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**Short-term spatial variation in the demography of a common Neotropical liana
is shaped by tree community structure and light availability**

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Abstract

We used matrix models to investigate the relation between population dynamics of the
liana *Mansoa difficilis* and environmental factors in fragmented Atlantic forest in
Brazil. The fate (growth and mortality) of individuals and the number of new
individuals were recorded for 3 years in 100 plots of 10 m × 10 m each. We used
multinomial logistic regressions to assess the influence of environmental factors on the
fate of individuals in different life stages. Adopting AIC for model selection, we tested
a range of models including different groups of environmental variables: soil nutrients,
water availability, light availability, and tree community structure. With the fates
predicted by the best model, we constructed a matrix model for each plot to calculate

population growth rate (λ) in that plot. The average λ was 0.962 for 2012–2013 and 0.941 for 2013–2014, both significantly lower than equilibrium ($\lambda = 1$). In both periods elasticity was higher for survival of large climbers than for other fates. The best models varied between life stages and periods, indicating that the impact of environmental factors on demographic rates changed through time. Model selection suggested that the influence of light availability on λ was less important than tree community structure, which allowed high population growth rates only in a small part of the forest. These findings support the notion that tree community characteristics are the key to understand and predict the observed recent increase in the density of lianas in the Neotropics.

Key-words: Brazil Tropical rainforest; demography; matrix model; population ecology; woody climber

Introduction

Lianas (woody climbers) are an abundant and diverse life form, and about half of the woody plant families include lianas (Putz 1984). They are key elements in tropical forest communities, with great structural and ecological importance, particularly in disturbed areas (Morellato and Leitão-Filho 1996; Schnitzer and Bongers 2002; van der Heijden et al. 2008). Lianas compete with trees above- and below-ground (Schnitzer 2005; Schröder et al. 2013; Álvarez-Cansino et al. 2014; Kainer et al. 2014), increase forest heterogeneity, and influence forest regeneration, dynamics, and structure (Schnitzer 2005; Nabe-Nielsen et al. 2009). Although lianas are important elements in forests, high liana loads have been demonstrated to reduce carbon retention, causing a negative impact on carbon stocks and, consequently, on global climate (Durán and Gianoli 2013; van der Heijden et al. 2013; Schnitzer et al. 2014). Lianas are particularly abundant in seasonally dry forests where they benefit from their deep roots, efficient vascular systems and fast control of stomatal conductance (Restom and Nepstad 2004; Schnitzer 2005; Dewalt et al. 2010; Chen et al. 2015). Álvarez-Cansino et al. (2014) showed that lianas compete with trees for water, and demonstrated that the presence of lianas strongly reduces the sap flow of trees in the dry season. Because lianas have a strong impact on forest dynamics, it is important to understand which biotic and abiotic factors influence their population growth, particularly for the most abundant species.

The Atlantic Forest in Brazil was formerly the second largest forest in South America, supporting high species richness and endemism (Myers et al. 2000; Ribeiro et al. 2009) and has the highest seed-plant diversity of Angiosperms in the country (Zappi et al. 2015). After intensive logging, only between 11%–16% of the forest remains intact, much of it as <100 ha fragments (Ribeiro et al. 2009). In order to predict the fate of the remaining Atlantic forest and improve management it is important to investigate

how liana populations are affected by the environmental conditions in the forest fragments. This, in turn, can allow us to predict their impact on forest dynamics under future environmental conditions (Nabe-Nielsen 2004), allowing managers, for example, to interfere in fragmented forests' fate by dealing more appropriately with lianas.

During their ontogeny lianas are exposed to various environmental conditions. After germinating in the soil they remain upright for a while. At a certain stage they start climbing a host plant in order to reach the high light levels at the forest canopy, but they remain rooted in the soil for their entire life (Putz 1990). Therefore, various biotic and abiotic factors, such as light availability, the presence of host trees, the presence of a dry season and soil properties can affect liana density (Schnitzer and Bongers 2002); these effects may also vary among life stages (Nabe-Nielsen and Hall 2002; Gerwing 2004). The success of lianas that have not yet become dependent on physical support from trees can be influenced by various biotic and abiotic factors (Nesheim and Økland 2007), while climbing lianas are particularly influenced by host-tree availability (Nesheim and Økland 2007; van der Heijden and Phillips 2008). Environmental factors can be spatially autocorrelated (Legendre 1993), frequently forming patches and gradients (Legendre 1993). Therefore, individuals growing close to each other may have the same growing conditions throughout their lifespan. Many of the environmental factors mentioned above are directly or indirectly linked to forest disturbances, and the largest liana densities are consistently found in the disturbed parts of the forest (e.g. Putz 1984, Schnitzer and Bongers 2002). This suggests that the liana populations are growing fastest in disturbed forests.

