Ecology, 100(1), 2019, e02556

Dry conditions and disturbance promote liana seedling survival and abundance

María Natalia Umaña[1,2,8] Jimena Forero-Montaña,[3] Christopher J. Nytch,[3] Jill Thompson,[4]
María Uriarte,[5] Jess Zimmerman,[3,6] and Nathan G. Swenson[1,7]

[1]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109 USA*
[2]*Department of Biology, University of Maryland, College Park, Maryland 20742 USA*
[3]*Department of Biology, University of Puerto Rico, Río Piedras, Puerto Rico 00931 USA*
[4]*Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB United Kingdom*
[5]*Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, New York 10027 USA*
[6]*Department of Environmental Sciences University of Puerto Rico, Río Piedras, Puerto Rico 00936 USA*
[7]*Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming, China*

Citation: Umaña, M., Forero-Montaña, J., Nytch, C. J., Thompson, J., Uriarte, M., Zimmerman, J., and N. G. Swenson. 2019. Dry conditions and disturbance promote liana seedling survival and abundance. Ecology 100(1):e02556. 10.1002/ecy.2556

Abstract. Species composition and community structure in Neotropical forests have been severely affected by increases in climate change and disturbance. Among the most conspicuous changes is the proliferation of lianas. These increases have affected not only the carbon storage capacity of forests but also tree dynamics by reducing tree growth and increasing mortality. Despite the importance of lianas in Neotropical forests, most of the studies on lianas have focused on adult stages, ignoring dynamics at the seedlings stage. Here, we asked whether observed increases in liana abundance are associated with a demographic advantage that emerges early in liana ontogeny and with decreased precipitation and increased disturbance. To test this, we compared patterns of growth and survival between liana seedlings and tree seedlings using a long-term data set of seedling plots from a subtropical wet forest in Puerto Rico, USA. Then, we examined the effect of precipitation and land use history on these demographic variables. We found evidence for liana seedling survival advantage over trees, but no growth advantages. This survival advantage exhibited significant temporal variation linked with patterns of rainfall, as well as differences associated with land-use history in the study area. Furthermore, we found that neighborhood density has a negative effect on liana survival and growth. Our results indicate that liana proliferation is likely related to a survival advantage that emerges in early stages and is influenced by climatic conditions and past disturbance. Predicted climatic changes in rainfall patterns, including more frequent and severe droughts, together with increases in disturbance, could have a significant effect on seedling tropical communities by favoring lianas.

Key words: community dynamics; growth; land use history; Neotropical forest; precipitation; seedlings crowding; survival.

Introduction

The high levels of species diversity found in tropical plant communities are in part represented by a high number of liana species that reach their peak diversity in tropical regions (Gentry 1992). During the last few decades, the proportion of lianas has increased in the tropics, especially in the Americas (Phillips et al. 2002, Wright et al. 2004, 2015*b*, Schnitzer and Bongers 2011, Schnitzer 2015; but see Smith et al. 2017 for small-sized trees) resulting in alterations of forests structure and composition as well as reductions in carbon storage capacity of the forests (Chave et al. 2008, Ingwell et al. 2010, Schnitzer and Bongers 2011, van der Heijden et al. 2015, Lai et al. 2017). Despite the evident changes that tropical plant communities have been experiencing related to liana proliferation, explanations for the relative success of lianas in these environments remain unclear.

Previous studies have suggested that the success of lianas is caused by their superior competitive ability that reduces the recruitment and survival of adult trees (Schnitzer and Bongers 2002, Schnitzer 2005, Schnitzer and Carson 2010, Tobin et al. 2012). Given that lianas are structural parasites of trees (Stevens 1987), they do not need to invest in structure to support the main stem. Instead, lianas may invest more in photosynthetic and

---

Manuscript received 17 November 2017; revised 7 September 2018; accepted 11 October 2018. Corresponding Editor: Ivette Perfecto.

[8] E-mail: maumana@gmail.com

vascular tissues that improve their water and nutrient uptake efficiency (Putz 1983, Schnitzer 2005). In adult stages, leaves of lianas easily invade the canopy by extending long branches laterally that take advantage of the good light conditions in the canopy (Schnitzer and Bongers 2002). In addition, it has been suggested that lianas may suffer less from water stress and thus grow better than trees during dry periods (Schnitzer 2005). Although the majority of the studies assessing the negative effects of lianas and their demographic success have been focused on adult stages of lianas (Schnitzer and Carson 2010, Wright et al. 2015*a*), we still have little evidence on whether the demographic advantage of lianas is evident even at their earliest stages of ontogeny (but see Wright et al. 2004, Hogan et al. 2017) .

Since lianas are freestanding individuals during early ontogeny, biomass allocation for self-supporting structures is necessary and the observed advantages at adult stages may not be reflected at seedling stages. However, lianas may still have physiological traits, such as large and wide vessels accompanied with thick xylem walls, and greater stomatal control compared to trees, that would provide advantages for water-uptake strategies independently of the ontogenetic stage (Ewers 1985, Ewers et al. 1990, Angyalossy et al. 2015). These physiological traits might benefit liana species over trees during dry periods, and in areas of high disturbance that are usually drier and sunnier than the shaded understory (Bazzaz and Wayne 1994, Laurance et al. 2001, Wright et al. 2004, Schnitzer and Bongers 2011), allowing higher growth and survival rates even at early stages of development. Indeed, previous studies have found that (adult) liana abundance increases in disturbed areas (Perez-Salicrup et al. 1998, Dewalt et al. 2000, Letcher and Chazdon 2009), yet, no studies have shown this for early ontogenetic stages.

