

ARTICLE

Liana versus tree seedling responses to spatial and temporal variation in dry season severity

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Funding information

Yale University; UK Natural Environment Research Council, Grant/Award Number: NE/J011169/1; Lewis B. and Dorothy Cullman Foundation; US National Science Foundation, Grant/Award Numbers: 1623775, 1845403; Ohio State University; Yale School of the Environment; New York Botanical Garden

Handling Editor: Sunshine A. Van Bael

Abstract

Lianas are key components of tropical forests, particularly at sites with more severe dry seasons. In contrast, trees are more abundant and speciose in wetter areas. The seasonal growth advantage (SGA) hypothesis postulates that such contrasting distributions are produced by higher liana growth relative to trees during seasonal droughts. The SGA has been investigated for larger size classes (e.g., ≥ 5 cm diameter at 1.3 m, dbh), but rarely for seedlings. Using eight annual censuses of $>12,000$ seedlings of 483 tree and liana species conducted at eight 1-ha plots spanning a strong rainfall gradient in central Panama, we evaluated whether liana seedlings had higher growth and/or survival rates than tree seedlings at sites with stronger droughts. We also tested whether an extreme El Niño drought during the study period had a more negative effect on tree compared to liana seedlings. The absolute density of liana seedlings was similar across the rainfall gradient, ranging from 0.32 individuals/m² (0.20–0.49, 95% credible interval [CI]) at the driest end of the gradient and 0.27 individuals/m² (0.13–0.51 95% CI) at the wettest end of the gradient. The relative density of liana seedlings compared to tree seedlings was higher at sites with stronger dry seasons (0.27, 0.21–0.33, 95% CI), compared to wetter sites (0.12, 0.04–0.20 95% CI), due to lower tree seedling densities at drier sites. However, liana seedlings did not grow or survive better than tree seedlings in drier sites compared to wetter sites. Tree seedlings were more negatively impacted in terms of mortality by the extreme El Niño drought than liana seedlings, with an increase in annual mortality rate of 0.013 (0.003–0.025 95% CI) compared to lianas of -0.009 (-0.028 to 0.008 95% CI), but not growth. Our results indicate that lianas do not have a SGA over trees at the seedling stage. Instead, higher survival of liana versus tree seedlings during severe droughts or differences in liana versus tree fecundity or germination across the rainfall gradient likely explain why liana seedlings have higher relative densities at drier sites.

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KEYWORDS

2015–2016 El Niño event, dry season severity, extreme drought, growth, hierarchical Bayesian models, mortality, Panama, rainfall gradient, seasonal growth advantage, tropical forest

INTRODUCTION

In tropical forests, lianas (i.e., woody vines) are a crucial component of forest structure and diversity (Schnitzer et al., 2012) and are involved in many ecological interactions and ecosystem processes (Arroyo-Rodríguez et al., 2015; di Porcia e Brugnera et al., 2019). For example, lianas reduce biomass growth and reproductive output of trees (Estrada-Villegas et al., 2022), and increasing liana density is associated with decreases in forest carbon stocks (Durán & Gianoli, 2013). Trees and lianas, however, show marked and opposite patterns in their distributions across lowland tropical forests. While trees are more abundant and speciose in wetter areas (DeWalt et al., 2010; Gentry, 1982), lianas reach higher diversity and greater relative and absolute abundance in sites that experience longer dry seasons (DeWalt et al., 2010; Parolari et al., 2020; Schnitzer, 2005). Such contrasting distributional patterns, plus the fact that liana abundance has been increasing in recent decades in many tropical forests (Schnitzer et al., 2021), make it essential to investigate the mechanisms that regulate liana and tree abundance.

The seasonal growth advantage (SGA) hypothesis (Schnitzer, 2005) may explain the opposing patterns of tree and liana distributions. The SGA hypothesis postulates that lianas are able to grow more than trees during seasonal droughts because lianas take greater advantage of high solar radiation in the canopy (due to low cloud cover) and better tolerate the low water availability in the soil, in part due to increased water use efficiency (Maréchaux et al., 2017; Schnitzer, 2005, 2018; Schnitzer & van der Heijden, 2019). In comparison, trees grow very little, if at all, during seasonal or extreme droughts due to low tolerance for water limitation (Schnitzer, 2018; Schnitzer & van der Heijden, 2019). Over time, these small differences in growth are expected to increase liana size and survival, resulting in higher liana relative abundance at sites with increasingly severe dry seasons relative to sites with mild or no dry seasons (Schnitzer, 2005).

To date, most studies investigating the SGA have focused on larger size classes (e.g., ≥ 5 cm dbh) rather than seedlings. Ignoring whether the SGA also occurs at early life stages hinders our understanding of the mechanisms that explain tropical forest diversity and composition because the seedling stage is one of the strongest bottlenecks in the plant life cycle, and seedling growth

and survival play a crucial role in shaping the diversity, abundance, and distribution of tropical plant species (Comita & Engelbrecht, 2009; Green et al., 2014). We currently do not know whether the SGA of lianas occurs at the seedling stage or whether it only emerges at later life stages. If liana seedlings possess the same traits that confer an advantage to liana adults under dry conditions, then we would expect to find evidence of the SGA at the seedling stage as well. However, like trees, lianas start their life as free-standing seedlings in the forest understory and both life forms show almost identical life history trade-offs in terms of growth and survival (Gilbert et al., 2006). Although liana and tree seedlings show differences in some morphological and physiological traits (Pasquini et al., 2015; van der Sande et al., 2019), they are similar in other key traits (Manzané-Pinzón et al., 2018; van der Sande et al., 2013), which may partially explain why the trade-off between growth and survival between the two life forms is so similar. Therefore, liana and tree species may show similar patterns of growth and mortality with respect to water availability at the seedling stage, such that the SGA would only be evident at later ontogenetic stages.

