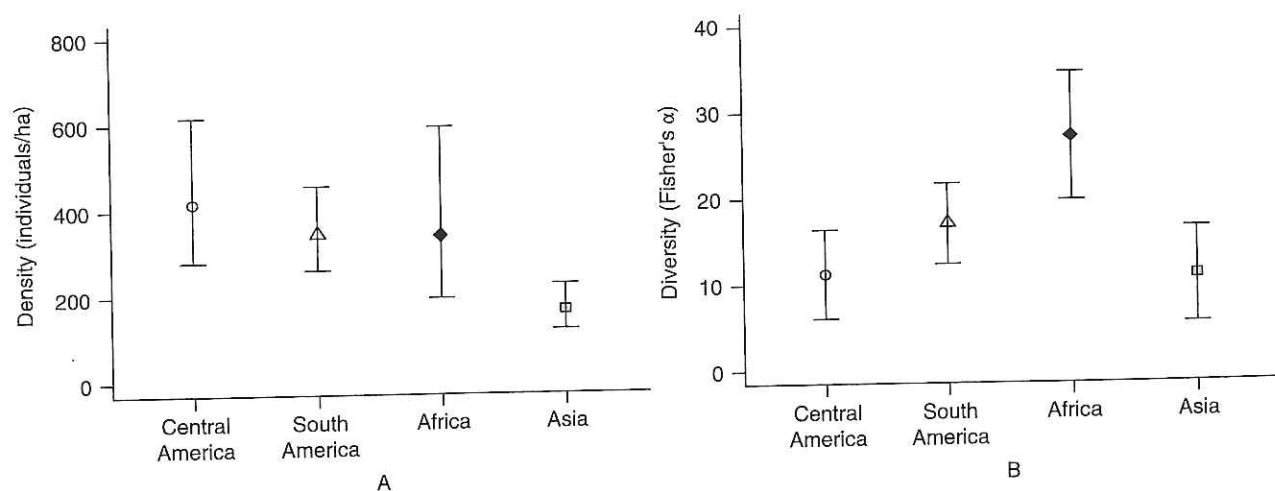


Fig. 11.2 Mean density (A) and diversity (B) of lianas ≥ 2.5 cm in diameter for the four biogeographical regions with MAP and DSL kept at their average values (LSmeans). Density was back-transformed. Diversity is measured as Fisher's α . Bars represent 95% confidence intervals. For density (A), there were 6 sites in Central America, 11 in South America, 3 in Africa, and 9 in Asia. For diversity (B), the number of sites included were 4 in Central America, 5 in South America, 2 in Africa, and 8 in Asia.

sites averaged 163 lianas ha^{-1} , whereas the other three biogeographical regions averaged 365 lianas ha^{-1} . Nonetheless, liana density differed greatly within biogeographical regions, particularly in South America where one site in Brazil (Gerwing & Vidal 2002) and one in Bolivia (Pérez-Salicrup et al. 2001) supported twice as many lianas as the other South American sites. Liana density did not differ among Africa, Central America, and South America even when these two high-density sites in South America were removed from the analysis.

Liana diversity, as measured by Fisher's α , varied almost nine times among sites (range: 4.2–35.7) and also differed among biogeographical regions. African sites had 59% greater diversity than South American ones, and 140% greater diversity than Central American and Asian sites at similar levels of MAP and DSL (Fig. 11.2B). Only two sites represented African forests, which is unlikely to be representative of all of Africa. The deficits in the data notwithstanding, the underlying diversity of the liana species pool appears greatest in Africa and South America.

Patterns of liana density and diversity among biogeographical regions in the GLD were similar to those

reported by Gentry (1991). In Gentry's global analysis, African forests supported much higher liana densities than Australasian forests and more than neotropical forests. In addition, species richness was roughly equivalent in African and neotropical forests and much greater than in Asian sites (Gentry 1991). In both the GLD and Gentry datasets, Asian forests appear to contain substantially fewer lianas and lower liana diversity than other biogeographical regions. The GLD suggests that Central American sites have lower diversity than South American sites, when controlling for MAP and DSL. Thus far, Central and South American forests have not been directly compared in Gentry's dataset.