Studies on population dynamics are powerful tools to understand the life history of a species and its stability in time and space (Crone et al. 2011). Moreover, investigating population dynamics of lianas and how they relate to environmental

variation can help to understand the reason for their increasing abundance in the Neotropics (Phillips et al. 2002). Although liana population dynamics are likely related to environmental variation, the relative impact of different kinds of environmental variables on the lianas' vital rates remains poorly studied (but see Escalante et al. 2004; Nabe-Nielsen 2004; Kouassi et al. 2008).

In this study we investigated how the population dynamics of an abundant and ecologically important liana species, *Mansoa difficilis* (Cham.) Bureau & K. Schum. (Bignoniaceae), relates to environmental variation in a fragment of the Atlantic Seasonal Semideciduous Forest with a history of anthropogenic disturbance. Our main objective was to evaluate the effects of biotic and abiotic environmental variation on the population dynamics of the species in order to better understand possible feedbacks between liana and forest dynamics. We tested the following hypotheses: (1) Although no logging has taken place in the study area for the last 100 years, the forest is still recovering from past disturbances. We therefore expected the population to be declining, after having experienced optimal conditions immediately after logging ceased. (2) We expected growth and survival to be related to light availability and soil variables for small individuals, but to be more related to host tree availability for larger, climbing individuals. (3) Since lianas are in general light demanding and invariably dependent on host trees, we expected the population to grow faster in parts of the forest with gaps and a high number of potential host trees, higher biomass, open canopy and low average canopy height. (4) We expected population growth rates for *M. difficilis* to be more similar for plots that were closer together.

Methods

Study site

The study was carried out on a slope in Ribeirão Cachoeira Forest (22°50' S, 46°55' W), a 245-ha fragment of Tropical Seasonal Semideciduous Forest located in the Campinas Protection Environmental Area, SE Brazil. In the east-west direction the fragment is crossed by the Cachoeira stream, a tributary of the Atibaia River, the main water provider to Campinas municipality. The regional climate is subtropical humid, with rainy summers and dry winters (Cwa classification, Peel et al. 2007). The rainy season occurs from October to March (spring-summer), when average total precipitation is 1020 mm and the average temperature is 24 °C; the dry season lasts from April to September, when average precipitation is 344 mm and average temperature is 20 °C (data from 2004 to 2014, CIIAGRO 2015). The altitude varies between 630 m and 760 m a.s.l. and the soil forms a catena along the slope, with sandy Red-Yellow Argisol (FAO's Acrisol) in the lower portion and Litholic Neosol (FAO's Leptosol) in the upper portion (LCF personal observation).

The sampling area (6.48 ha) was located in the south portion of the fragment, on the left bank of the Cachoeira brook. We collected the data in 100 randomly positioned permanent plots of 10 m × 10 m each (see Cielo-Filho et al. 2007 for more details on how the plots were installed) according to the unrestricted randomization procedure (Greig-Smith 1983).

Study species

Mansoa difficilis occurs in Bolivia, Paraguay, Argentina and Brazil from the Amazon Forest in the north to the Atlantic Forest in the south (Lohmann and Taylor 2014), being especially abundant in the seasonal forests (Hora and Soares 2002). *Mansoa difficilis*

flowers mainly from October to December, during the rainy season (Garcia et al. 2014). This species is cultivated as ornamental due to its abundant inflorescences with rose-true purple (Smithe 1974), large flowers (Lorenzi and Souza 1995). In the Ribeirão Cachoeira forest, it represents about 20% of all lianas with diameter ≥ 1 cm at 1.3 m from the rooting point (van Melis 2013) and occurs throughout the forest, both in gaps and closed canopy (LCF personal observation). Its individuals climb their host plants using trifid tendrils. Individuals in seasonal semideciduous forest flower synchronously during the rainy season (Morellato and Leitão-Filho 1996). Only individuals that have reached the canopy reproduce (LCF, personal observation), presumably because they require high light levels to do so, similarly to most liana species (Campbell and Newbery 1993). *Mansoa difficilis* does not reproduce every year (Garcia et al. 2014) and does not form a seed bank (Grombone-Guaratini and Rodrigues 2002). The species is pollinated by bees, and their seeds are dispersed by wind (Scudeller et al. 2008).

