Liana Abundance and Diversity Increase with Rainfall Seasonality along a Precipitation Gradient in Panama

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Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama

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Abstract

In tropical regions, rainfall gradients often explain the abundance and distribution of plant species. For example, many tree and liana species adapted to seasonal drought are more abundant and diverse in seasonally-dry forests, characterized by long periods of seasonal water deficit. Mean annual precipitation (MAP) is commonly used to explain plant distributions across climate gradients. However, the relationship between MAP and plant distribution is often weak, raising the question of whether other seasonal precipitation patterns better explain plant distributions in seasonally-dry forests. In this study, we examine the relationship between liana abundance and multiple metrics of seasonal and annual rainfall distribution to test the hypothesis that liana density and diversity increase with increasing seasonal drought along a rainfall gradient across the isthmus of Panama. We found that a normalized seasonality index, which combines MAP and the variability of monthly rainfall throughout the year, was a significant predictor of both liana density and species richness, whereas MAP, rainfall seasonality and the mean dry season precipitation (MDP) were far weaker predictors. The strong response of lianas to the normalized seasonality index indicates that, in addition to the total annual amount of rainfall, how rainfall is distributed throughout the year is an important determinant of the hydrological conditions that favor liana proliferation. Our findings imply that changes in annual rainfall and rainfall seasonality will determine the future distribution and abundance of lianas. Models that aim to predict future plant diversity, distribution, and abundance may need to move beyond MAP to a more detailed understanding of rainfall variability at sub-annual timescales.

Introduction

A central goal in ecology is to explain the distribution of organisms. In tropical regions, rainfall gradients often explain the abundance and distribution of many plant species. For example, tree species that are adapted to strong seasonal drought tend to dominate tropical dry forests and, by contrast, tree species that dominate tropical wet forests are not adapted to seasonal drought, and thus they survive poorly in dry forests (Engelbrecht et al. **2007**, Condit et al. 2013). Tropical lianas (woody vines), which are a diverse and abundant component of tropical forests (Schnitzer and Bongers **2002**, Schnitzer **2018**), tend to be particularly abundant and diverse in highly seasonal tropical forests, decreasing in relative abundance and diversity with increasing mean annual precipitation (Schnitzer **2005**, Swaine and Grace **2007**). Identifying the climate characteristics that best describe the variation in plant abundance provides critical insights into the determinants of plant distribution (Schnitzer **2005**, 2018, Condit et al. 2013).

Mean annual precipitation (MAP) is a common measure to quantify the amount of water stress experienced by plants and, therefore, MAP is often used to explain plant distributions (Condit et al. 2000, Schnitzer **2005**, DeWalt et al. **2015**). However, temporal rainfall variability, soil type and soil hydrology can confound the assumed relationship between MAP and plant water stress. For example, MAP includes the wet season rainfall, which often exceeds the soil water holding capacity, leading to water losses via surface runoff and deep recharge that are unavailable to support plant activity (Feng et al. 2012). Furthermore, MAP may fail to adequately describe the duration of time that plants experience seasonal drought, which may have a strong direct effect on plant distribution (Manzané-Pinzón et al. **2018**).

For example, the unique distribution of tropical lianas is thought to be driven by their ability to grow more than co-occurring trees during seasonal drought. Thus, accurately describing the amount of rainfall at a given site and how that rainfall is distributed throughout the year is particularly important to explaining the distribution of

lianas throughout the tropics. Specifically, lianas are thought to have a seasonal growth advantage, and by managing water stress better than trees, lianas may be able to take advantage of abundant dry-season solar radiation, and thus grow more than trees during the dry season (Schnitzer **2005**, 2018). Indeed, evidence is accruing that lianas grow better than co-occurring trees during the dry season than the wet season (Schnitzer **2005**, Schnitzer and van der Heijden **2019**), and that lianas are able to photosynthesize and maintain water status better than co-occurring trees during the dry season (Cai et al. **2009**, Chen et al. **2015**, Smith-Martin et al. **2019**). Therefore, the distribution of lianas may be better explained by the seasonal distribution of rainfall than MAP, since seasonal rainfall distribution is likely a better proxy for the time that plants experience water stress (DeWalt et al. 2010, 2015, Manzané-Pinzón et al. **2018**).