Here, we use a long-term dataset on seedling dynamics including >12,000 individuals of 483 tree and liana species collected at eight sites along a pronounced rainfall gradient spanning the Isthmus of Panama to test the SGA hypothesis in both space and time. We evaluated whether liana seedlings have an advantage (e.g., higher growth and/or lower mortality) relative to tree seedlings at sites that experience more severe dry seasons compared to sites with milder dry seasons. Additionally, we compared the growth and mortality response of tree versus liana seedlings to a severe supra-annual drought associated with the extreme 2015–2016 El Niño event (Browne et al., 2021). Given that previous studies have found that adult lianas have an advantage compared to adult trees under drier conditions (Schnitzer & van der Heijden, 2019), we predicted (1) that liana seedlings would have higher growth rates and/or lower mortality rates than tree seedlings at sites that experience stronger annual drought, leading to a pattern of increasing relative density of liana versus tree seedlings as dry season severity increases across the precipitation gradient; and (2) that the extreme El Niño drought event that occurred during our study would have a more negative effect on growth and survival for tree seedlings compared to liana seedlings.

MATERIALS AND METHODS

Study area

In this study, we censused free-standing, woody seedlings in eight previously established 1-ha forest plots across the Isthmus of Panama (Figure 1) (Browne et al., 2021). We selected accessible lowland sites in mature, protected, seasonal tropical moist forest that spanned the rainfall gradient between the Pacific and Caribbean coasts. Across this 65-km gradient, mean annual precipitation ranges from ~1600 to ~3200 mm (Condit et al., 2013; Umaña et al., 2021). Plant-available soil phosphorus covaries across this gradient, with higher values at drier sites (Condit et al., 2013). Drier sites along the gradient also tend to have high understory light availability (Gaviria & Engelbrecht, 2015). There is high turnover in tree species composition across the gradient, although many tree species occur at multiple sites along the gradient (Pyke et al., 2001; Umaña et al., 2021). The species composition of lianas shows relatively high overlap across sites: Manzané-Pinzón et al. (2018) reported that 45 out of the 63 liana species encountered in their study were present in all six of the sites where they surveyed liana seedlings.

Seedling censuses

We established 400 1-m² seedling plots within each 1-ha plot from September to December 2013 (Browne et al., 2021).

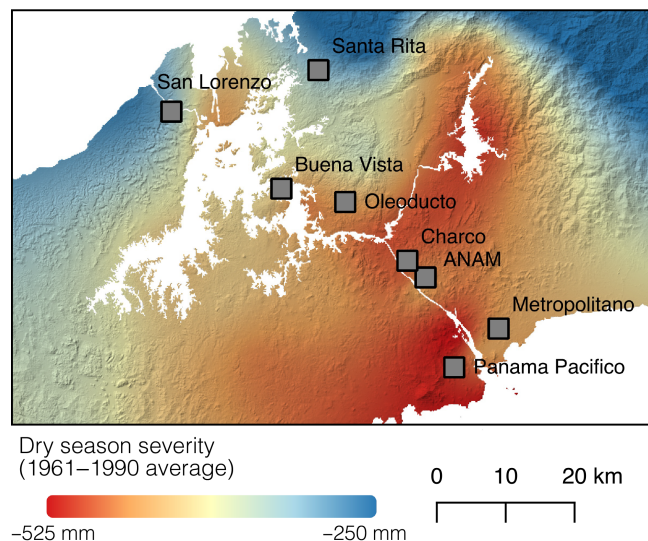


FIGURE 1 Map of study area showing eight census sites across the Isthmus of Panama (gray squares). Red to blue shading indicates long-term dry season severity (1961–1990 average), with redder shades showing more intense dry seasons than bluer shades.

The seedling plots were spaced every 5 m to maximize spatial coverage over the 1-ha plot and facilitate long-term monitoring. Within each 1-m² seedling plot, we tagged, identified, and measured all woody seedlings ≥ 200 mm in height and < 1 cm dbh (diameter at 1.3 m above ground) following the protocol of Comita et al. (2007). We then re-censused seedling plots annually at the beginning of the annual dry season (November–February). For this analysis, we include census data from 2013 to 2022, which encompasses eight annual census intervals. During each census, we measured the stem height of woody seedlings and evaluated if they were dead or alive, as well as marking and measuring newly recruited seedlings ≥ 200 mm tall. The seedling census included tree and shrub seedlings (hereafter referred to simply as “trees”), but not palm seedlings. Liana seedlings were included in the seedling census if they were not yet twining or climbing on other plants or along the ground. Once tagged, we continued to record the status of liana seedlings that later began twining/climbing but did not remeasure their height. We did not census the sites Oleoducto in 2019 and 2020 and Panamá Pacifico in 2018 due to limited site access.