Collection of environmental data

During the three years of data collection we estimated the forest canopy openness index using a spherical convex densiometer at breast height in the centre of each plot (Lemmon 1956). We collected 500 g of topsoil (first 20 cm) in the centre of each plot using an auger, from which organic matter, pH, P, K, Ca, Mg, potential acidity, cation exchange capacity, sum of bases, base saturation, silt, clay and coarse, fine and total sand were measured. The soil depth was measured with an auger on three locations in each plot. To estimate the content of available water in each plot, one undeformed soil sample was collected in the centre of each plot using a volumetric ring (50 mL). The soil chemical and textural analyses and the water retention curves were performed at Instituto Agronômico de Campinas (Camargo et al. 2009). In each plot, the maximum

height and trunk diameter at breast height (DBH) were measured for every tree with DBH ≥ 5 cm.

Collection of demographic data

Following Schnitzer et al. (2006), liana stems with independent roots were considered separate individuals in this study. Liana stems sharing roots were considered to be one single branched individual, and only the largest branch was tagged. We tagged all individuals of *M. difficilis* in each one of the 100 plots. During the years 2012, 2013 and 2014 we recorded the fate (death, growth or stasis) of all individuals and tagged new recruits, i.e., the free-standing individuals that entered the population. The individuals were classified into four stages (Table 1): free-standing (individuals that are upright and not climbing), searchers (individuals lying on the ground searching for a support to climb), small climbers (individuals climbing in the understory), and large climbers (individuals climbing in the canopy). We recensused the population once every year, at the end of the rainy season (March-April). No individual flowered in the plots, and we did not observe any seedlings in the plots, free-standing individuals being the earliest ontogenetic stage that we could record. Because we censused the population in March–April each year, it is likely that the newly recruited free-standing individuals originated from seedlings that had emerged from seeds produced in October–December of the previous year.

Population projection matrix construction

We summarized the species' life cycle with a life cycle graph (**Fig. 1**), which was subsequently used to construct a stage-based matrix model (Lefkovitch 1965) for each of the intervals included in our study. This allowed us to project the model $\mathbf{n}(t+1) =$

$\mathbf{A}\mathbf{n}(t)$, where $\mathbf{A}$ is the projection matrix and $\mathbf{n}(t)$ is a vector of stage abundances at the time t (Caswell 2001). The projection time (t) was one year. From one year to the next, plants can grow from stage j to stage i (G_{ij}), survive without changing stage (S_i) or regress (R_{ij}) from stage j to stage i . G_{ij} was calculated as the proportion of plants in stage j at time t that had grown to stage i in time $t + 1$. S_i was calculated as the proportion of plants in stage i at time t that remained in the stage i at time $t + 1$. R_{ij} was calculated as the proportion of individuals that regressed from stage j at time t to stage i at time $t + 1$. The fertility (F_i) of large climbers was obtained as the average number of free-standing recruits produced per large climber, i.e., the total number of free-standing recruits divided by the number of large climbers.

For each of the annual transition matrices that were constructed on the basis of all individuals in the 100 plots (one matrix for the period of 2012–2013 and one for the period 2013–2014), we calculated the population growth rate (λ) and the elasticity of λ with respect to each of the elements in the transition matrix employing the R package ‘popbio’ (Stubben and Milligan 2007). The elasticity of a given matrix element can be interpreted as the proportional contribution of that element to λ (Caswell 2001). We also obtained the 95% confidence interval of λ by bootstrap resampling of the original data with 1000 replacements using the percentile method (Caswell 2001).

Multinomial logistic regression for matrix transition entries and spatial variation in λ

