

SHORT COMMUNICATION

The demography of a dominant Amazon liana species exhibits little environmental sensitivity

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Abstract: Despite its high plant diversity, the Amazon forest is dominated by a limited number of highly abundant, oligarchic tree and liana species. The high diversity can be related to specific habitat requirements in many of the less common species, but fewer studies have investigated the characteristics of the dominant species. To test how environmental variation may contribute to the success of dominant species we investigated whether the vital rates of the abundant liana *Machaerium cuspidatum* is sensitive to canopy height, topographic steepness, vegetation density, soil components and floristic composition across an Ecuadorian Amazon forest. The population was inventoried in 1998 and in 2009. Plants were divided into seedling-sized individuals, non-climbers and climbers. Out of 448 seedling-sized plants 421 died, 539 of 732 non-climbers died, and 107 of 198 climbers died. There was weak positive effect of dense understorey on the relative growth rate of climbers. The mortality of seedling-sized plants was higher in areas with intermediate slope, but for larger plants mortality was not related to environmental variation. The limited sensitivity of the vital rates to environmental gradients in the area suggests that ecological generalism contributes to the success of this dominant Amazonian liana.

Key Words: ecological generalism, liana, mortality, relative growth rate, tropical rain forest, woody climbers

Lianas – woody climbers – are great competitors, affecting tree survival and growth (Tobin *et al.* 2012) as well as forest structure (Schnitzer & Bongers 2002). The abundance of lianas is reported to have been increasing in the Amazon forest over the last 20 y (Laurance *et al.* 2014), which may have a global impact due to lower carbon uptake capacities in tropical forests with high liana densities (Schnitzer *et al.* 2014).

In the Amazon forest, a limited number of liana (Burnham 2002) and tree species (Macía & Svenning 2005, Pitman *et al.* 2001, ter Steege *et al.* 2013) dominate the plant communities. Most of the dominant tree species are widely distributed, but dominant only in a few places (ter Steege *et al.* 2013). The dominance of few widely distributed species characterizes the oligarchy hypothesis (Pitman *et al.* 2001). High local diversity of plants is

often related to local habitat variability, with most species occurring in some parts of the forest. Many species are associated with a particular kind of topography, which is often associated with particular edaphic conditions, forest structure and dynamics (Baldeck *et al.* 2013, John *et al.* 2007, Queenborough *et al.* 2007, Svenning 1999). Most of the dominant tree species in the Amazon have, in contrast, been characterized as generalists (Duque *et al.* 2003, Pitman *et al.* 2001), occurring on a range of soil types and topographic positions (Pitman *et al.* 2001). Not only can the distribution of trees be related to environmental factors, but also their vital rates. In the Amazon, tree mortality can be related to soil factors (Phillips *et al.* 2004) and water availability (Phillips *et al.* 2009). Although the density of lianas has increased in the Amazon forest in the last 30 y (Phillips *et al.* 2002), there is no work demonstrating how the vital rates of dominant liana species relate to environmental heterogeneity.

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Our aim was to investigate how sensitive the vital rates of a dominant Amazonian liana species are to environmental variation using a long-term study. We tested the influence of environmental variation (maximum canopy height, understorey density, floristic composition, soil components and topographic steepness) on the relative growth rate (RGR) and mortality of the liana *Machaerium cuspidatum* Kuhl. & Hoehne (Fabaceae) over an 11-y period at Yasuní National Park, Ecuador. As palms and their relation with the environment are well known in the Amazon forest (Kristiansen *et al.* 2012, Svenning 1999, 2002; Svenning *et al.* 2009), we used the palm species composition (Vormisto *et al.* 2000) as a proxy for general floristic variation and related environmental drivers.

The study site in the Yasuní National Park in Amazonian Ecuador (00°40'S, 76°23'W) is located in an old-growth tropical moist forest with little annual variation in precipitation and temperature (Nabe-Nielsen 2001) and with relatively small natural gaps (Svenning 1999). Floodplain, terra firme and swamp are the three local major habitats (Svenning 1999). The forest has a high diversity and low density of lianas (Nabe-Nielsen 2001). The soil is acidic and silt is prominent (Tuomisto *et al.* 2003). The average yearly precipitation is 2255 mm, and the average temperature is 24.7°C (data from 1995 to 2009 – Estación Científica Yasuní, <http://www.yasuni.ec/>).

Machaerium cuspidatum is a shade-tolerant liana (Nabe-Nielsen 2004) that is abundant and widely distributed in the Amazonian rain forest of Colombia, Peru, Bolivia, Brazil and Ecuador (Lozano & Klitgaard 2006). It is one of the most abundant liana species in the Yasuní National Park, eastern Ecuador (Burnham 2002, Burnham & Romero-Saltos 2015, Nabe-Nielsen 2002). The individuals of *M. cuspidatum* with diameter ≥ 1 cm in Yasuní National Park are more abundant in low-canopy and dense-understorey areas (Nabe-Nielsen & Hall 2002). The population growth rate is most influenced by survival of large individuals and relatively insensitive to recruitment due to low survival rate of seedlings (Nabe-Nielsen 2004).

All individuals of *M. cuspidatum* in seven 20 × 250-m transects in a terra firme area were censused in 1998 and re-censused in 2009 (1378 individuals in total). Three transects were located in terra firme areas close to the Tiputini river and four transects were far from the river, c. 8 km further west. In both years, the diameter of each individual was measured with a calliper at the first point above the roots where the stem was regular, which was painted to assure the next measurement was taken in the same place. Mortality was recorded in the last census.