PATTERNS RELATED TO PRECIPITATION

Liana density

Liana abundance was negatively associated with mean annual precipitation and positively associated with dry season duration using the GLD dataset (Fig. 11.3; Table 11.2). Liana density declined most quickly with

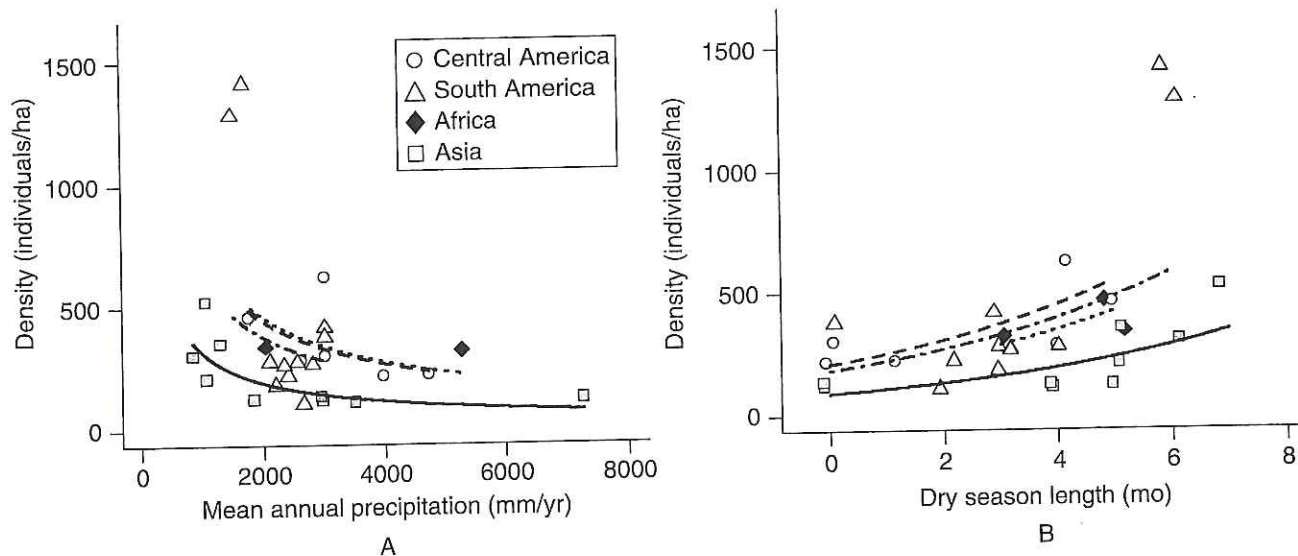


Fig. 11.3 Bivariate relationships between liana density and (A) mean annual precipitation and (B) dry season length for the four biogeographical regions. Each point represents the liana density for a site listed in Table 11.1. In (A), the point for Ituri (Africa) is not visible behind Cocoli (Central America) at 1750 mm yr^{-1} . The points in (B) are jittered so that they are visible. Lines represent the regression equations calculated from the best-fitting bivariate model (MAP or DSL) for Central America (dashed), South America (dashed and dotted), Africa (dotted), and Asia (solid). In (A), the regression lines for Central America and Africa overlap. In (A), density = $\text{intercept} \times \text{MAP}^{-0.739}$ with intercept = 121,176 for Central America; 103,708 for South America; 125,713 for Africa; and 52,300 for Asia. In (B), density = $\text{intercept} \times \exp(0.193[\text{DSL}])$ with intercept = 207 for Central America; 182 for South America; 160 for Africa; and 88 for Asia.

Table 11.2 Model coefficients and *t*-values from the best-fitting models explaining log(density) and Fisher's α diversity of lianas. For each variable, we examined bivariate models for the MAP or DSL parameters as well as overall models potentially including both parameters. All models also included biogeographical region. Multiple R^2 values are provided for each model.