Determining an estimate of rainfall that accurately captures seasonal plant water stress is a critical advance in modeling the distribution of plant species and growth forms. Here we use new methods to quantify seasonal drought and the distribution of rainfall over the year to assess which factors best determine the distribution of lianas across a rainfall gradient in central Panama. We quantified rainfall variability at the monthly and annual scales to test the hypothesis that liana density and diversity (both in absolute terms and relative to trees) increase with increasing seasonal drought along the rainfall gradient across the isthmus of Panama.

Material and methods

Quantifying liana and tree abundance and diversity

We determined liana and tree density and diversity in eleven 1-ha plots in forests that were distributed across the isthmus of Panama from north to south (Fig. 1). The plots were all in closed canopy, lowland forest that were a mix of old growth and late secondary growth. All forests were located adjacent to the Panama Canal, which crosses the 65-km wide isthmus of Panama. For more details on the plots and forests used in this study, see Pyke et al. (2001) and Condit et al. (2013).
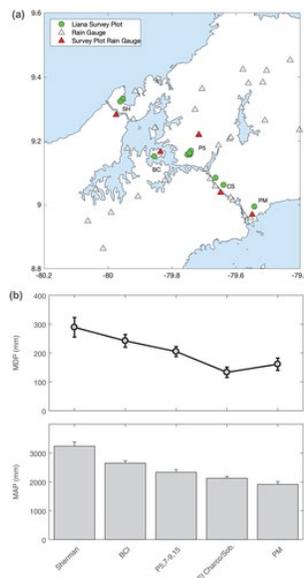
Figure 1 Isthmus of Panama precipitation gradient. (a) Locations of liana survey plots and rain gauges. Green circles indicate the eleven liana survey plots, open triangles indicate all rain gauges, and red triangles indicate rain gauges nearest to the liana survey plots. (b) Mean annual precipitation (MAP) and mean dry season precipitation (MDP) at the liana survey plots.

During a 13-month period, from December 2010 until January 2012, we measured the diameter of all lianas ≥5 cm diameter in the entire 1-ha plot and the diameter for all lianas ≥1 cm in the center 40 × 40 m of the plot

for all 11 plots. We scaled the small liana data (1–9.9 cm diameter) to 1 ha and present all data at the 1 ha scale. We identified lianas to species and measured liana diameter at 1.3 m from the rooting point using census protocols established by Gerwing et al. (2006) and Schnitzer et al. (2008). The seasonal growth advantage hypothesis to explain liana abundance across rainfall gradients depends on both the ability of lianas to grow more during the dry season than the wet season, as well as greater competitive ability of lianas than trees in more seasonal forests compared to aseasonal forests (Schnitzer **2005**, 2018, Schnitzer and van der Heijden **2019**). Therefore, we calculated both absolute liana density and species richness, as well as liana density and species richness relative to that of trees. To calculate the relative measures of liana density and richness, we used data on the trees ≥10 cm that were measured in each of the 1 ha plots (for more details Condit et al. 2013). Tree diameters were measured at 1.3 m from the soil surface using census protocols established by Condit (**1998**).

Rainfall variability

We characterized rainfall variability using local rain gauge data that were obtained from the Smithsonian Tropical Research Inst. (STRI) Physical Monitoring Program (<**https://biogeodb.stri.si.edu/physical_monitoring/**>), which provides access to data collected by STRI as well as data collected by the Panama Canal Authority (ACP). Data were collected from 31 rain gauges in the ACP dataset plus 3 rain gauges operated by STRI. The gauge nearest to each of the 11 liana survey plots (3 from STRI and 2 from ACP) was assigned to that plot. Rainfall measurement frequency ranged between 5 min and 1 h and the rainfall record length ranged between 16 and 47 yr. Rainfall data sources and attributes are summarized in Table 1. Rainfall data were aggregated to monthly, seasonal and annual scales for analysis. The dry season was defined as 1 January–1 May for all sites, since all sites are within 65 km and they all generally experience the same weather patterns.

Table 1. Rainfall data sources and attributes.[1]

Site name	Mean annual precipitation (mm)	Mean dry season precipitation (mm)	Frequency	Years	Source
Sherman (SH)	3236	289	15-min	1998–2016	STRI
Barro Colorado Island (BCI)	2649	242	5-min	1971–2017	STRI
Parcela 5.7–9.15 (P5)	2332	205	1-h	1999–2014	ACP
El Charco y Soberania (CS)	2132	131	1-h	1979–2001	ACP
Parque Metropolitano (PM)	1911	166	15-min	1975–2007	STRI
ACP rain gauge network (31 sites)	1811–3648	133–522	Daily	Variable (5–47 yr)	ACP

[a] [1]All rainfall data can be accessed at: <https://biogeodb.stri.si.edu/physical_monitoring/>.