The transects were divided into 5 × 5-m subplots; in each subplot we measured: (1) maximum canopy height, classified into six categories: 0–2 m, 2–5 m, 5–10 m,

10–20 m, 20–40 m and ≥ 40 m; (2) topographic steepness, divided in four classes: depression, flat ($< 10^\circ$), slope ($\geq 10^\circ$ and $< 30^\circ$) and steep slope ($\geq 30^\circ$); and (3) the understorey vegetation density, divided into dense vegetation and sparse vegetation. Canopy height was measured in both censuses, and we used the mean value in the data analyses. The understorey density did not change between years ($\chi^2 = 0.420$, $df = 1$, $P = 0.516$); we used data from 2009 in the analyses. Three soil samples were collected in each transect for chemical analyses, which were made following van Reeuwijk (2002) in the laboratories of the Department of Bioscience at Aarhus University. All palm individuals were identified in a sub-transect of 5 × 250-m within each 20 × 250-m transect. Soil and palm data were sampled in 2012. From 1995 to 2012 the palm community remained stable (Balslev, unpubl. data).

For data analysis, the *M. cuspidatum* population was divided into three classes: seedling-sized plants, non-climbers and climbers. We used this classification because the transition to becoming a climber is a key phase in the life history of lianas and is known to improve their fitness (Gianoli 2015). We refer to individuals ≤ 30 cm long as seedling-sized. Non-climbers have length > 30 cm and can be upright or lie on the ground; climbers are > 30 cm long and attached to a host plant. The soil data were summarized as the first axis of a Principal Component Analysis (PCA) with the soil components calcium, potassium, magnesium and sodium. We used Beals smoothing function on palm data (De Caceres & Legendre 2008) to obtain a probability of occurrence of palms in the 5 × 5-m subplot where there were no palms. Then, we summed the calculated value for every five subplots, repeated the summed value in these plots, and did Hellinger transformation (Legendre & Gallagher 2001). We summed the values to avoid many subplots with zeros. We used the second axis of a PCA with the transformed palm species distribution to characterize variation in the palm species composition that were associated with environmental variation. The first axis only captured spatial variations in the species composition. In the areas of the 20 × 250-m transect where there were no palm data available, we used the PCA second axis score of the adjacent 5 × 5-m subplot. The influence of environmental factors on RGR of each class was tested by Akaike Information Criterion (AIC) model selection with linear regression and linear mixed model (LMM). RGR was logit transformed for seedling-sized plants. Mortality was treated as a binary variable, and the influence of environmental factors on it was tested by AIC model selection with generalized linear model (GLM) and generalized mixed model (GLMM). Mean maximum canopy height, steepness, soil, palm species composition and understorey density were treated as fixed effects in all models. Transect

number, region (close or far from the river), and transect within regions were treated as random effects. We used backward stepwise for model selection, as recommended by Zuur *et al.* (2009). For Beals smoothing function and Hellinger transformation we used the vegan package (<http://CRAN.R-project.org/package=vegan>) for R (R Development Core Team). The mixed effect models were made in lme4 package (<http://www.inside-r.org/packages/lme4/versions/1-0-4>) for R (R Development Core Team).

Over 11 y, 421 of 448 seedling-sized plants died, 539 of 732 non-climbers died, and 107 of 198 climbing individuals died. The mean relative growth rate of the surviving seedling-sized plants (\pm 1SE) was $0.164 \pm 0.062 \text{ mm mm}^{-1} \text{ y}^{-1}$, of non-climbers it was $0.096 \pm 0.021 \text{ mm mm}^{-1} \text{ y}^{-1}$ and for climbers it was $0.094 \pm 0.018 \text{ mm mm}^{-1} \text{ y}^{-1}$. The models selected for RGR based on AIC did not include any random factor, and only the model for climber growth was significant ($F = 3.98$, $r^2 = 0.04$, $P = 0.049$). The only variable retained in this model, understorey density, had a weak positive effect on the RGR (estimates = -0.010 , t test = -1.99 , $P = 0.05$). For mortality, only the model selected for seedling-sized plants was significant. It included mean maximum canopy height and slope, but no random effects. The mortality of seedling-sized plants was higher (58.4%) in areas with intermediate (10° – 30°) steepness than elsewhere (estimates = -0.690 , t test = -2.04 , $P = 0.042$). The models selected for non-climbers and climbers included transect as a random effect, but none of the variables was significant in these models.

Many species of liana in tropical forests are generally described as light demanding (Castellanos 1991, Schnitzer & Bongers 2002). Over the short term (1998–2000), *M. cuspidatum* seedlings (individuals ≤ 30 cm high) have been found to grow more in places with higher light availability (Nabe-Nielsen 2002). However, in the long term (1998–2009) the vital rates of the species were uncorrelated with a range of environmental variables that are all related to variation in light availability (maximum canopy height, steepness and understorey density). Although the mortality of seedling-sized plants was higher in areas with intermediate slope and the RGR of climbing individuals was higher in dense understorey, the effect was weak for the RGR of climbing individuals, and the vital rates were not related to any other type of environmental variation. The most parsimonious models did not suggest that the vital rates varied among transects with different environmental conditions either, e.g. between bottomland and ridgetop habitats.

The weak relationship between the vital rates of *M. cuspidatum* and the studied environmental factors indicate that the species can be regarded as an ecological generalist. Whereas lianas are generally characterized as species that respond to high-light environments and

availability of suitable supports by growing fast (Putz 1984), this is not the case for *M. cuspidatum*. Two studies from the Ecuadorian Amazon have shown that the three most dominant tree species are all relatively indifferent to environmental heterogeneity (Pitman *et al.* 2001). The present study suggests that ecological generalism may play a similar role in explaining the prevalence of the most abundant liana species.

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