Variable	R^2	Coefficient	t^a	Parameter
(A) Density				
	0.45			MAP only
		-0.739	-3.44*	log(MAP)
	0.52			DSL only
		0.193	4.10**	DSL
	0.57			Overall
		-0.402	-1.72	log(MAP)
		0.140	2.56*	DSL
(B) Diversity				
	0.71			MAP only
		7.24e-03	2.07*	MAP
		-8.34e-07	-1.88*	MAP ²
	0.64			DSL only
		-0.76	-1.10	DSL
	0.71			Overall
		7.24e-03	2.07*	MAP
		-8.34e-07	-1.88*	MAP ²

Notes: * $0.05 < P < 0.1$, * $P < 0.01$, ** $P < 0.001$

^a *df* for each model parameter for (A) density are 1,24 for the MAP and DSL bivariate models, and 1,23 for the overall model. *df* for (B) diversity are 1,13 for the MAP and overall models, and 1,14 for the DSL model.

increases in precipitation at the lowest MAP values in the dataset. For each biogeographical region, liana density was predicted to be 2.7 times as high in seasonally dry forests with 5-month dry seasons than in rain forests with no dry months. The best-fitting overall model for density, which explained 57% of the variance, included biogeographical region, log(MAP), and DSL (Table 11.2). In addition, the length of the dry season explained more of the variation in liana density than mean annual precipitation.

The clear relationship between rainfall patterns and liana density in the GLD contrasts with previous reports based on the Gentry data. Using data solely from Gentry's neotropical dataset, neither Gentry (1982, 1991) nor van der Heijden and Phillips (2008) found an association between liana density and MAP or DSL. In contrast, Schnitzer (2005) found a significant negative relationship between liana density and MAP using all of Gentry's data from neotropical and paleotropical sites as well as his own data from the steep rainfall gradient across the isthmus of Panama. The lack of a relationship between liana abundance and climatic variables in Gentry's dataset appears,

for some reason, restricted to the neotropics. In the GLD, the negative relationship between liana density and MAP and the positive relationship between liana density and DSL are apparent for both neotropical and paleotropical sites (Fig. 11.3A). Gentry's neotropical dataset covers longer gradients in MAP than the GLD (Gentry: 400–9000 mm yr⁻¹; GLD: 850–7250 mm yr⁻¹) and DSL (Gentry: 0–11 mo; GLD: 0–7 mo), and includes sites located on unusual soil types (e.g., floodplains and white sands) that may obscure the relationship with MAP and DSL. Further analyses of both datasets are needed to determine the source of the discrepancy (see below). In addition, the GLD requires more liana surveys in areas on the low and high ends of the gradients in MAP and DSL.

Liana diversity

Species diversity appeared to have a hump-shaped relationship with MAP but was not related to DSL in the GLD analysis (Fig. 11.4; Table 11.2). The best-fit model explained 71% of the variance in Fisher's α , but DSL did