We used multinomial logistic regressions (MLRs) to calculate how transition probabilities for plants in different stages (i.e., individual fates) depended on environmental variation. Multinomial logistic regression is recommended when the subordinated variable (individual fates, in this case) is categorical, and there are several predictor variables (Ledolter 2013). Before calculating the MLRs and in order to reduce

collinearity, we removed highly correlated environmental variables. Whenever two variables had Spearman correlation $r > 0.7$, the variable we considered as most biologically meaningful was retained. Using all pairwise correlations, we retained the variables P, K, Ca, clay, silt, organic matter, fine sand, content of available water, river distance, soil depth, canopy openness, above-ground biomass (AGB), number of trees per plot and maximum canopy height. To organize analyses and facilitate interpretation of results, we arranged the variables in four subsets (Table 2): (i) variables related to soil nutrients, (P, K and Ca), (ii) water-related variables (those that affect soil water conditions: clay, silt, fine sand, organic matter, available water content, distance from the river and soil depth), (iii) light availability (canopy openness), and (iv) variables related to tree community structure (tree AGB, number of trees per plot, and maximum canopy height). Only trees with trunk diameter ≥ 5 cm at breast height were included. We applied arcsine transformation to canopy openness. Above ground biomass was calculated using the formula by Chave et al. (2005):

$$AGB = \exp(-2.977 + \ln(\rho D^2 H)),$$

where ρ is wood density (g cm^{-3}), D is diameter at breast height (cm) and H is the height (m) of trees. We used the mean ρ for Atlantic Forest, 0.701 g cm^{-3} (Chave et al. 2006).

In the MLRs, the fates of individuals in a particular life stage (in all 100 plots) were used as dependent variables, and the environmental variables as independent variables. We chose fate stasis as the reference fate against which other fates were compared. The other fates included death, growth to the next stage, growth by two life stages in one time period, shrinking one stage, and shrinking two stages in one period. For every stage we constructed 14 multinomial logistic regressions, one for each possible combination of variable subsets (Appendix Table A1). In each case, the best model was selected employing the Akaike Information Criterion (AIC). MLR's were

conducted with the R package ‘nnet’ (Venables and Ripley 2002). After selecting the best model for each life stage we used the ‘predict’ function in R to calculate the predicted value of all the transition probabilities corresponding to the environmental conditions found in each plot. The predicted transition probabilities were subsequently used to construct a transition matrix for each plot and period, excluding plots without individuals. In each matrix, fertility was based on the entire population for the corresponding period. Matrix projection was then performed for each plot as had been done for the full dataset. We tested the per-plot spatial autocorrelation in λ using Moran’s I with Bonferroni correction index (Legendre and Legendre 2012) in R (R code address for Moran’s I function <https://github.com/MarioJose/r-functions/tree/master/correlogI>).

We constructed maps of the variation of λ among plots for each period. For each period and plot we calculated the elasticities of λ and the mean elasticity matrix for all 100 plots.

Results

Population dynamics

The number of *Mansoa difficilis* individuals varied from 661 in 2012 to 636 individuals in 2013 and 563 in 2014 (Table 1). The population growth rate was significantly <1 in both periods ($\lambda_{2012-2013} = 0.962$, 95% CI: 0.935–0.978; $\lambda_{2013-2014} = 0.941$, 95% CI: 0.933 – 0.979) (Table 3). This supports hypothesis 1, that the population is declining after having experienced optimal conditions in the years after logging ceased. In both periods, the elasticity of λ was higher for stasis of large climbers (60.2% in 2012–2013 and 70.8% in 2013–2014) than for any other transition (Table 4).

Fate-environment relationships at different stages

In accordance with hypothesis 2, growth and survival of small individuals were mostly influenced by soil conditions whereas larger, climbing individuals were more influenced by host tree availability (Appendix Table A2). In the first period, transitions of free-standing individuals (i.e., whether they remained in the same size class or turned into searchers or small climbers) were related to soil nutrients and tree community structure; in the second period, only the tree community structure influenced transitions of these individuals. The mortality of free-standing lianas was positively related to potassium in the first period, and negatively related to trees per plot (tree community) in both periods (Appendix Table A1). The transitions of searchers were related to soil nutrients in the first period, but to water-related variables in the second period (Appendix Table A2). The mortality of searchers was related to soil nutrients in the first period and to water-related variables in the second period (Appendix Table A1). The transitions of small climbers were related to canopy openness and tree community structure in the first period, but only to canopy openness in the second period (Appendix Table A2). Mortality of small climbers was related to tree community in the first period and to canopy openness in the second period (Appendix Table A1). Finally, transitions of large climbers in the first period were negatively related to the number of trees per plot and positively related to maximum canopy height, while in the second period, they were positively related to canopy openness (Appendix Tables A1 and A2). The mortality of large climbers was related to tree community in the first period and to canopy openness in the second (Appendix Table A1).