We calculated rainfall seasonality as the normalized seasonality index. The normalized seasonality index, S, combines MAP and the relative entropy, D, a measure of the rainfall variability between months,

$$S = D \frac{\text{MAP}}{\text{MAP}_{\text{max}}}$$

(1)

where MAP_{max} is the maximum MAP across all sites (Feng et al. 2013). The relative entropy of the monthly rainfall distribution relative to a uniform distribution is defined as:

$$D = \sum_{mo=1}^{12} P_{mo} \log_2 \left(\frac{P_{mo}}{q_{mo}} \right)$$

(2)

where P_{mo} is the monthly precipitation normalized by MAP and the uniform distribution is denoted as $q_{mo} = 1/12$ for all months, mo. Relative entropy is a measure of the seasonal rainfall distribution, which takes a value of 0 when rainfall is distributed uniformly throughout the year and a maximum value of $\log_2(12) = 3.585$ when all rainfall is concentrated in one month (Feng et al. 2013). Therefore, S takes large values only when annual rainfall and seasonal rainfall variability are high, but can take low values for either low annual rainfall or low seasonal rainfall variability.

Statistical analysis

We regressed measures of liana abundance and diversity, both absolute and relative to trees, against four rainfall descriptors. These descriptors included climatic means of annual precipitation, dry season precipitation, relative entropy, and the normalized seasonality index. To quantify relationships between liana abundance and diversity and rainfall descriptors, as well as among rainfall descriptors, we used ordinary least squares regression in MATLAB.

Results

Rainfall gradient

Rainfall characteristics varied from north to south along the Isthmus at Panama at both seasonal and annual scales (Fig. 1). MAP decreased from north to south, from 3236 mm at Fort Sherman to 1911 mm at Parque Metropolitano (mean = 2399 mm, SD = 479 mm, CV = 0.20). Mean dry season precipitation (MDP) varied much less in absolute terms, with a mean of 194 mm and a standard deviation of 63 mm (CV = 0.32) and was similarly oriented north to south. Therefore, most of the MAP variability across sites, in terms of absolute rainfall, occurred during the wet season. However, the CV of MDP was 60% higher than the CV of MAP, indicating that there was even more variability in MDP (relative to the mean) than for MAP.

The distribution of rainfall throughout the year, or rainfall seasonality, was markedly different across the rainfall gradient and paralleled the gradients in MAP and MDP. Our empirically derived measure of MDP was positively correlated with MAP (Fig. **2**a). This relationship was significant for the rain gauges closest to the liana survey plots, as well as all rain gauges in the ACP network (Fig. **2**a). By contrast, rainfall seasonality, as measured by the relative entropy, D, was negatively correlated with MAP (Fig. **2**b) and MDP (Fig. **2**c). Relative entropy was more strongly related to MDP than MAP. Lower MAP (and MDP) was associated with higher relative entropy – that is, dry sites had a more uneven rainfall distribution throughout the year than did the wet sites. These relationships were significant across all ACP rain gauges, but not across the liana survey plots.
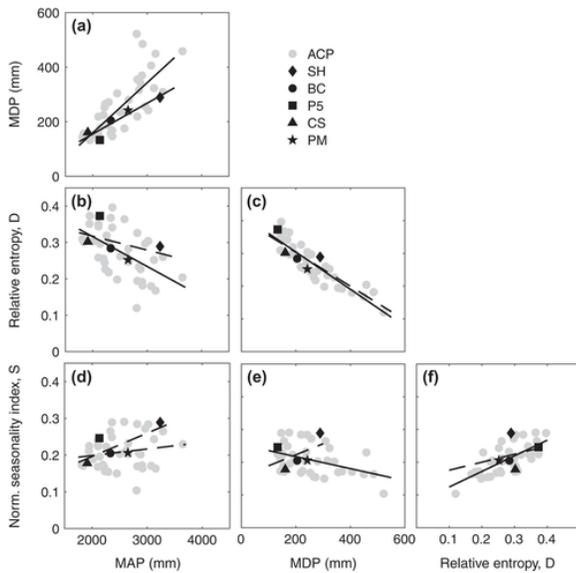
Figure 2. Seasonal and annual-scale rainfall variability across the Isthmus of Panama. Rainfall descriptors include: mean annual precipitation (MAP), mean dry season precipitation (MDP), relative entropy (D), and normalized seasonality index (S). The black symbols correspond to the five rain gauges near the liana survey plots and the gray circles correspond to 29 additional rain gauges in the study area. Lines correspond to least squares linear regressions with solid lines indicating significance with $p < 0.05$. Regression parameters are listed in Supplementary material Appendix 1 Table A1. Different shaped symbols represent different sites: Sherman (◆), Barro Colorado Island (★), Parcelas 5.7–9.15 (•), El Charco y Soberania (■), and Parque Metropolitano (▲).