We included census observations that met the following criteria: the seedling had a known survival status, known height in the prior census ≥ 200 and ≤ 1300 mm, had a species-level identification, that liana seedlings were free-standing, and ≤ 3.5 year interval between census observations for the seedling. After filtering for these criteria, the overall dataset contained 45,070 observations from 12,641 individuals across 483 different species (381 tree and shrub species and 102 liana species).

Dry season severity

To estimate the degree of annual drought at each 1-ha plot, we estimated dry season severity, which is defined as the most extreme cumulative rainfall deficit of evapotranspiration exceeding precipitation reached during the annual dry season (Condit et al., 2013). Lower values indicate more severe drought conditions during the dry season (Condit et al., 2013). We used two metrics of dry season severity from Browne et al. (2021): long-term dry season severity estimates (1961–1990 average) at each site (Figure 1), and dry season severity during the 2015–2016 El Niño (Appendix S1: Figure S1), which represented one of the most severe droughts in Panama’s recent history (Spinoni et al., 2019). Across sites, the estimates of long-term dry season severity and dry season severity during the 2015–2016 El Niño were strongly correlated with each other (Pearson’s $r = 0.98$, $p < 0.0001$).

Seedling density

We calculated seedling densities separately for lianas and trees per 1-m² seedling plot for each census and included zeroes for plots not containing any seedlings and only counting alive seedlings. To produce a site-level estimate of seedling density, we first averaged across the 400 seedling plots within each 1-ha site and then averaged across the eight censuses. We calculated liana relative density by dividing liana absolute density by total seedling density.

To test the hypothesis that tree and liana seedling absolute densities show differing patterns in response to long-term dry season severity across sites, we used a linear regression to model average tree and liana seedling densities (averaged across all censuses) at each site as a function of long-term dry season severity, growth form (i.e., whether the seedling density estimate was for lianas or trees), and the interaction between growth form (liana/tree) and dry season severity. We used a lognormal error distribution to ensure that predicted density estimates did not go below zero. To assess the relationship between liana relative densities and long-term dry season severity, we fit a linear regression with liana relative density at each site as the response variable and long-term dry season severity as the predictor variable.

Growth and mortality models

To estimate how growth and mortality rates varied between tree seedlings and liana seedlings, we fit hierarchical Bayesian models separately for growth and mortality, similar in form to the models presented in Browne et al. (2021). We used relative growth rates (RGRs) (cm cm⁻¹ year⁻¹) as our metric of growth following the equation:

$$\text{RGR} = \frac{\ln(\text{Height}_2) - \ln(\text{Height}_1)}{(t_2 - t_1)}, \quad (1)$$

where t_2 = time two, t_1 = time one, Height_2 = height at time 2, and Height_1 = height at time 1. We ran analyses with RGR calculated in two forms: (1) only positive growth rates and (2) all growth rates, including positive, zero, and negative growth rates. To normalize the distribution of growth rates and aid in model convergence, we used a Box-Cox transformation ($\lambda = 0.15$) when only positive growth rates were included and a modulus transformation when all growth rates were included (Browne et al., 2023; Condit et al., 2017). We then back-transformed RGR values to their original scale for presentation in all figures. For growth models, we

assumed transformed RGR to be normally distributed for each individual observation i :

$$\text{RGR}_i \sim \text{Normal}(\hat{y}_i, \sigma). \quad (2)$$

For mortality models, we assumed the response variable (1 = dead, 0 = alive) to be Bernoulli distributed and adjusted to account for varying census interval lengths (time):

$$\text{Mortality}_i \sim \text{Bernoulli}\left(\text{logit}(\hat{y}_i)^{\text{time}}\right). \quad (3)$$

Model 1: Overall growth and mortality rates

To estimate overall (i.e., for all sites combined) growth and mortality rates for tree and liana seedlings, we fit a model with the following form:

$$\hat{y}_i \sim \alpha_0 + \alpha_{1\text{spp}} + \alpha_{2\text{c,s}} + \alpha_{3\text{p}} + \beta_1 \times \text{InitialHeight}_i + \beta_2 \times \text{Liana}_i, \quad (4)$$

$$\alpha_{1\text{spp}} \sim \text{Normal}(0, \sigma^2), \quad (5)$$

$$\alpha_{2\text{c,s}} \sim \text{Normal}(0, \sigma^2), \quad (6)$$

$$\alpha_{3\text{p}} \sim \text{Normal}(0, \sigma^2), \quad (7)$$

where \hat{y}_i is either Box-Cox-transformed RGR or mortality status (1 = dead, 0 = alive) for observation i , α_0 is the overall intercept, $\alpha_{1\text{spp}}$ is a species-level (spp) random intercept to control for inherent differences in vital rates across species, $\alpha_{2\text{c,s}}$ is a random effect predicted separately for each census-site combination, $\alpha_{3\text{p}}$ is a plot-level random effect for each 1 × 1 m seedling plot p to control for spatial autocorrelation at small scales, β_1 estimates the effect of height at the previous census on either RGR or mortality, and β_2 estimates the overall difference in growth or mortality rates for lianas versus tree seedlings where $\text{Liana}_i = 1$ if a species is a liana and $\text{Liana}_i = 0$ when a species is not a liana. We did not explicitly account for repeated measures of the same individual because including an individual-level random effect prevented model convergence, but by including random effects for species and plot and including seedling height, we account for the majority of factors that would lead to nonindependence of measurements taken on the same individual. To account for differences in mean seedling height across species, we log-transformed and standardized (mean = 0 and SD = 1) initial seedling height within each species following Browne et al. (2021). We found

similar results when using an upper height cutoff of 400 mm to confirm that results were similar when looking at only smaller seedlings (Appendix S1: Figures S1 and S2).