Spatial variation in population dynamics

Partially supporting hypothesis (3), the population grew faster in sites with gaps and high number of trees, higher biomass, open canopy and low average canopy height. Consequently, the predicted population growth rate varied in space (**Fig. 2**), and was generally higher in areas with a high number of potential host trees. In the first period, mean λ was 0.906 ± 0.092 (mean $\pm$ standard deviation), and 13 plots had $\lambda < 0.80$, 23 plots had $0.80 \leq \lambda \leq 0.89$, 57 plots had $0.90 \leq \lambda \leq 0.99$, one plot had $\lambda = 1$ and three plots had $\lambda > 1$ (1.006, 1.008 and 1.029). The plots with positive population growth were characterized by an intermediate number of trees per plot and intermediate biomass, open canopy, and low average canopy height. In the period 2013–2014, $\lambda = 0.930 \pm 0.053$, 24 plots had $0.80 \leq \lambda \leq 0.89$, 68 plots had $0.90 \leq \lambda \leq 0.99$, five plots had $\lambda = 1$ and no plot had $\lambda > 1$. From the first to the second period λ increased in 49 plots and decreased in 48 plots. The plots in which λ increased had low average canopy height, and the plots in which the λ decreased had high average canopy height. In one plot λ increased to 1, and in one it increased to >1 from the first to the second period. In these two plots small and large climbers remained in the same life class from one period to another, the transition stasis of these two life classes had the highest elasticity values, i.e., the transitions that influenced the variation in λ most strongly. In one plot λ decreased from 1 to <1 and in three plots the λ decreased from >1 to <1 . In these four plots, several free-standing, searcher and small climber individuals died. Three plots were without any individuals of the study species.

The highest mean elasticity value for the 97 plots was found for survival of large climbers in both periods (0.597 ± 0.314 and 0.820 ± 0.383 , in the first and second period, respectively) (Table 5). In two plots elasticity for free-standing stasis was higher

than 96%. Both of these plots were characterized by low light availability due to a closed canopy.

Contrary to our hypothesis (4) that both the environmental conditions and population growth rates are more similar for plots that were close together, we found no autocorrelation in λ per plot for either period (**Fig. 3**).

Discussion

*Population dynamics of *Mansoa difficilis* in relation to forest disturbance*

Because lianas depend on host trees to reach the forest canopy, changes in tree community structure lead to changes in liana population dynamics (van der Heijden and Phillips 2008; Dalling et al. 2012). The presence of many short trees in Ribeirão Cachoeira forest and high abundance of lianas (3,806 individuals.ha⁻¹, van Melis 2013) are likely to be the result of anthropogenic disturbances in the past. Although no logging has occurred for at least 100 years (Furtado et al. in press), the forest therefore appears to still be recovering from past disturbances. As this recovery leads to a gradual decrease in the number of trees that are suitable as hosts for young climbing lianas, we expected the population growth rate of *Mansoa difficilis* to be <1 (hypothesis 1). This was supported by our findings.

Liana populations are commonly reported to have $\lambda \geq 1$ (Escalante et al. 2004; Nabe-Nielsen 2004; Kouassi et al. 2008; Balcázar - Vargas et al. 2015), but this was not the case for *M. difficilis*. One likely explanation for this difference is that the previous studies of liana population dynamics were conducted in late successional forests, where new gaps with suitable host trees appeared approximately as fast as the suitable hosts disappeared in the remainder of the forest. Although the abundance of lianas is generally high in fragmented and disturbed areas and in treefall gaps (Schnitzer and

Bongers 2002; Campbell et al. 2015), liana biomass has been observed to increase with forest age (Letcher and Chazdon 2009). Recently fragmented areas can promote fast increase in the density of early successional lianas, but the abundance and composition of lianas change with forest regeneration stage due to changes in light and support availability (DeWalt et al. 2000; Letcher 2015). Another possible reason why we did not observe a positive population growth rate for *M. difficilis* could be the irregular reproduction of the species, as it does not produce fruits every year (Garcia et al. 2014). Therefore, the high population densities we currently observe in the area could result from a few years with great reproduction and rapid population growth.

The highest elasticity of λ was for stasis of large climbers in both periods. This is consistent with the general importance of stasis of the oldest or largest life stages for woody plants (Silvertown and Franco 1993; Caswell 2001) and with previous studies of climbers in tropical forests (Escalante et al. 2004; Nabe-Nielsen 2004; Kouassi et al. 2008). The higher elasticity for stasis of large climbers may be due to the duration of this stage, which is the longest one. The higher elasticity for stasis of large climbers indicates that small changes in this matrix element could directly influence the population growth rate (Silvertown et al. 1996).