At the local scale, individual crowding might also affect seedling performance. Previous studies have shown that density of neighboring seedlings influences individual performance (Packer and Clay 2003, Kobe and Vriesendorp 2011, Comita et al. 2014), and this effect could vary across species depending on their life-history strategies. For instance, large-seeded species are less negatively affected by high density of conspecific neighbors than smaller-seeded species (Lebrija-Trejos et al. 2016). Given that lianas exhibit a set of strategies that are different from trees (Ewers 1985, Ewers et al. 1990, Angyalossy et al. 2015), the use of resources may overlap more among liana individuals than between lianas and trees. This greater overlap in resource use could result in lower performance of liana seedlings where higher densities of liana neighbors are present (Wright et al. 2015*a*).

In this study, we compared seedling performance between lianas and tree species in a subtropical wet forest in Puerto Rico and linked it to biotic and climatic factors. We combined a 10-year demographic inventory of seedling plots with local rainfall data and neighborhood crowding to investigate the following questions: (1) Do lianas have advantageous demographic performance (i.e., growth and survival) relative to trees at the seedling stage? (2) Are liana seedlings responding differentially to abiotic factors such as local climatic conditions and land use history? (3) How is this potential advantage related with local neighborhood crowding? We predict that demographic advantages for lianas should emerge at early ontogenetic stages, likely associated with physiological characteristics that allow them a more efficient use of resources (i.e., water availability). The variability in climatic and local abiotic conditions should favor liana seedlings over tree seedlings in dry and disturbed conditions. In addition, we expect a negative neighborhood density effect on liana survival and growth.

METHODS

Study site

We compiled seedling information data from the 16-ha Luquillo Forest Dynamic Plot (LFDP; 18°20′° N, 65°49′° W) located in northeastern Puerto Rico, which is part of the Smithsonian's Forest-GEO network. This forest is classified as a subtropical wet forest with a mean annual temperature of 25.2°C, mean annual rainfall of 3,500 mm/yr, and elevation from 333 to 428 m above sea level (Thompson et al. 2004). In the past, the plot was affected by natural (hurricanes) and human disturbances that severely altered species composition and dynamics. Two major hurricanes that impacted the island during the study period were Hurricane Hugo in September 1989, some months before the establishment of the LFDP, and hurricane Georges in 1998 (Brokaw and Grear 1991, Zimmerman et al. 1994, Thompson et al. 2004). In addition, in the early 1900s, the north portion of the plot was greatly affected by agriculture based on coffee and fruit plantations that were later abandoned after the hurricane San Felipe II 1928, while selective logging was practiced on the south portion of the plot until 1944 (Thompson et al. 2002). Based on aerial photographs taken in 1936 (Foster et al. 1999, Thompson et al. 2002), we classified the 16-ha plot in two categories: low-intensity land use (≥80% of canopy cover) and high-intensity land use (<80% of canopy cover) to examine the role of past disturbance on liana seedling survival.

Seedling censuses

We used information from 120 seedling-plot stations distributed along the LFDP. Each station consisted of three seedling plots of 1 × 1 m established at a distance of ~2 m from each other. From 2007 to 2016 (starting in January), all the seedling plots were annually monitored for growth, recruitment, and survival. All freestanding seedlings (>0–100 cm in height) were tagged, identified, and measured. When plots had new recruits, these individuals were included in the new census following the same methodology previously explained. We classified all individual seedlings across the entire census according to their habit as liana or tree. We found a total of 15 liana species (*Cissampelos pareira* L., Menispermaceae; *Cissus verticillata* (L.) Nicolson & C.E. Jarvis, Vitaceae; *Dioscorea alata* L., Dioscoreaceae; *Dioscorea polygonoides* Humb & Bonpl. Ex Willd., Dioscoreaceae; *Hippocratea volubilis* L., Celastraceae; *Heteropterys laurifolia* (L.) A. Juss, Malpighiacecae; *Ipomoea repanda* Jacq., Convolvulaceae; *Marcgravia rectiflora* Triana & Planch, Marcgraviaceae; *Paullinia pinnata* L., Sapindanceae; *Pinzona coriacea* Mart. & Zucc., Dilleniaceae; *Rourea surinamensis* Miq., Connaraceae; *Schlegelia brachyantha* Griseb., Schlegeliaceae; *Securidaca virgate* Sw., Polygonaceae; *Smilax coriacea* Spreng., Smilacaceae; *Smilax domingensis* Willd., Smilacaceae) and 77 species of trees (Appendix S1: Table S1). For the analyses, we combined seedling information at the station level, and our sample size was 120.

Climatic data

We used information about local daily precipitation that has been measured at the El Verde meteorological station from 1974 to 2014. This station is situated <0.5 km to the south of the LFDP. Our analyses used annual precipitation values that were computed from daily precipitation data from 2007 to 2014. These data were obtained from the LTER website (*available online*).[9]

Data analyses

We recorded annual seedling survival across the 120 stations and calculated relative growth rates for each individual seedling as $\frac{\log(H_{t+\Delta t})-\log(H_t)}{\Delta t}$, where H indicates seedling height at successive time steps t. Then, we assessed the proportion of liana and tree seedlings that survived at each station.