Model 2: Site-level growth and mortality rates predicted by long-term dry season severity

To estimate whether growth and mortality rates at a site for tree and liana seedlings were dependent on dry season severity, we fit a model where site-level random intercepts varied separately for tree seedlings versus lianas:

$$\hat{y}_i \sim \alpha_0 + \alpha_{1\text{spp}} + \alpha_{2c} + \alpha_{3p} + \alpha_{4s,l} + \beta_1 \times \text{InitialHeight}_i, \quad (8)$$

where parameters are the same as in Model 1, except α_{2c} is a census-level (*c*) random intercept and $\alpha_{4s,l}$ is a site-level (*s*) random intercept estimated separately based on whether an individual is a liana or tree seedling (*l*).

To determine whether dry season severity at a site could explain variation in overall growth and mortality rates for either tree or liana seedlings, we fit a second-level regression within each growth and mortality model where:

$$\alpha_{4s,l} \sim \text{Normal}(\alpha_l + \beta_{2l} \times \text{DSS}_s, \sigma_l). \quad (9)$$

Under this formulation, β_{2l} estimates the slope of the relationship between dry season severity (DSS, average from 1961 to 1990, lower numbers indicate more severe dry seasons) and overall growth or mortality rates at a site (depending on the model), estimated separately for tree and liana seedlings. We then compared whether β_2 for tree seedlings was higher or lower than β_2 for liana seedlings using draws from the posterior distribution.

Model 3: Growth and mortality response to El Niño

To estimate how growth and mortality responses to the extreme 2015–2016 El Niño differed for tree seedlings and liana seedlings, we fit a model of the following form:

$$\hat{y}_i \sim \alpha_0 + \alpha_{1\text{spp}} + \alpha_{2c,l} + \alpha_{3p} + \alpha_{4s} + \beta_1 \times \text{InitialHeight}_i, \quad (10)$$

where parameters were similar to those in Model 2 above, but $\alpha_{2c,l}$ is a random effect predicted separately for tree seedlings and liana seedlings for each census. We then

estimated the impacts of the 2015–2016 El Niño on growth and mortality separately for tree and liana seedlings (*l*) as a derived parameter where the El Niño growth or mortality response was the difference between the growth or mortality estimate in the census interval including the El Niño compared to the average growth or mortality estimates of the remaining non-El Niño census intervals:

$$\text{NinoMortResponse}_l = \alpha_{2\text{NinoYear},l} - \text{mean}(\alpha_{2\text{NonNinoYears},l}). \quad (11)$$

Using this estimate, for model visualization, we present the absolute change in annual RGR in units of $\text{cm cm}^{-1} \text{ year}^{-1}$ and annual mortality rate, respectively, between the El Niño census interval compared to the remaining non-El Niño census intervals.

For El Niño models only, we excluded the site Oleoducto because a localized storm unrelated to the El Niño caused a large amount of tree falls during the census interval covering the El Niño. As a result, we observed an abnormally high rate of seedling growth in Oleoducto following the El Niño. To avoid falsely ascribing this phenomenon to the impacts of El Niño related drought, we excluded Oleoducto from the El Niño analysis. We present results including Oleoducto in the El Niño analysis in Appendix S1: Figure S4.

We fit models with Stan (Carpenter et al., 2017) using the “brms” package (Bürkner, 2017) for seeding density models and the “rstan” package v. 2.21.2 (Stan Development Team, 2017) for growth and mortality models. We used weakly-informative priors of Half-Normal(0,1) for variance parameters, Student_t(5,0,2.5) for coefficients in mortality models, and Normal(0,1) for coefficients in growth models following the Stan prior choice recommendations (Stan Development Team, 2017). For all models, we ran four independent chains for 1500 iterations, with 750 iterations of burn in, for a total of 3000 post-burn in samples. We checked chain convergence visually and by ensuring the potential scale reduction factor statistic (“rhat”) was <1.10 (Kéry, 2010).

For parameter estimates of interest, we calculated the Probability of Direction (Pd), which is the probability that a parameter estimate is strictly positive or negative, whichever is most probable. Probability of direction varies between 50% and 100% and is calculated based on the posterior distribution of the parameter estimate, such that it is the proportion of the posterior distribution that is of the median’s sign (Makowski et al., 2019). Pd values are strongly correlated with frequentist *p*-values such that $p_{\text{one-sided}} = 1 - p_d$ and $p_{\text{two-sided}} = 2 \times (1 - p_d)$. We used the “language of evidence” (Muff et al., 2022) to interpret Pd values (see Appendix S1 for details).