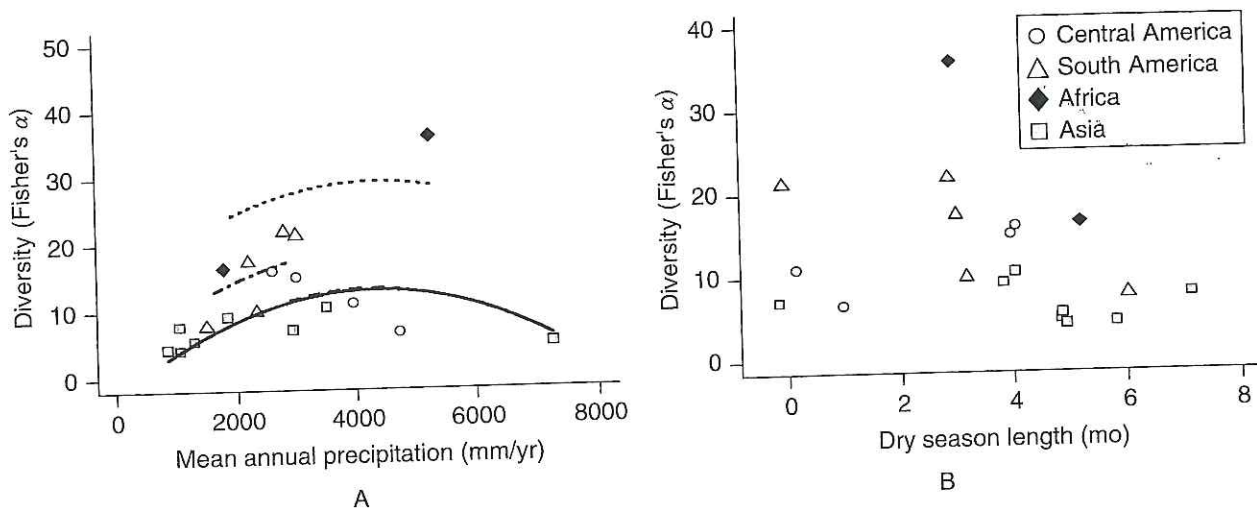


Fig. 11.4 Bivariate relationships between liana diversity (Fisher's α) of lianas ≥ 2.5 cm diameter and (A) mean annual precipitation and (B) dry season length for sites of Africa, Central America, South America, and Asia that contained at least 25 liana individuals. Each point represents the mean Fisher's α as calculated over individual plots at a site. Lines represent the regression equations calculated from the best-fitting bivariate model (MAP or DSL) for Central America (dashed), South America (dashed and dotted), Africa (dotted), and Asia (solid). In (A), the regression lines for Central America and Asia overlap. The intercept = -2.53 for Central America; 3.31 for South America; 13.4 for Africa; and -2.77 for Asia. Note that MAP and MAP² were only marginally significant in the model ($P = 0.06$ and 0.08 , respectively; Table 11.2). In (B), the DSL parameter was not significantly different from 0 (Table 11.2).

not contribute significantly and MAP and MAP² were only marginally significant (Table 11.2). Interestingly, the Asian plots in the GLD spanned 100% of the range in the dataset of MAP (850–7250 mm yr⁻¹) and DSL (0–7 mo) but spanned only 20% of the range in Fisher's α (Asia: 4.2–10.4; GLD: 4.2–35.7).

Thus far, only the neotropical Gentry dataset has been used to study the relationship between liana species richness and climatic variables, and therefore an analysis using the pantropical dataset is awaiting. Climatic variables are more strongly associated with species richness in Gentry's neotropical dataset than in the GLD. When differences in density are accounted for, greater liana species richness was positively, linearly related to MAP and negatively related to DSL in Gentry's neotropical dataset (van der Heijden & Phillips 2009). In addition, DSL explained more variation in species richness than MAP (van der Heijden & Phillips 2009). In the GLD, there is an indication that Fisher's α diversity may be greatest at intermediate levels of rainfall but appears unrelated to dry season length. Therefore, in contrast with the Gentry dataset, neotropical diversity in the GLD dataset does not appear to increase linearly with MAP or negatively with DSL.

GLD versus the Gentry dataset

Why do the relationships between liana abundance and diversity and climatic variables differ between Gentry's dataset and those of the GLD? Because Gentry's data were conducted in very small areas and with narrow transects, they may be a poor estimate of liana density or diversity. Using the fairly homogeneous 50-ha plot on Barro Colorado Island (BCI), Panama, Schnitzer et al. (2012; unpublished data) reported that the coefficient of variation for liana density decreased considerably up to 1 ha, indicating that samples <1 ha are likely a poor representation of forest-wide liana density. The minimum sampling area for a robust estimate of species richness was even greater; >5 ha was necessary for a precise estimate of plot-level liana diversity based on the BCI 50-ha plot (Schnitzer et al. 2012). The large areas sampled for each site in the GLD relative to those in Gentry's dataset likely include areas of both high and low liana density and species richness. In contrast, the small number of replicates and limited total areas sampled for each site in the Gentry dataset may fail to provide an accurate and representative estimate of site-wide liana density and richness.