In order to compare annual seedling survival between lianas and trees, we built a null model in which we shuffled the habit (i.e., liana or tree) of all the individuals within one station (three seedling plots), keeping the total number of lianas and trees for each station constant. Next, we recalculated the proportion of surviving lianas. Because the local conditions within each station may change from site to site we restricted randomizations to each station. In total, we used 999 randomizations such that at the end we had 999 null estimates of the proportion of surviving lianas in each station for each year. We estimated the standardized effect size (SES) for the proportion of liana survival by subtracting the mean values of the null distribution from the observed values and dividing by the standard deviation of the null distribution. Positive SES values indicate a higher proportion of liana survival over trees, given observed individuals of lianas and trees, whereas negative values indicate the opposite.

We used a similar null model to test whether the relative growth rate of liana seedlings was significantly higher than tree seedlings. We randomized the habit (liana or tree) for all individuals within each plot 999 times and then we estimated mean relative growth rates for lianas. Next, we calculated SES mean relative growth rates for lianas in the same way it was described above, and the meaning of positive and negative values remain the same as well.

To explore the role of temporal variability in precipitation and land-use effects on liana seedling survival and growth advantage, we fit models for SES survival and SES growth, respectively, which included as fixed effects the mean annual rainfall from the year prior to the census, and the land-use category at the station level. Station was modeled as a random effect to account for spatial variation. The data used for these analyses span the period between 2007 and 2014, given that rainfall information is only available for these years. To facilitate interpretation, the mean annual rainfall variable was centered at its average and divided by its standard deviation.

Considering that local neighborhood might influence the demographic performance of seedlings we evaluated whether the density of neighbor individuals had a significant effect on liana seedling survival and growth. To accomplish this, we fit models in which SES liana survival and SES liana growth were modeled as a function of liana seedling density or total density including tree and liana seedlings. To account for spatial variation, the variable station was modeled as a random effect. Census was also modeled as a random effect. All models were fit by implementing linear mixed-effects models with normal-distributed errors by using the lme4 package (Bates et al. 2015) in R 3.4.0 (R Development Core Team, 2017). Confidence intervals for each parameter were computed by bootstrap.

RESULTS

Comparing survival and growth between lianas and trees

We found that during 2007–2016 the total number of seedlings (lianas and trees) increased from about 7,000 to 11,500 across the 120 stations. In addition, the proportion of liana seedlings increased from ~0.4 to more than 0.6 (Fig. 1). Liana survival was significantly higher than tree survival during the first two-year intervals (2007–2008 and 2008–2009), in 2012–2013, and in the last two-year intervals (2014–2015 and 2015–2016), marginally significant in 2009–2010, nonsignificant in 2013–2014, and significantly lower than trees in 2010–2011 and 2011–2012 (Fig. 2). On the other hand, seedling growth rates were in general no different for lianas and trees, except in the time intervals of 2008–2009 and 2010–2011 where growth rates were significantly lower for lianas than trees (Fig. 2).

Effects of climate and land-use history on liana seedling survival

We examined whether the variation in SES liana survival and SES growth were influenced by mean annual

---

[9] http://luq.lter.network/

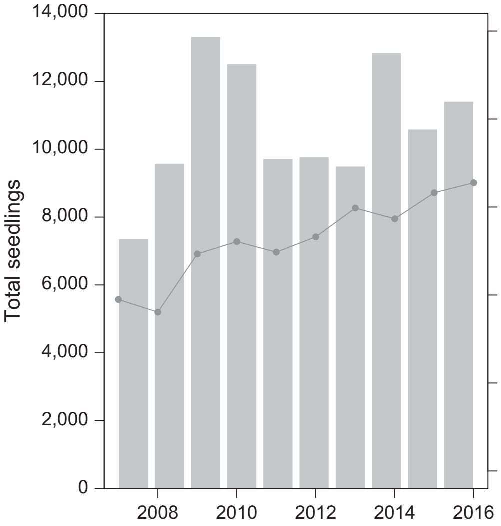

FIG. 1. Bar plot showing changes in the total number of seedlings across 120 sites in LFDP, Puerto Rico from 2007 to 2016. The gray line represents changes in the proportion of lianas over time.

precipitation from 2007 to 2014 and land-use history. We found that SES liana survival was significant and negatively associated with mean annual precipitation (Fig. 3). In addition, we found that SES liana survival was significantly lower in the portion of the plot with high-intensity land use than in the area that experienced low-intensity land use (Fig. 4; Appendix S1: Table S2). Similar analyses for SES liana growth showed a non-significant effect of annual mean precipitation and land use (Appendix S1: Table S3).

Effects of neighborhood crowding on liana seedling demography

To evaluate whether variation in tree and liana seedling demography was associated with neighborhood density, we examined the relationship between SES liana values of growth and survival with the total density of neighbors and the density of liana neighbors. We found that the density of lianas had a significant negative effect on liana survival, while the effect of total density was not significant (Fig. 5; Appendix S1: Tables S4 and S5). For the analyses considering growth rates and neighborhood density effects, we found that high density of seedlings and high density of lianas were negatively correlated with liana growth rates (Fig. 5; Appendix S1: Tables S6 and S7).