RESULTS

We found moderate evidence that densities of tree seedlings and liana seedlings responded differently to long-term dry season severity across the gradient (Figure 2a; $Pd = 0.95$ of liana by dry season severity interaction term). Densities of tree seedlings increased at sites with less severe dry seasons, while densities of liana seedlings remained relatively constant across the gradient (Figure 2a). Specifically, liana seedling density was predicted to be 0.32 individuals/m² (0.20 to 0.49, 95% credible interval [CI]) at the driest end of the gradient and 0.27 individuals/m² (0.13–0.51 95% CI) at the wettest end of the gradient. In contrast, tree seedling density was predicted to more than double across the gradient from 0.85 individuals/m² (0.52–1.32 95% CI) at the driest end of the gradient and 2.03 individuals/m² (0.99–3.64 95% CI) at the wettest end of the gradient. As a result, we found strong evidence that the relative density of liana seedlings was higher at sites with more severe dry seasons compared to sites with less severe dry seasons (Figure 2b; $Pd = 0.99$).

At the driest end of the gradient, relative density of lianas was predicted to be 0.27 (0.21–0.33 95% CI), compared to 0.12 (0.04–0.20 95% CI) at the wettest end of the gradient.

For both tree and liana seedlings, there was a trend of decreasing seedling growth and mortality with decreasing long-term dry season severity across the gradient (Figure 2c,d). However, contrary to expectation, we found little to no evidence that liana and tree seedlings differed in the slope of the relationship for either growth rates (Pd tree > liana = 0.53; Figure 2c) or mortality rates (Pd tree > liana = 0.68; Figure 2d). Including negative growth rates did not change qualitative results (Appendix S1: Figure S3).

We found strong evidence that tree seedlings showed a stronger mortality response during El Niño than liana seedlings (Pd tree response > liana response = 0.99; Figure 3c,d), with tree seedlings showing an average increase in annual mortality rate of 0.013 (0.003–0.025 95% CI) compared to lianas of -0.009 (-0.028 to 0.008 95% CI). We found moderate to strong evidence that the

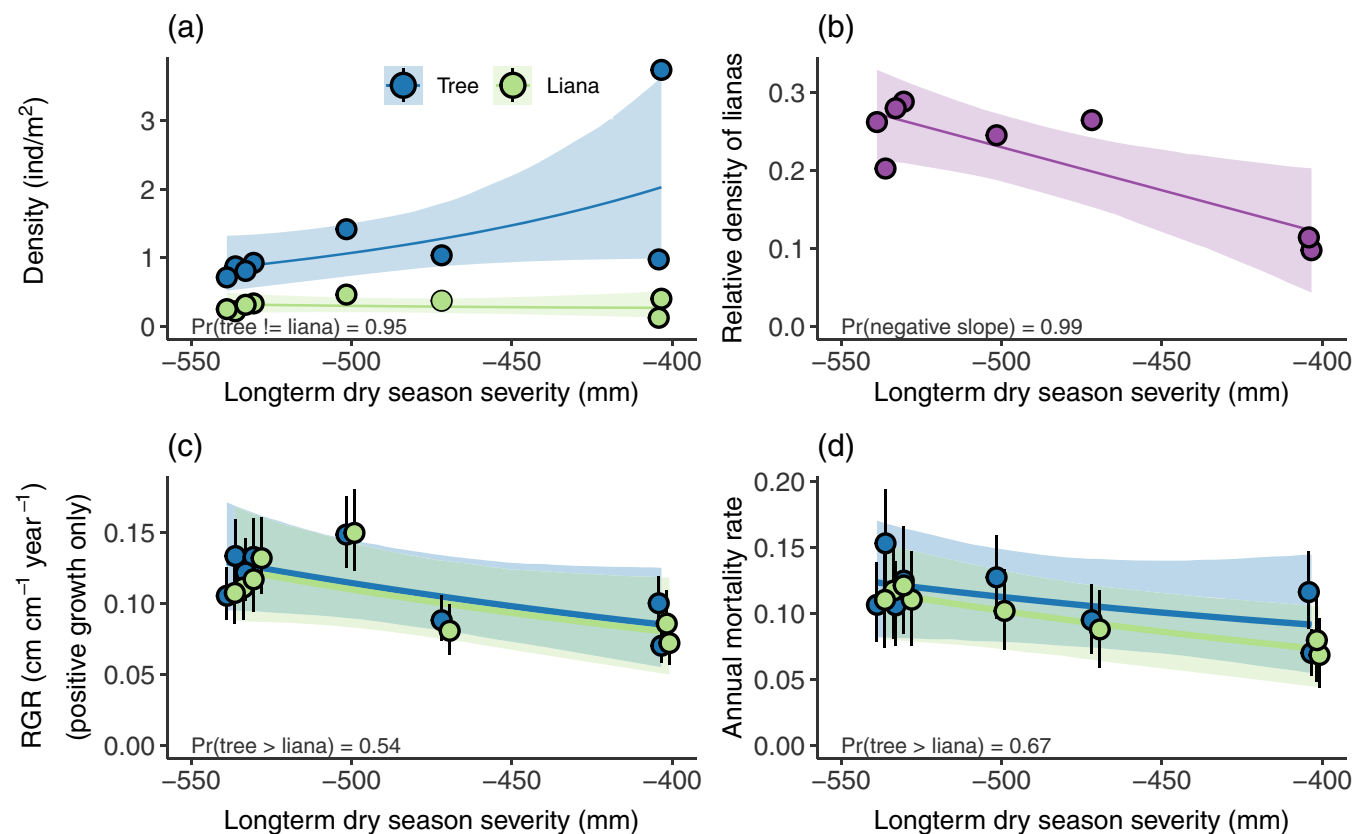


FIGURE 2 (a) Relationship between long-term dry season severity (in millimeters) and seedling density for tree seedlings and liana seedlings. Points show the mean seedling density averaged across censuses. Solid line shows the line of best fit from a linear regression, and shaded area shows the 95% credible interval. (b) Relationship between long-term dry season severity and relative density of lianas. Solid line shows the line of best fit from a linear regression, and shaded area shows the 95% credible interval. (c, d) The relationship between long-term dry season severity at a site (1961–1990 average) and the annual relative growth rates and mortality rates, respectively, for tree seedlings and liana seedlings. Points show the mean growth or mortality rate at a site, along with the 95% credible interval. Points are slightly jittered along the x-axis to reduce overlap for presentation purposes only.