Alternatively, the limited number of sites in the GLD compared to the large number in Gentry's dataset, particularly in the neotropics, may obscure the true relationships. Nonetheless, none of these possibilities explain why climatic variables were strongly related to liana diversity but not density in Gentry's dataset for the neotropics, with the opposite pattern found in the GLD for the neotropics and paleotropics. Assuming that there are no major errors in either dataset, it could be that processes shaping liana communities differ among biogeographical regions. We can only test this hypothesis after more sites are added to the GLD, particularly in western and eastern Africa and at the ends of the gradients in climatic variables. These additions would then allow us to examine whether relationships with climatic variables differ among regions (i.e., a region \times MAP or region \times DSL interaction).

TROPICAL ISLANDS

Relatively few liana inventories are available for tropical islands, but the few surveys conducted in the Caribbean suggest that Puerto Rico, Jamaica, and Dominica support fewer lianas and lower species diversity than mainland tropical forests (Gentry 1991; Rice et al. 2004; DeWalt & Ickes, unpublished data; Florens et al. 2012). Across 17 0.25-ha plots that span gradients of precipitation and hurricane disturbance on the island of Dominica, the average liana density was 76 individuals ≥ 2.5 cm diameter ha^{-1} , with a Fisher's α of 1.7 (Table 11.1). Dominica has roughly one-third of the liana density and only one-fourth of the liana diversity compared to Los Tuxtlas, Mexico, a continental rain forest site at similar latitude.

On Caribbean islands, and perhaps other oceanic islands, it appears that non-liana climbers are abundant. On Puerto Rico, about half of the climbers surveyed in tropical wet forest were species of *Marcgravia* (Rice et al. 2004), which are considered "lianescent hemiepiphytes," "hemiepiphytic lianas," or "epiphytic lianas" because they establish as seedlings in the ground, climb with adventitious roots, and can become facultative epiphytes if their climbing stems degenerate. In some cases, epiphytic *Marcgravia* can produce new aerial roots and reestablish contact with the ground (DeWalt & Ickes, pers. obs.). On Dominica, species in two genera within the Marcgraviaceae, *Marcgravia* and *Schwartzia*, were particularly

abundant (DeWalt & Ickes, pers. obs.), and, in some sites, almost every tree ≥ 10 cm diameter had a least one *Marcgravia umbellata* stem/root appressed to the trunk. These non-liana climbing species contribute to forest structure, but they are difficult to census using methods designed for lianas (e.g., Gerwing et al. 2006; Schnitzer et al. 2008).

TEMPERATE AND SUBTROPICAL FORESTS

Lianas are more diverse and typically more abundant in tropical than temperate forests, with subtropical forests in between (Gentry 1982, 1991; Schnitzer & Bongers 2002; Schnitzer 2005; Ladwig & Meiners, Chapter 15 in this volume). Unfortunately, the GLD currently includes few subtropical or temperate forests. The only samples from temperate forests are from Australia, and these plots are small (0.03 ha each; Gallagher & Leishman 2012), such that the density estimates for 1 ha are likely overinflated. The subtropical montane forest of Argentina and Australia support relatively high liana density (Argentina = 323 individuals ha^{-1} ; Australia = 474 individuals ha^{-1}) but low diversity (Argentina Fisher's $\alpha = 2.1$; Australia Fisher's $\alpha = 2.2$ for lianas ≥ 1.0 cm at the Iluka site). Temperate forests of Australia had similar liana density and even lower diversity (800 individuals ha^{-1} ; Fisher's $\alpha = 1.2$ for lianas ≥ 1.0 cm). Thus, even liana-rich and liana-dense temperate and subtropical forests tend to have only a fraction of the diversity of tropical forests. Gentry (1991) also found that temperate forests have few liana species. He further noted that temperate forests of the southern hemisphere, such as the Valdivian forests of Chile, tend to have double the liana density and species richness as northern hemisphere temperate forests. In North America, liana abundance appears to be positively related to disturbance and is particularly abundant along edges (Londré & Schnitzer 2006). However, liana densities vary substantially among North American broadleaf forest stands, even those located in close proximity to each other (Londré & Schnitzer 2006). In summary, other than disturbance, little is known about the climatic and other factors that drive liana density and diversity in temperate forests, and more sites in temperate, as well as subtropical, forests of the northern and southern hemispheres are needed in the GLD.