DISCUSSION

An increasing number of studies have shown that tropical forests are experiencing remarkable changes in structure and dynamics (Phillips and Gentry 1994, Condit 1998, Allen et al. 2010, Enquist and Enquist 2011), which includes an outstanding proliferation of lianas in the Neotropics (Phillips et al. 2002, Schnitzer and Bongers 2011, Delgado et al. 2016, Hogan et al. 2017). Determining whether these changes are also present in earlier ontogenetic stages and linked to abiotic and biotic factors is a central goal in ecology and conservation biology. In this study, we sought to investigate whether lianas exhibit a demographic advantage during seedling stages, thereby helping to further elucidate the drivers of the increasing abundance of lianas in Neotropical forests. Our findings suggest that liana seedlings exhibit a survival advantage associated with dry years and high-intensity land-use portions of the forest. These results have important implications for forest structure, diversity, and dynamics in the context of global climate change, wherein more severe and frequent extreme drought events are predicted to occur in tropical environments (IPCC 2013).

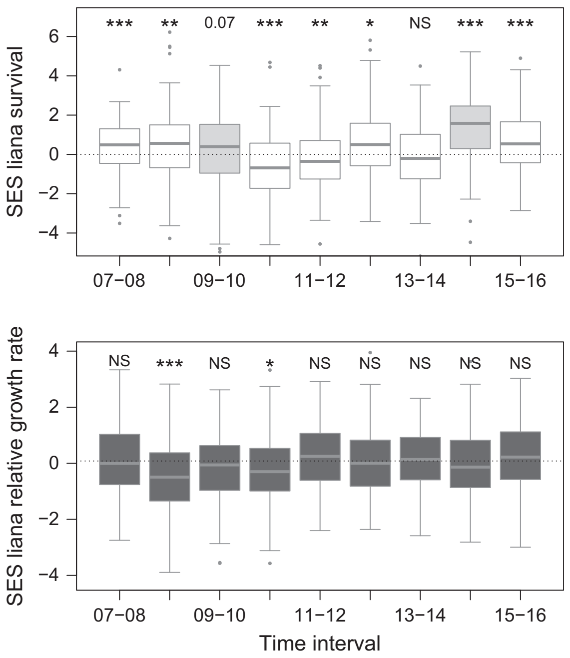

FIG. 2. Standardized effect size of the proportion of liana seedling survival and liana relative growth rates relative to trees in seedling communities over 10 years (from 2007 to 2016). White box plots show the results based on survival and dark-gray box plots show the results based on relative growth rates. The two light-gray box plots in the top figure show El Niño Southern Oscillation events that occurred during the study period. Positive standardized effect sizes (SES) values indicate higher growth rates or higher proportion of liana seedling survival over trees given observed individuals of lianas and trees, whereas negative values indicate the opposite. The values on top of the box plot indicate the level of significance of Wilcoxon signed-rank test, with ***$P < 0.001$, **$P < 0.01$, *$P \leq 0.05$; and NS, $P > 0.05$. Box plot components are mid line, median; box edges, inter-quartile range; whiskers, and points, outliers.

Liana seedlings are increasing over time

By looking at the general patterns that describe the changes in seedling number and proportion of liana

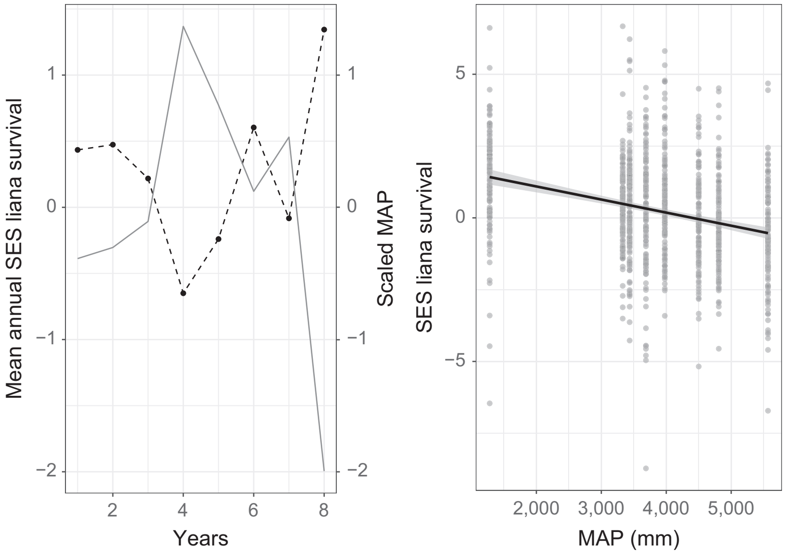

FIG. 3. Relationship between mean annual precipitation at El Verde Field Station and SES liana survival. The gray line shows the variation in scaled annual precipitation from 2007 to 2014. The black dashed line shows the temporal variation in mean annual SES liana survival at intervals from 2007–2008 to 2014–2015. The plot at the right shows the result of the model testing for the relationship between mean annual precipitation (MAP) and SES liana survival. Each point represents a station.