The normalized seasonality index, S, which combines rainfall relative entropy (D) and annual rainfall (Eq. 1), showed varying responses to MAP, MDP and D. The normalized seasonality index increased with MAP, however, this relationship was not significant and was weaker across all sites compared to the liana survey plots (Fig. **2**d). The normalized seasonality index decreased significantly with MDP for all sites, but increased non-significantly for the liana survey plots (Fig. **2**e). Finally, S increased with D consistently across all rain gauges (Fig. **2**f). This relationship was significant across all ACP rain gauges, but not significant across the liana survey plots. The fact that D was negatively related to MAP and positively related to S suggests that S and MAP capture different information regarding rainfall variability. In addition, S was more strongly related to D than MAP. Therefore, across this rainfall gradient, dry sites tended to have lower dry season rainfall, more variable rainfall across months, and a lower seasonality index. Regression results are reported in the Supplementary material Appendix 1 Table A1.

Monthly contributions to the relative entropy varied markedly across the liana survey plots and did not follow the gradient in MAP (Fig. 3). BCI had the lowest relative entropy ($D = 0.25$) and the second highest rainfall (MAP = 2649 mm), whereas CS had the highest relative entropy ($D = 0.37$) and the second lowest rainfall (MAP = 2132 mm). Low relative entropy sites (SH, BCI and P5) were characterized by monthly rainfall that was consistently closer to the mean than the high relative entropy sites (CS and PM). The site with the highest relative entropy (CS) exhibited wet season rainfall that was consistently higher than the monthly mean and wet season deviations from the mean were much larger than dry season deviations.
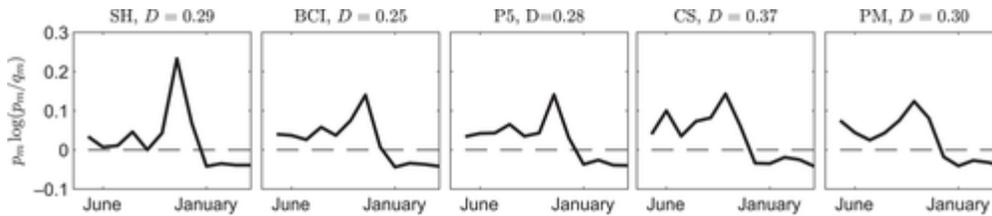
Figure 3. Monthly contributions to the relative entropy, *D*, for the rain gauges near the five liana survey plots. From left to right, Sherman (SH), Barro Colorado Island (BCI), Parcelas 5.7–9.15 (P5), El Charco y Soberania (CS) and Parque Metropolitano (PM).