CONCLUSION AND FUTURE DIRECTIONS

The GLD is becoming a valuable dataset for determining biogeographic patterns of liana abundance and diversity. Furthermore, the GLD can be used to examine additional interesting relationships such as change in the liana community among forests and continents, and across abiotic gradients. For instance, we could examine how liana phylogenetic and functional composition differs among biogeographical regions and changes along climatic gradients. These kinds of analyses can be accomplished only with a large database, such as the GLD, that has species identifications, individual stem measurements, and relatively large plot sizes. In particular, we could test whether certain climbing types are more common under particular climatic regimes and verify that root climbers are more common in wetter, less seasonal temperate and tropical forests, as was found using Gentry's global dataset (Durigon et al. 2013). We could also use the GLD to test liana community-assembly mechanisms (*sensu* Webb et al. 2002). However, many more sites are needed in the GLD, particularly in Africa, where we have few sites and liana diversity is high (e.g., Bongers and Ewango, Chapter 3 in this volume; Thomas et al., Chapter 2 in this volume), and in Asia in areas outside of India, such as Peninsular Malaysia, Vietnam, and Cambodia.

As more sites are added to the GLD and information about trees also is added to the liana datasets, we can begin to examine whether lianas and trees co-vary in their patterns of abundance and diversity. Swaine and Grace (2007) found that liana species represent a greater percentage of the flora as annual rainfall decreases along a climatic gradient in Ghana. We could test whether lianas represent a greater proportion of the woody plant density or diversity in sites with lower MAP and greater DSL with plot-level surveys of both lianas and trees. Gentry's dataset suggests that the strength of the relationship between climatic variables and species richness in the neotropics is not as strong for lianas as it is for trees and shrubs (Gentry 1982; van der Heijden & Phillips 2009). We have yet to compile comparable diversity estimates for trees at sites for which we have liana diversity estimates to be able to conduct an independent assessment of this pattern.

Additional questions that we plan to address include: why do liana abundance and diversity vary with climatic factors (DeWalt et al. 2010; Šímová et al. 2011), and why are particular biogeographical regions

especially liana-rich or liana-poor? Functional traits such as deeper roots, more efficient water transport, and larger xylem vessels may promote liana proliferation in drier areas in which trees are less competitive (Schnitzer 2005; Swaine & Grace 2007), though the ubiquity of such traits among the hundreds of liana species still needs to be tested. If there are contrasting patterns between liana and tree abundance across climatic gradients, as found by Schnitzer (2005), determination of the mechanisms for these differences may give insight into the factors that control liana abundance across broad abiotic gradients. Furthermore, if lianas continue to increase over time in abundance, productivity, and biomass in neotropical forests (reviewed by Schnitzer & Bongers 2011; Schnitzer, Chapter 30 in this volume; Schnitzer et al., Chapter 7 in this volume), then determination of the mechanisms responsible for liana distribution will help explain why lianas are increasing in tropical forests. It will also be critical to predict the forest types where lianas will play increasing ecological roles in the future. Building the GLD by adding more liana surveys with species identifications from tropical continental forests (in areas such as Amazonian Brazil, Queensland Australia, West Africa, East Africa, and mainland areas of Southeast Asia); tropical islands; and temperate forests will help to document these important patterns and may enable us to determine the evolutionary, biogeographical, and ecological processes that influence liana density and diversity.

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