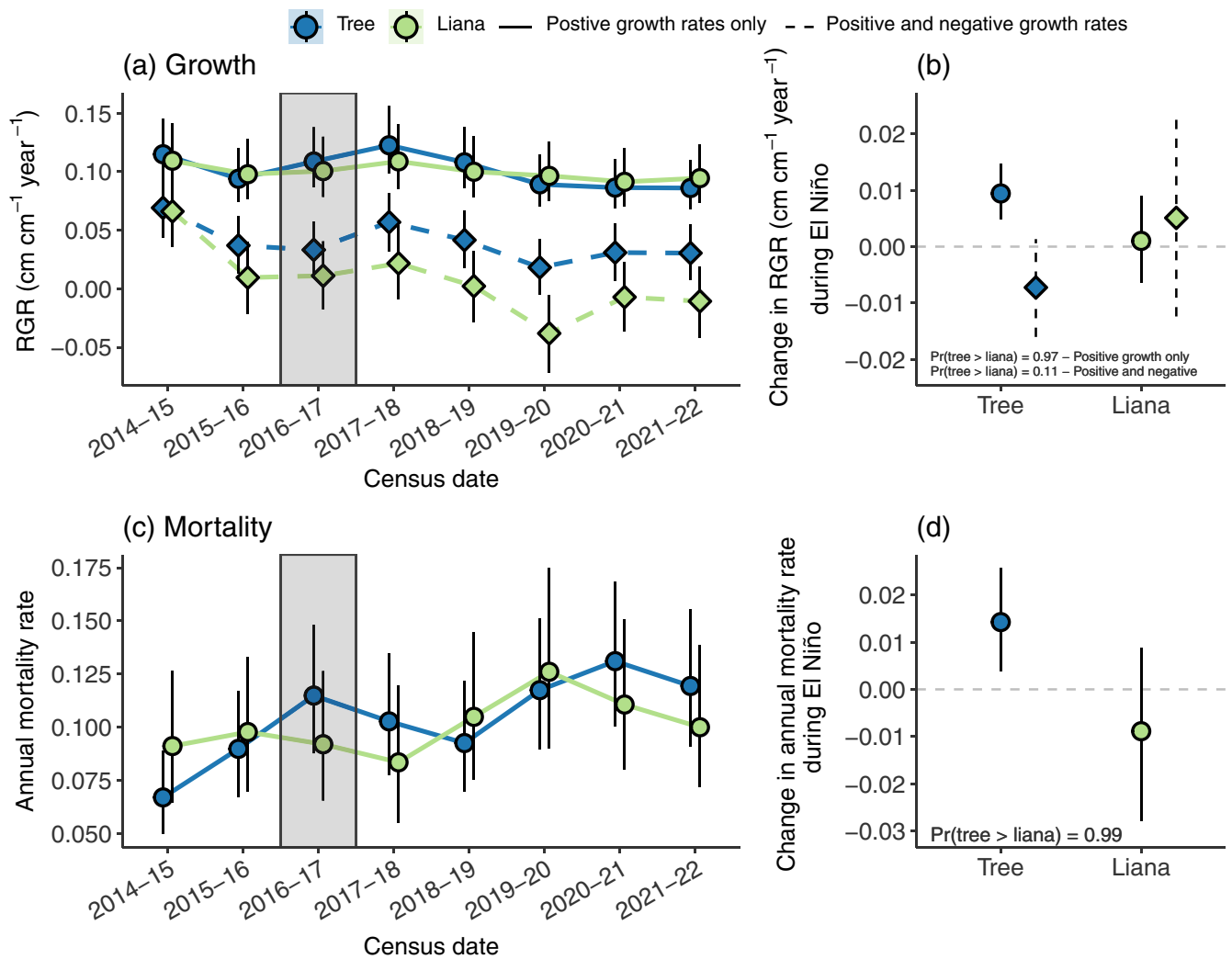


FIGURE 3 (a) Annual relative growth rates (RGRs) and (c) annual mortality rates for tree seedlings and liana seedlings during each census interval, with the census period covering the 2015–2016 El Niño shaded in gray. RGR estimates including only positive growth rates are shown with solid lines, and estimates with negative growth rates included are shown with dashed lines. For each panel, points indicate the mean estimate and vertical lines indicate the 95% credible interval. We excluded Oleoducto because it suffered a localized storm unrelated to the El Niño, which caused many tree falls that subsequently increased seedling growth. Failing to exclude Oleoducto from our analyses would have erroneously assigned an effect of El Niño on seedling growth. (b) Overall percentage of change in annual RGRs (RGR estimates with only positive growth rates included shown with solid lines and filled circles, and RGR estimates both positive and negative growth rates included shown with dashed lines and filled diamonds) and (d) annual mortality rates for tree seedlings and liana seedlings during the El Niño compared to other census intervals.

growth response to the 2015–2016 El Niño was more positive in tree seedlings than liana seedlings when only positive growth rates were included (Pd tree response > liana response = 0.97; Figure 3a,b), with annual RGRs increasing in tree seedlings by 0.012 (−0.010 to 0.041 95% CI) and in liana seedlings by 0.003 (−0.009 to 0.016 95% CI). When negative growth rates were included alongside positive growth rates, there was no evidence that growth response during El Niño was stronger for tree seedlings than liana seedlings (Pd tree response > liana response = 0.11; Figure 3b).