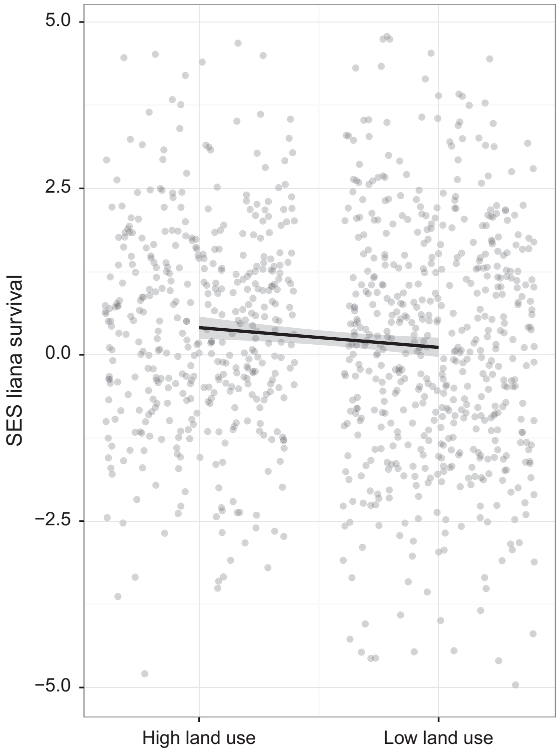

FIG. 4. Land use effect on SES liana survival. Dots indicate seedling stations, the black line represents the mean estimate, and the shaded gray area shows the 95% credible intervals. Values for this covariate are summarized in Appendix S1: Table S2.

individuals over time (Fig. 1), a clear feature of the seedling community in Puerto Rico is a high and increasing proportion of liana individuals. This trend is consistent with patterns of adult lianas in other Neotropical forests (Phillips et al. 2002, Schnitzer and Bongers 2011), and with a previous study in the same site examining the recruitment success for some liana and tree species from 2008 to 2010 (Muscarella et al. 2013). The proportion of lianas during 2007 to 2016 ranged from approximately 40% to more than 60%, almost three times the proportion of lianas found in Barro Colorado Island (BCI), Panama during eight years of monitoring (1994–2002; Wright et al. 2004). This first result highlights, then, that lianas represent an increasingly important component of the seedling community in this forest.

Temporal and spatial variability in liana seedlings demography is associated with rainfall and disturbance

The observed increase in liana seedlings is likely associated with a survival advantage that was evidenced in our results (Fig. 2). This pattern, however, was not consistently found across the whole study period. There was important interannual variation in liana demographic success associated with temporal seasonality related to local climatic conditions, in which liana-seedling survival was enhanced during periods of low annual precipitation (Fig. 3). Although, for seedling stages, drought is perhaps one of the key causes of plant mortality in tropical forests (Bunker and Carson 2005, Engelbrecht et al. 2007, Nepstad et al. 2007, Kraft et al. 2011, Saatchi et al. 2012, Comita and Engelbrecht 2014, O'Brien et al. 2017), our results suggest that liana seedlings are less affected by dry conditions. This demographic advantage of lianas during dry periods has been also reported in a recent analysis using a subset of species of the seedling community in the LFDP (Uriarte et al. 2017), and in