Liana density and diversity

Liana density (in both absolute terms and relative to trees) was strongly related to rainfall seasonality, as quantified by *S* (Fig. 4). Specifically, liana absolute density and relative density were highest in the least seasonal (dry) sites and decreased with increasing seasonality (i.e. the wetter sites; Fig. **4**c, f), increasing MAP (Fig. **4**a, d), and increasing *D* (Fig. **4**b, e). Liana species richness (in absolute terms and relative to trees) followed the same patterns as liana density (Fig. 5). Specifically, liana species richness was highest in the least seasonal (and dry) sites, and decreased with increasing seasonality (Fig. **5**c, f), increasing MAP (Fig. **5**a, d), and increasing *D* (Fig. **5**b, e).
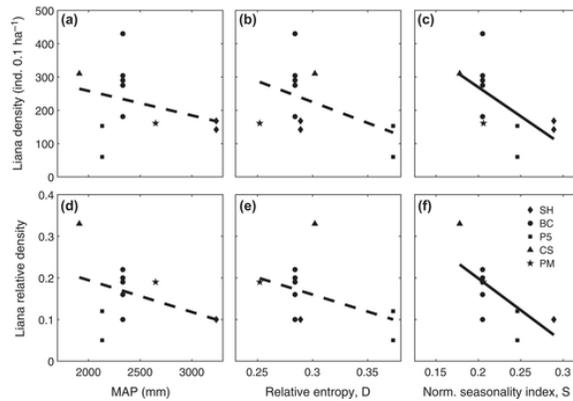
Figure 4. Liana density in absolute terms (a–c) and relative to trees (d–f) as a function of mean annual precipitation (MAP), relative entropy (*D*) and normalized seasonality index (*S*). Lines correspond to least squares linear regressions with solid lines indicating significant (p < 0.05) and dashed lines indicating non-significant relationships (p > 0.05). Regression parameters are listed in Table 2. Different shaped symbols represent different sites: Sherman (◆), Barro Colorado Island (★), Parcelas 5.7–9.15 (•), El Charco y Soberania (■) and Parque Metropolitano (▲).
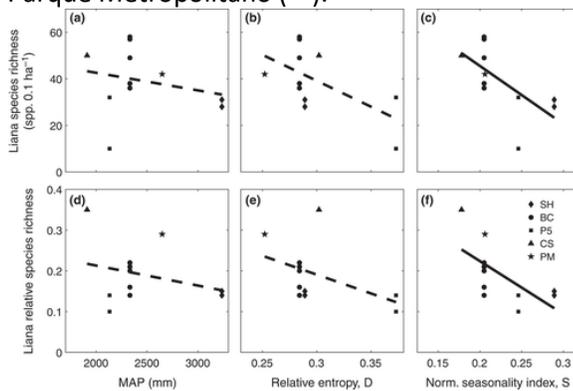
Figure 5. Liana species richness in absolute terms (a–c) and relative to trees (d–f) as a function of mean annual precipitation (MAP), relative entropy (*D*) and normalized seasonality index (*S*). Lines correspond to least squares linear regressions with solid lines indicating significant (p < 0.05) and dashed lines indicating non-significant

relationships (p > 0.05). Regression parameters are listed in Table 2. Different shaped symbols represent different sites: Sherman (◆), Barro Colorado Island (★), Parcelas 5.7–9.15 (●), El Charco y Soberania (■) and Parque Metropolitano (▲).

While liana density and richness, both in absolute terms and relative to trees tended to decrease with S, MAP and D, only the relationships between lianas and S were statistically significant (Table 2). The normalized seasonality index explained between 38% and 52% of the variance in liana density and species richness, in both absolute and relative terms, and the regressions were all significant ($p < 0.05$). MDP was the weakest predictor across all liana measures, explaining almost none of the variance between liana density and richness (Table 2). By contrast, MAP explained between 5% and 18% of the variance in liana density and species richness, respectively; however, none of the regressions were significant. Relative entropy (D) was the second-best predictor of liana density and species richness, explaining between 16% and 36% of the variance. However, the relationship with D absolute species richness was the only regression that was significant ($p = 0.051$).

Table 2. Regression results for rainfall predictors (mean annual precipitation, mean dry season precipitation and normalized seasonality index) and liana density and species richness in both absolute terms and relative to trees in the sampling plots. Asterisks denote significant relationships (p < 0.05)

	Mean annual precipitation (MAP)		Mean dry season precipitation (MDP)		Relative entropy (D)		Normalized seasonality index (S)	
	r^2	p	r^2	p	r^2	p	r^2	p
Liana density (ind. 0.1 ha^{-1})	0.090	0.37	0.0002	0.97	0.21	0.16	0.38	0.045*
Liana species richness (spp. 0.1 ha^{-1})	0.053	0.50	0.0069	0.81	0.36	0.051	0.43	0.030*
Liana relative density	0.18	0.20	0.019	0.69	0.16	0.22	0.52	0.012*
Liana relative species richness	0.080	0.40	0.0005	0.95	0.22	0.14	0.42	0.032*

Discussion

Previous studies on the climatic drivers of liana distribution focused primarily on MAP and dry season length as predictors (Schnitzer **2005**, Swaine and Grace **2007**, van der Heijden and Phillips **2009**, DeWalt et al. 2010, 2015). These two drivers, however, are coarse predictors of the amount of water limitation that plants actually experience. For MAP, the much greater (and highly variable) amount of wet season precipitation may poorly predict the amount of dry season rainfall, thus obscuring the amount of water stress that plants experience. Dry season length is normally measured in months (DeWalt et al. 2010, 2015), and thus may underestimate the length of drought that plants experience if heavy rainfall occurs toward the second half of the final month of the dry season. Indeed, in the current study, we found that MAP and MDP explained less than 18% of the variation in the measures of liana density and richness.