DISCUSSION

We found little support for the prediction that liana seedlings exhibit higher growth rates or lower mortality rates than tree seedlings in sites that experience stronger annual droughts across a gradient of dry season severity. While growth rates and mortality rates tended to be higher in drier sites than in wetter sites for both liana and tree seedlings, there were no strong differences in growth and mortality between liana and tree seedlings across sites. Yet, the relative density of liana

seedlings was higher in sites that experience stronger annual droughts, although the absolute density of liana seedlings remained almost the same across the precipitation gradient. Our results suggest liana seedlings might have an advantage over tree seedlings, but not from the expected higher growth and lower mortality predicted by the SGA hypothesis. Other processes, such as lower liana seedling mortality during extreme droughts (observed in this study), higher adult liana fecundity, or higher liana germination success, could potentially drive the observed patterns. This suggests that the SGA hypothesis might not be applicable to early life stages in the plant life cycle, but that greater differences in liana growth and survival relative to trees occur at later life stages.

A potential explanation of this unexpected result is that liana and tree seedlings are likely facing similar trade-offs when growing in the understory as freestanding individuals despite some differences in morphology and physiology. Liana and tree seedlings are, in some respects, different in terms of morphology (e.g., internode length) and physiology (e.g., capacity to power photosynthetic reactions) (Pasquini et al., 2015). Yet, seedlings of the two life forms are indistinguishable in terms of other morphological (e.g., wood density) and physiological traits (e.g., stomatal conductance) (van der Sande et al., 2013). Despite some differences as freestanding seedlings, lianas and trees show similar life history trade-offs in terms of growth and survival at this early life stage (Gilbert et al., 2006). Moreover, lianas occur as freestanding seedlings across the precipitation gradient (Manzané-Pinzón, 2012), and many liana species only start to exhibit their climbing habits well after the seedling stage (Campanello et al., 2016). Higher liana growth rates at sites with greater dry season severity probably occur at later life stages, when lianas exhibit more acquisitive traits than trees (Medina-Vega et al., 2021). In fact, the benefit of higher water-use efficiency of lianas compared to trees may be smaller at the seedling stage due to lower water demand relative to large individuals in the canopy.

We found mixed support for the prediction that the extreme drought associated with the 2015–2016 El Niño would lead to stronger negative effects on tree seedlings than on liana seedlings. Consistent with our expectations, tree seedlings showed increased mortality during the El Niño drought, while lianas did not show a mortality response to the El Niño. Increased mortality during El Niño for tree seedlings, as previously shown in Browne et al. (2021), is likely caused by drought stress. The lack of mortality response to El Niño in liana seedlings is likely due to their higher tolerance and resistance to drought stress (Maréchaux et al., 2017; Zhu & Cao, 2010). Contrary to our expectations, however, liana seedlings

showed no response to the El Niño in terms of growth, while tree seedlings showed increased growth in the El Niño year compared to other years, but only when RGRs were calculated for seedlings with positive growth. This suggests that a subset of tree seedlings are able to avoid stem breakage or dieback and take advantage of factors that promote growth during El Niño events, such as decreased cloud cover and higher understory light availability (Browne et al., 2021; Wright et al., 1999). However, as a whole, when negative and zero growth rates are included, tree seedlings do not show a positive growth response, as ~22% of tree seedlings experienced zero or negative growth during the El Niño, presumably due to the indirect and direct effects of drought stress. The lack of growth response in liana seedlings was unexpected, especially because the SGA hypothesis theorizes that lianas gain an advantage during dry periods through higher growth. Perhaps liana seedlings were unable to profit from higher availability of understory light because young lianas allocate less biomass to roots compared to young trees (Smith-Martin et al., 2020), and so were probably not as effective as tree seedlings at acquiring the little soil moisture that was available during the extreme drought. Therefore, the tree seedlings that did not have access to sufficient water died because of their low drought resistance, but those that had access to water were able to take advantage of the higher understory light availability to grow more.

Previous observational and experimental studies in Panama have also found that the effects of severe supra-annual droughts on liana and tree seedlings were not as strong as predicted. Umaña et al. (2020) analyzed changes in liana and tree seedling abundance in seasonal moist forest in the BCI 50-ha plot in Panama over a 16-year study that also spanned the 2015–2016 El Niño. They found only a small increase in liana relative abundance during the extreme drought of 2016. In comparison, there were larger increases in liana relative abundance in previous years with less severe dry seasons (Umaña et al., 2020). In a water addition experiment during the 1997–1998 El Niño dry season in an old-growth forest in central Panama, Bunker and Carson (2005) found no evidence for differential growth or mortality responses to irrigation of liana versus tree seedlings. In fact, and in line with our results, they found that liana seedlings grew significantly less than tree seedlings during the dry season (Bunker & Carson, 2005).