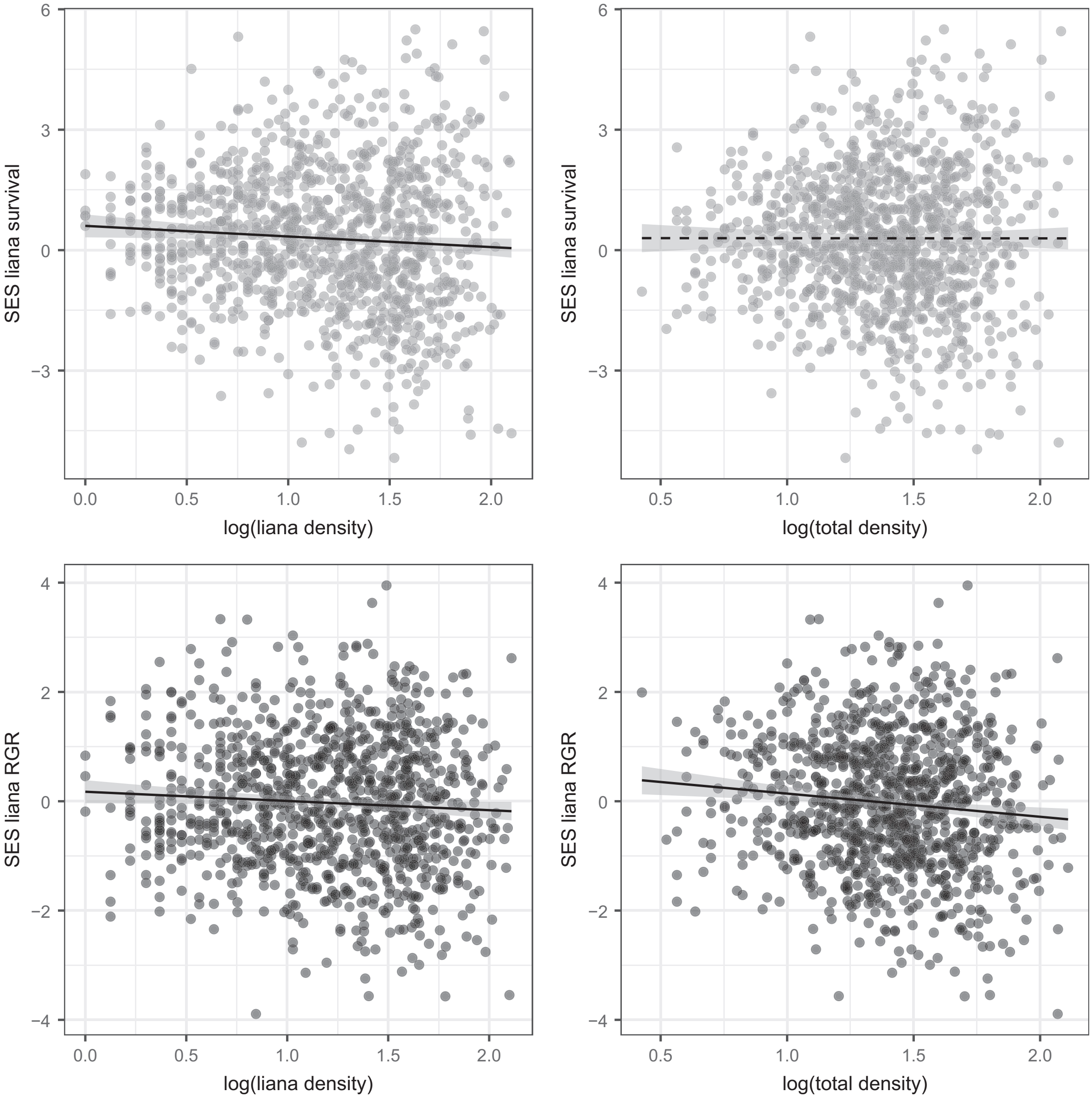

FIG. 5. Crowding effect on liana demography. Top plots with gray dots show relationships using SES liana survival. Bottom plots with black points show relationships using SES liana relative growth rate. Black lines show significant relationships and the dashed line shows a nonsignificant relationship.

other tropical forests for adult lianas (Swaine and Grace 2007). Further, Wright et al. (2004) found high variation in seedling densities in Barro Colorado Island related to dry and warm periods associated with El Niño Southern Oscillation (ENSO) events, where higher recruitment occurred during the ENSO years. In our study, ENSO occurred during 2009–2010 and 2014–2015, coinciding with the years when survival advantage was detected for liana seedlings and when precipitation was particularly low (Fig. 3). Nevertheless, longer time series would be needed to thoroughly test the link between liana seedling advantages and ENSO events in Puerto Rico.

The observed superior survival of liana seedlings relative to trees suggests that lianas might exhibit physiological and ecological characteristics that allow them to attain better performance than trees at early ontogenetic stages. For example, recent studies have shown that lianas have a greater stomatal control, which helps to regulate water loss under low water conditions (Cai and Bongers 2007, Cai et al. 2009). Other studies have found that lianas are deep rooted, which enables them to access water at great depths during dry periods (Restom and Nepstad 2004, discussed by Schnitzer 2005, Swaine and Grace 2007). Lianas are also equipped with the largest and widest vessels among the vascular plant species, which allow great conductivity. This same attribute also contributes to enhanced vulnerability (Ewers 1985, Ewers et al. 1990, Angyalossy et al. 2015); however, lianas have also thick xylem walls that help avoid water transport failure (Masrahi 2014). These characteristics are likely developed during early stages and provide physiological benefits that allow liana seedlings to perform better under drought conditions (Schnitzer 2005).

Another potential factor that influences the success of lianas in Puerto Rico is related to the history of human and natural disturbances. Many studies have suggested that adult lianas benefit from disturbance (Perez-Salicrup et al. 1998, Laurance et al. 2001, Schnitzer and Bongers 2002) and are linked to successional processes (Letcher and Chazdon 2009, Alves et al. 2012, Hogan et al. 2017). Currently, the plant community in the LFDP is recovering from past disturbance after hurricanes Hugo and Georges (Zimmerman et al. 1994, Thompson et al. 2002, 2004, Uriarte et al. 2009) and varied land-use history that occurred before 1934. We evaluated the response of liana seedlings to land-use and hurricane effects by integrating land-use information based on aerial canopy photographs taken two years after human activities ceased in the plot. The results suggest that the spatial variation in liana seedling survival throughout the LFDP is explained by differences in past disturbance (Fig. 4), emphasizing the variable roles of hurricanes and anthropogenic influences on the current proliferation of liana seedlings in this forest. In agreement with these findings, Hogan et al. (2017) found that abundance of adult lianas and liana seed rain increased after 2001, especially in the high land-use intensity portion of the LFDP. Our results, therefore, indicate that the positive effect of disturbance on lianas is also evidenced during early ontogenetic stages.

Our study also shows that growth and seedling survival are not necessarily coupled. Overall, significant differences in survival between trees and lianas were more frequent than differences in growth. One potential explanation for these results is that differences in growth may occur at shorter temporal scales. For example, Schnitzer (2005) showed intra-annual variability in growth, where liana species tend to exhibit faster growth than trees during the dry season compared with the wet season. Another explanation might simply be that growth rates are noisier than survival rates.

Crowding effects on liana seedlings

The demographic advantages of liana seedlings observed during dry years are sensitive to liana crowding effects, which decrease liana density after years of high recruitment (Fig. 5). When analyzing the role of neighborhood density on liana survival, we found that liana seedling survival is negatively related to the total number of liana neighbors (Fig. 5). For growth, the results showed that not only the liana density but also the density of all neighbors have negative effects on liana growth. These negative crowding effects are likely associated with years of high recruitment that are followed by periods of high mortality (Appendix S1: Fig. S1).