By contrast, liana density and species richness, particularly relative to trees, were predicted best by the normalized seasonality index (S). In fact, S explained 52% of the variation in relative liana density and 42% of the variation in liana relative species richness. The normalized seasonality index may explain liana abundance and diversity better than MAP because S combines seasonal and annual rainfall descriptors that contain different information that directly affects the hydrologic conditions that appear to confer an advantage to lianas (Schnitzer **2018**). The normalized seasonality index is defined as the product of the entropy of the monthly rainfall distribution relative to a uniform distribution and the annual rainfall normalized by the maximum annual rainfall across all sites (Feng et al. 2013). Liana density and diversity were highest for low values of S, which occur in sites that have either a relatively low annual rainfall or a relatively even distribution of rainfall across the year (low D). By contrast, across the entire set of rain gauges, low annual rainfall generally occurred with low dry season rainfall and high entropy (Fig. **2**b). Therefore, the combination of low annual rainfall and low entropy was critical to identifying sites with potential for higher liana density and diversity.

The El Charco and Soberania sites (denoted as CS) clearly demonstrate the role of rainfall seasonality in predicting liana density and diversity. Compared to the other sites, CS exhibited relatively low liana density and diversity, less than what would be predicted by the regressions with MAP (Fig. 4, 5). In addition, CS had the highest relative entropy, driven largely by wet season rainfall that was consistently greater than the monthly average rainfall (Fig. 3). Our results show that high relative entropy was associated with low liana density and diversity (Fig. 4, 5). Therefore, the seasonality index provided a better overall prediction of liana density and diversity, because it combines the effects of MAP and D, as exemplified by the observations at CS.

The strong negative response of lianas to the normalized seasonality index suggests that some combination of annual rainfall and the distribution of rainfall throughout the year favor lianas in more arid and less seasonally variable climates. Liana density and richness had a weak response to either annual rainfall or seasonality alone. A strong and significant pattern of changing liana density and richness emerged when annual rainfall and relative entropy were combined multiplicatively (and relative to the highest obtainable mean annual rainfall) to obtain the normalized seasonality index. Therefore, the seasonality index appears to provide a weighting of these two factors that is a strong predictor of liana distribution across coincident gradients of annual rainfall and its seasonal distribution.

One reason that rainfall seasonality improves predictions of liana distribution beyond that of annual rainfall alone may be that rainfall seasonality provides additional information of the seasonal variation of soil moisture availability. Although annual rainfall would seem to be strongly related to the dry season rainfall (Fig. 2), annual rainfall cannot by itself predict the length and severity of seasonal soil water deficits. For example, along this same rainfall gradient in Panama, Manzané-Pinzón et al. (**2018**) reported that the density of liana seedlings, particularly relative to adult tree density, was higher in sites with limestone soils that had low water retention

than in adjacent sites with clayey soils that had better water retention. The results reported here provide further evidence that the distribution of lianas is driven by the seasonal water availability, which emerges from complex interactions between climate, soil and vegetation characteristics.

The strong positive correlation between liana density and diversity and rainfall evenness is consistent with the hypothesis that lianas have a competitive advantage during the dry season. Lianas are thought to maintain a competitive advantage during the dry season because they can capitalize on high dry season solar radiation while limiting the detrimental effects of low water availability imposed by soil water deficit (Schnitzer **2005**, 2018). Indeed, from **2011** until 2016 canopy lianas in central Panama grew as much during the four-month dry season as they did during the eight-month wet season, while trees realized the vast majority of their growth during the wet season (Schnitzer and van der Heijden **2019**, van der Heijden et al. **2019**). Lianas appear to be able to maintain higher levels of photosynthesis and better water status than trees during the dry season relative to the wet season (Cai et al. **2009**, Chen et al. **2015**, Smith-Martin et al. **2019**). How lianas are able to reduce the effects of drought compared to trees remains unknown; however, lianas seem to be able to maintain both high hydraulic conductance and hydraulic safety, whereas these properties in trees are negatively correlated (van der Sande et al. **2019**). This ability of lianas to fix carbon while resisting embolism may explain their high dry-season growth rates (Schnitzer and van der Heijden **2019**). The capacity of lianas to grow well during the dry season, which includes the potential to exploit dry-season rain pulses, may enable lianas to accumulate in seasonal tropical forests (Schnitzer **2005**, 2018, Schnitzer and van der Heijden **2019**), thus explaining the strong correlation between liana density and diversity and *S*.