In contrast to the aforementioned results, stronger effects of El Niño-related droughts have been reported at other tropical forest sites. Abundance of liana seedlings showed a sharp increase after the 2015–2016 El Niño in a seasonally dry forest in Brazil (Marimon et al., 2020) and a wet forest in Puerto Rico (Umaña et al., 2019).

Interestingly, liana seedlings showed higher survival than tree seedlings in Puerto Rico during seasonal droughts, but lianas and trees showed no difference in growth rates (Umaña et al., 2019). Studies across more sites will determine whether higher liana seedling growth occurs during supra-annual droughts and translates into increases in liana seedling density.

Finally, we found support for the prediction that the abundance of liana seedlings relative to tree seedlings increases in sites with more severe annual dry seasons (Manzané-Pinzón et al., 2018). While the absolute density of lianas in the community did not vary based on dry season severity, their relative abundance in the community was higher in drier sites than in wetter sites. This pattern could be driven directly by water availability or by other factors that covary across the rainfall gradient, namely, soil phosphorous and understory light availability. However, in a nutrient addition experiment, also in central Panama, Schnitzer et al. (2020) found that neither phosphorus, nitrogen, nor potassium addition significantly increased liana relative growth or mortality rates relative to controls. This suggests that the higher relative densities of liana seedlings at the drier sites are unlikely to be due to enhanced liana performance under higher phosphorous levels at those sites. Drier sites along the gradient also tend to be more open and have more deciduous canopies, leading to higher understory light levels (Gaviria & Engelbrecht, 2015). If liana seedlings benefit more from increased light availability at the drier sites compared to tree seedlings, we would expect to see liana growth and mortality responding more strongly to changing long-term dry season severity across the gradient. Instead, both tree and liana seedlings showed a similar trend of decreasing seedling growth and mortality with decreasing long-term dry season severity across the gradient (Figure 2c,d). More generally, the higher relative density of liana seedlings at drier sites does not appear to be driven by differences in average growth or mortality rates between tree and liana seedlings. Instead, such a pattern could potentially be explained by higher growth and survival of adult trees in wetter sites, leading to differences in adult abundance and fecundity, resulting in higher tree seed availability and more trees seedlings recruiting at wetter than at drier sites. Additional data on seed production are needed to determine whether fecundity of adult lianas and trees contribute to patterns of liana and tree seedling densities across the gradient.

In conclusion, we found mixed support for the hypothesis that lianas should outperform tree seedlings in drier conditions, with tree and liana seedlings showing similar spatial patterns of growth and mortality across the dry season severity gradient, and tree seedlings showing higher growth but also higher mortality in response

to the extreme drought associated with the 2015–2016 El Niño. The SGA has been detected by comparing liana and tree growth on adult individuals between seasons (Schnitzer & van der Heijden, 2019). Our results suggest that the SGA hypothesis does not appear to apply to the seedling stage. Further studies assessing the fecundity of adult trees and lianas between sites that differ in dry season severity and examining the transition from the free-standing mode to the climbing mode in liana seedlings across species (e.g., Campanello et al., 2016) will help us circumscribe the limits of the SGA hypothesis. Liana abundance is expected to increase in areas where dry seasons will become longer and more severe. Therefore, improved understanding of the mechanisms that explain plant abundance and performance across ontogenetic stages will help predict the future of tropical forests.

AUTHOR CONTRIBUTIONS

Sergio Estrada-Villegas, Liza S. Comita, Eric Manzané-Pinzón, and Luke Browne conceived the study. Liza S. Comita, Eric Manzané-Pinzón, and Luke Browne participated in data collection. Luke Browne performed data analysis with input from Sergio Estrada-Villegas and Liza S. Comita. Sergio Estrada-Villegas and Luke Browne wrote the first draft of the manuscript, and all authors contributed to interpretation and writing. All authors approve of the submitted version of the manuscript.

ACKNOWLEDGMENTS

This work was supported by funding from the UK Natural Environment Research Council grant NE/J011169/1, the US National Science Foundation grants 1623775 and 1845403, Yale University, and the Ohio State University. SE-V was supported by the Cullman Fellowship from the Yale School of the Environment and the New York Botanical Garden. We are grateful for the tireless efforts of Lourdes Hernández Hassán, Luis Aguilar, Guillermo Aguilar, Mitzila Gaitan, Roni Saenz, Osmar Agrazal, Biancolini Castro, Moises Perez, and others who have made the yearly censuses possible. We thank the Comita and Queenborough labs for helpful feedback on the manuscript. We thank the Yale Center for Research Computing for use of the research computing infrastructure. The research was conducted in Panama under permits from the Ministry of Environment (MiAmbiente) and the Agencia Panama Pacifico (APP).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and model code (Browne et al., 2024) are available from Figshare: [10.6084/m9.figshare.24415828](https://doi.org/10.6084/m9.figshare.24415828).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Estrada-Villegas, Sergio, Luke Browne, Eric Manzané-Pinzón, and Liza S. Comita. 2024. "Liana versus Tree Seedling Responses to Spatial and Temporal Variation in Dry Season Severity." *Ecosphere* 15(11): e70058. <https://doi.org/10.1002/ecs2.70058>