CONCLUSION

Our study indicates that lianas exhibit a demographic advantage that starts early in ontogeny and is associated with past disturbance and drought. Predicted increases in anthropogenic activities and natural disturbances, together with more frequent severe droughts in tropical forests, are likely to drive compositional changes in plant communities (Woods 1989, Enquist and Enquist 2011, Esquivel-Muelbert et al. 2016) and potentially lead to continued increases in liana abundances. The integration of long-term information that considers fluctuations in climatic phenomena is key to predict alterations in structure and composition of tropical seedling communities in response to environmental change. Future studies should include analyses of relevant functional traits to provide additional insights into the underlying physiological mechanisms.

ACKNOWLEDGMENTS

We thank several field assistants and staff involved in recording the data on seedling census during these past years. Masha van der Sande, Michael O'Brien, and an anonymous reviewer provided helpful comments on earlier versions of the manuscript. Financial support was provided by two grants from the National Science Foundation, DEB-0614658 and DEB-1122325. Additional support was provided by grants DEB-0620910, DEB-129764, and DEB-1546686 from NSF to the Department of Environmental Science, University of Puerto Rico, and to the International Institute of Tropical Forestry USDA Forest Service, as part of the Luquillo Long-Term Ecological Research Program. The U.S. Forest Service (Department of Agriculture) and the University of Puerto Rico gave additional support.

LITERATURE CITED

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Alves, L. F., M. A. Assis, J. van Melis, A. L. S. Barros, S. A. Vieira, F. R. Martins, L. A. Martinelli, and C. A. Joly. 2012. Variation in liana abundance and biomass along an elevational gradient in the tropical Atlantic Forest (Brazil). Ecological Research 27:323–332.

Angyalossy, V., M. R. Pace, and A. C. Lima. 2015. Liana anatomy: a broad perspective on structural evolution of the vascular system. Pages 251–287 *in* S. A. Schnitzer, F. Bongers, R. J. Burnham, and F. E. Putz, editors. Ecology of lianas. John Wiley & Sons, Hoboken, New Jersey, USA.

Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bazzaz, F. A., and P. M. Wayne. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap—understory continuum. Pages 349–390 *in* M. M. Caldwell and R. W. Pearcy, editors. Physiological ecology: a series of monographs, texts, and treatises. Exploitation of environmental heterogeneity by plants. Ecophysiological processes above- and belowground. Academic Press, San Diego, California, USA.

Brokaw, N. V. L., and J. S. Grear. 1991. Forest structure before and after hurricane Hugo at three elevations in the Luquillo mountains, Puerto Rico. Biotropica 23:386–392.

Bunker, D. E., and W. P. Carson. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. Journal of Ecology 93:794–806.

Cai, Z., and F. Bongers. 2007. Contrasting nitrogen and phosphorus resorption efficiencies in trees and lianas from a tropical montane rain forest in Xishuangbanna, south-west China. Journal of Tropical Ecology 23:115.

Cai, Z. Q., S. A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. Oecologia 161:25–33.

Chave, J., J. Olivier, F. Bongers, P. Chatelet, P. Forget, P. van der Meer, N. Norden, B. Riera, and P. Charles-Dominique. 2008. Above-ground biomass and productivity in a rain forest of eastern South America. Journal of Tropical Ecology 24:355–366.

Comita, L. S., and B. M. J. Engelbrecht. 2014. Drought as a driver of tropical tree species regeneration dynamics and distribution patterns. Pages 261–308 *in* D. A. Coomes, D. F. R. Burslem, and W. D. Simonson, editors. Forests and global change. Cambridge University Press, Cambridge, Massachusetts, USA.

Comita, L. S., S. A. Queenborough, S. J. Murphy, J. L. Eck, K. Xu, M. Krishnadas, N. Beckman, and Y. Zhu. 2014. Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. Journal of Ecology 102:845–856.

Condit, R. 1998. Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. Climatic Change 39:413–427.

Delgado, D. L., J. Figueroa, and C. Restrepo. 2016. Using multiple traits to assess the potential of introduced and native vines to proliferate in a tropical region. Ecology and Evolution 6:8832–8845.

Dewalt, S. J., S. A. Schnitzer, and J. S. Denslow. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. Journal of Tropical Ecology 16:1–19.

Engelbrecht, B. M. J., L. S. Comita, R. S. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. Nature 447:80–82.

Enquist, B. J., and C. A. F. Enquist. 2011. Long-term change within a Neotropical forest: assessing differential functional and floristic responses to disturbance and drought. Global Change Biology 17:1408–1424.

Esquivel-Muelbert, A., et al. 2016. Seasonal drought limits tree species across the Neotropics. Ecography 40:618–629.

Ewers, F. W. 1985. Xylem structure and water conduction in conifer trees, dicot trees, and lianas. IAWA Bulletin 6:309–317.

Ewers, F. W., J. B. Fisher, and S. T. Chiu. 1990. A survey of vessel dimensions in stems of tropical lianas and other growth forms. Oecologia 84:544–552.

Foster, D., M. Fluet, and E. Boose. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. Ecological Application 9:555–572.

Gentry, A. H. 1992. The distribution and evolution of climbing plants. Pages 3–49 *in* F. E. Putz and H. A. Mooney, editors. The biology of vines. Cambridge University Press, Cambridge, Massachusetts, USA.

Hogan, J. A., S. Mayorquín, K. Rice, J. Thompson, J. K. Zimmerman, and N. Brokaw. 2017. Liana dynamics reflect land-use history and hurricane response in a Puerto Rican forest. Journal of Tropical Ecology 33:155–164.

Ingwell, L. L., S. Joseph Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. Journal of Ecology 98:879–887.