We chose to examine liana density and species richness in both absolute terms, as well as relative to trees because both metrics provide different information about the ability of lianas to take advantage of seasonal drought. The increase in absolute liana density and richness with decreasing measures of precipitation and seasonality indicates that lianas in forests that are consistently dry throughout the year are performing better than lianas in wetter forests. Integrated over decades, consistently higher dry season growth ultimately can result in an accumulation of lianas (Schnitzer **2005**, 2018). For example, Schnitzer and van der Heijden (**2019**) demonstrated that canopy liana growth rate was far higher during the dry season than the wet season, and thus lianas in seasonal forests likely have a period of high growth during the year that lianas in aseasonal forests lack. If this annual period of high growth ultimately results in higher reproduction, establishment and survival, then lianas would be expected to accumulate more in forests with longer dry periods. Forests with low annual rainfall and more evenly distributed rainfall (i.e. low entropy) are expected to have longer seasonal droughts, which would thus give lianas a relatively larger growth advantage.

By contrast, relative measures of liana density and richness allow us to test whether lianas would be expected to accumulate relative to trees in forests that are seasonally dry during some part of the year because lianas can capitalize on high dry season radiation while minimizing water stress better than co-occurring trees (Schnitzer **2005**2015, **2018**). For example, in a seasonal tropical forest in central Panama, Schnitzer and Van Der Heijden (**2019**) demonstrated that canopy tree growth rate was far higher during the wet season than the dry season – the opposite pattern of lianas (see also Schnitzer **2005**). Therefore, if liana density and richness increase with liana performance across a rainfall gradient, and tree density and richness do not, we would expect that the pattern of liana accumulation in the forests where they have a seasonal growth advantage to be strongest relative to that of trees, which is what we found. In fact, the stronger relationship of relative liana density and richness than absolute density and richness is exactly what we would have predicted based on the original mechanistic explanation for liana density and diversity both within and across forests (Schnitzer **2005**).

In this study, we standardized the dry season length from January until May, since all sites are within 65 km and they all generally experience the same weather patterns. However, the dry season length actually varied considerably across the sites, even at this small spatial scale. When we defined the dry season length as the

period when potential evapotranspiration exceeds precipitation (sensu; Condit et al. 2000, 2013), we found that the dry sites also had much longer dry seasons. Specifically, the dry season lengths increased from 111 d in the wet site (SH) to 137 d at the driest site (PM) – a 23% increase in dry season length. The intermediate sites had dry seasons that lasted 120 d (BCI) and 123 d (P5), whereas the dry season at CS was 143 d. Therefore, the dry sites were not only drier during the core dry-season months, but they also had predictably longer dry seasons, which supports our finding that liana density and diversity are greatest in sites with stronger seasonal droughts. However, dry season length and MDP were not strong predictors of liana abundance or diversity (Supplementary material Appendix 1).

Our findings demonstrate that detailed descriptors of rainfall that explicitly include rainfall variability better describe liana distributions and are likely to provide improved forecasts of forest structure. Furthermore, more detailed descriptors of rainfall will likely better predict the changes in forest structure in a changing climate. Rainfall patterns are changing in many parts of the tropics, including changes to both annual rainfall and rainfall seasonality (Feng et al. 2013, Greve et al. 2014, Chadwick et al. 2016). In Panama, increases in liana abundance and productivity have occurred at the same time as annual rainfall decreased 20% between 1930 and 1990 (Schnitzer and Bongers **2011**). However, changes in the seasonal distribution of rainfall during this period likely have had a much greater influence on relative liana density and diversity than mean annual rainfall alone. The strong response of lianas to dry season rainfall and rainfall seasonality implies that changes in annual rainfall and rainfall seasonality will determine future distribution and abundance of lianas which will influence the structure of future tropical forests. Models that aim to predict future liana distribution and abundance may require a detailed understanding of rainfall variability on monthly and annual timescales.