IPCC. 2013. Climate Change 2013: The Physical Science Basis. *In* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley, editors. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, 1535 pp.

Kobe, R. K., and C. F. Vriesendorp. 2011. Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. Ecology Letters 14:503–510.

Kraft, N. J. B., et al. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. Science 333:1755–1758.

Lai, H. R., J. S. Hall, B. L. Turner, and M. van Breugel. 2017. Liana effects on biomass dynamics strengthen during secondary forest succession. Ecology 98:1062–1070.

Laurance, W. F., D. R. Perez-Salicrup, P. Delamonica, P. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology 82:105–116.

Lebrija-Trejos, E., P. Reich, A. Hernández, and S. J. Wright. 2016. Species with greater seed mass are more tolerant of conspecific neighbours: a key driver of early survival and future abundances in a tropical forest. Ecology Letters 19:1071–1080.

Letcher, S. G., and R. L. Chazdon. 2009. Lianas and self-supporting plants during tropical forest succession. Forest Ecology and Management 257:2150–2156.

Masrahi, Y. S. 2014. Ecological significance of wood anatomy in two lianas from arid southwestern Saudi Arabia. Saudi Journal of Biological Sciences 21:334–341.

Muscarella, R., M. Uriarte, J. Forero-Montaña, L. S. Comita, N. G. Swenson, J. Thompson, C. J. Nytch, I. Jonckheere, and J. K. Zimmerman. 2013. Life-history trade-offs during the seed-to-seedling transition in a subtropical wet forest community. Journal of Ecology 101:171–182.

Nepstad, D. C., I. M. Tohver, D. Ray, P. Moutinho, and G. Gardinot. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. Ecology 88:2259–2269.

O'Brien, M. J., R. Ong, and G. Reynolds. 2017. Intra-annual plasticity of growth mediates drought resilience over multiple years in tropical seedling communities. Global Change Biology 23:4235–4244.

Packer, A., and K. Clay. 2003. Soil pathogens and *Prunus serotina* seedling and sapling growth near conspecific trees. Ecology 84:108–119.

Perez-Salicrup, D. R., V. L. Sork, and F. E. Putz. 1998. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33:34–47.

Phillips, O. L., et al. 2002. Increasing dominance of large lianas in Amazonian forests. Nature 418:770–774.

Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. Science 263:954–958.

Putz, F. E. 1983. Liana biomass and leaf area of a “Tierra Firme” forest in the Rio Negro basin, Venezuela. Biotropica 15:185–189.

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org

Restom, T. G., and D. C. Nepstad. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. Forest Ecology and Management 190:109–118.

Saatchi, S., S. Ase, Y. Malhi, L. E. O. C. Aragão, and L. O. Anderson. 2012. Persistent effects of a severe drought on Amazonian forest canopy. Proceedings of the National Academy of Sciences USA 110:2000–2009.

Schnitzer, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. American Naturalist 166:262–276.

Schnitzer, S. A., F. Bongers, R. J. Burnham, and F. E. Putz, editors. 2015. Ecology of lianas. John Wiley & Sons, Oxford, UK.

Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. Trends in Ecology & Evolution 17:223–230.

Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. Ecology Letters 14:397–406.

Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. Ecology Letters 13:849–857.

Smith, J. R., S. A. Queenborough, P. Alvia, H. Romero-Saltos, and R. Valencia. 2017. No strong evidence for increasing liana abundance in the Myristicaceae of a Neotropical aseasonal rain forest. Ecology 98:456–466.

Stevens, G. C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68:77–81.

Swaine, M. D., and J. Grace. 2007. Lianas may be favoured by low rainfall: evidence from Ghana. Plant Ecology 192:271–276.

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. Ecological Applications 12:1344–1363.

Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. I. Everham, and D. A. Schaefer. 2004. Luquillo forest dynamics plot, Puerto Rico, United States. University of Chicago Press, Chicago, Illinois, USA.

Tobin, M. F., A. J. Wright, S. A. Mangan, and S. A. Schnitzer. 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. Ecosphere 3:1–11.

Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. Ecological Monographs 79:423–443.

Uriarte, M., R. Muscarella, and J. K. Zimmerman. 2017. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. Global Change Biology 24:e692–e704.

van der Heijden, G. M. F., J. S. Powers, and S. A. Schnitzer. 2015. Lianas reduce carbon accumulation and storage in tropical forests. Proceedings of the National Academy of Sciences USA 112:13267–13271.

Woods, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. Biotropica 21:290–298.

Wright, S. J., O. Calderón, A. Hernandéz, and S. Paton. 2004. Are lianas increasing in importance in tropical forests? A 17-year record from Panama. Ecology 85:484–489.

Wright, A., M. Tobin, S. Mangan, and S. A. Schnitzer. 2015*a*. Unique competitive effects of lianas and trees in a tropical forest understory. Oecologia 177:561–569.

Wright, S. J., I. F. Sun, M. Pickering, C. D. Fletcher, and Y. Y. Chen. 2015*b*. Long-term changes in liana loads and tree dynamics in a Malaysian forest. Ecology 96:2748–2757.

Zimmerman, J. K., E. M. Everham, R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico—implications for tropical tree life-histories. Journal of Ecology 82:911–922.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2556/suppinfo

DATA AVAILABILITY

The data used in this study are archived at the Luquillo LTER data repository: https://doi.org/10.6073/pasta/45e4817e74b51b9533b1bd4115415569