Data deposition

Data available from the Dryad Digital Repository: <**https://doi.org/10.5061/dryad.c2fqz6141**> (Parolari et al. **2019**).

References

CaiZ. Q. et al. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. – *Oecologia* **161**: 25– 33.

ChadwickR. et al. 2016. Large rainfall changes consistently projected over substantial areas of tropical land. – *Nat. Clim. Change* **6**: 177– 181.

ChenY. J. et al. 2015. Water-use advantage for lianas over trees in tropical seasonal forests. – *New Phytol.* **205**: 128– 136.

ConditR.1998. *Tropical forest census plots: methods and results from Barro Colorado Island, Panama, and a comparison with other plots*. – Springer.

ConditR. et al. 2000. Quantifying the deciduousness of tropical forest canopies under varying climates. – *Int. J. Veg. Sci.* **11**: 649– 658.

ConditR. et al. 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. – *Proc. Natl Acad. Sci. USA* **110**: 5064– 5068.

DeWaltS. J. et al. 2010. Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. – *Biotropica* **42**: 309– 317.

DeWaltS. J. et al. 2015. Biogeographical patterns of liana abundance and diversity. – In: SchnitzerS. A. et al. (eds), *Ecology of lianas*. Wiley, pp. 131– 146.

EngelbrechtB. M. J. et al. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. – *Nature* **447**: 80– 82.

FengX. et al. 2012. On the effects of seasonality on soil water balance and plant growth. – *Water Resour. Res.* **48**: 1– 12.

FengX. et al. 2013. Changes in rainfall seasonality in the tropics. – *Nat. Clim. Change* **3**: 811– 815.

GerwingJ. J. et al. 2006. A standard protocol for liana censuses. – *Biotropica* **38**: 256– 261.

GreveP. et al. 2014. Global assessment of trends in wetting and drying over land. – *Nat. Geosci.* **7**: 716– 721.

Manzané-PinzónE. et al. 2018. Does soil moisture availability explain liana seedling distribution across a tropical rainfall gradient?– *Biotropica* **50**: 215– 224.

ParolariA. J. et al. 2019. Data from: Liana abundance and diversity increase with rainfall seasonality along a precipitation gradient in Panama. – *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.c2fqz6141>.

PykeC. R. et al. 2001. Floristic composition across a climatic gradient in a neotropical lowland forest. – *J. Veg. Sci.* **12**: 553– 566.

SchnitzerS. A.2005. A mechanistic explanation for global patterns of liana abundance and distribution. – *Am. Nat.* **166**: 262– 276.

SchnitzerS. A.2015. Increasing liana abundance in neotropical forests: causes and consequences. – In: SchnitzerS. A. et al. (eds), *Ecology of lianas*. Wiley, pp. 451– 464.

SchnitzerS. A.2018. Testing ecological theory with lianas. – *New Phytol.* **220**: 366– 380.

SchnitzerS. A.BongersF.2002. The ecology of lianas and their role in forests. – *Trends Ecol. Evol.* **17**: 223– 230.

SchnitzerS. A.BongersF.2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. – *Ecol. Lett.* **14**: 397– 406.

SchnitzerS. A.van der HeijdenG. M. F.2019. Lianas have a seasonal growth advantage over co-occurring trees. – *Ecology* **100**: e02655.

SchnitzerS. A. et al. 2008. Supplemental protocol for liana censuses. – *For. Ecol. Manage.* **255**: 1044– 1049.

Smith-MartinC. M. et al. 2019. Effects of dry-season irrigation on leaf physiology and biomass allocation in tropical lianas and trees. – *Ecology*, <https://doi.org/10.1002/ecy.2827>.

SwaineM. D.GraceJ.2007. Lianas may be favoured by low rainfall: evidence from Ghana. – *Plant Ecol.* **192**: 271– 276.

van der HeijdenG. M. F.PhillipsO. L.2009. Liana infestation impacts tree growth in a lowland tropical moist forest. – *Biogeosciences* **6**: 2217– 2226.

van der HeijdenG. M. F. et al. 2019. Effect of lianas on forest-level tree carbon accumulation does not differ between seasons: results from a liana removal experiment in Panama. – *J. Ecol.* **107**: 1890– 1900.

van der SandeM. T. et al. 2019. The hydraulic efficiency–safety trade-off differs between lianas and trees. – *Ecology* **100**: e02666.