Growth and survival in relation to environmental conditions

In Neotropical forests, liana abundance and richness are strongly related to soil properties (DeWalt et al. 2006; Addo-Fordjour and Rahmad 2015) and to small-scale disturbances such as treefall gaps (Schnitzer and Bongers 2002; Ledo and Schnitzer 2014), but the relative importance of soil properties and disturbance differ among liana life stages.

Overall, our findings matched our expectation (hypothesis 2) that the growth and survival of free-standing individuals are related to soil properties and light availability more than to tree community, but that they gradually become more related to host tree availability for small and large climbers. Lianas in early life are more influenced by abiotic and biotic factors (Nesheim and Økland 2007), whereas climbing lianas are more influenced by tree community (Nesheim and Økland 2007; van der Heijden and Phillips 2008). Indeed, we found that the fate of the study species' early stages (free-standing and searcher) was related to soil variables, whereas the fate of large climbers was related to the tree community. Hence, changes in host tree availability seem to reduce survival of large climbers and to have a large impact on the population growth rate as indicated by the high elasticity found for the survival of this life stage in the transition matrix. The mortality of large climbers was higher in sites with low AGB and fewer trees, which can be related to the lack of suitable physical support. The presence of lianas is often negatively related to AGB because lianas are more common in disturbed areas and gaps and because of competition between lianas and trees (Ledo et al. 2016). However, lower biomass indicates thinner trees, which are less suitable to host large lianas (Homeier et al. 2010). The largest liana individuals are more likely to be associated with very large host trees (Homeier et al. 2010). These are often found in areas with a sparse understory and a small number of smaller host trees. A high number of trees is more likely to benefit small liana individuals because the greater the number of trees the greater the availability of small host trees (Putz 1984). Host tree availability is often considered the most important factor influencing liana regeneration and dynamics in tropical forests (van der Heijden and Phillips 2008), and the proximity of the host tree is a key factor influencing liana climbing (Roeder et al. 2015).

Some of the significant multinomial regression models included non-significant terms. This suggests that they are over-parameterised, which can lead to a bias in model interpretation (Warren and Seifert 2011). The models for mortality and growth of free-standing individuals in the first period included the non-significant variables P, Ca, AGB and maximum canopy height, and also K in the model for growth. The models for growth of small climbers and mortality of large climbers in the first period included the non-significant parameter maximum canopy height. In the second period, the models for mortality of free-standing included the non-significant variables AGB and maximum canopy height. The model for growth of free-standing included non-significant variables AGB and trees per plot. The mortality of searchers in the second period included the non-significant parameters organic matter and river distance. The mortality of small and large climbers, and growth of small climbers in the second period, included the non-significant variable canopy openness. Elimination of the non-significant terms would, however, make it more difficult to directly compare the significance of the different factors that we had *a priori* identified as potentially important for liana growth and mortality, which is why we kept all parameters in the models.

Spatial and temporal variation in population dynamics

The demographic rates of *M. difficilis* were mainly related to characteristics of the tree community, and λ was <1 in plots with low above-ground biomass. Generally, λ was higher in parts of the forest with intermediate biomass and intermediate number of trees, which supports our hypothesis (3), that the population would grow faster in parts of the forest with a high number trees, high biomass, open canopy and low average canopy height. These sites favoured the survival of large climbers. Survival of large climbers had the highest mean elasticity in all plots and in both periods. This shows that any

change in forest dynamics that influences the survival of large climbers may influence the population growth rate on a fine spatial scale.

The population growth rates were no more similar in nearby plots than in distant ones, thus refuting our expectation (hypothesis 4) that the population growth rates for *M. difficilis* would be more similar for plots that were closer together. The λ values predicted for the different plots based on the multinomial regressions varied among the plots depending on local environmental conditions. This illustrates how liana population dynamics can be tightly linked to the regeneration status of different parts of the forest. Temporal variability in the environmental conditions appeared to be the cause of the highly dynamic local population growth rates.

Our study supports the notion that changes in abundance and size-class distribution of lianas with forest age can be explained by the variability in growth and mortality of individuals growing under different environmental conditions (Dewalt et al. 2000). Increases in liana abundance are often linked to increasing levels of atmospheric CO₂ (Phillips et al. 2002; Schnitzer and Bongers 2011), drought (Schnitzer et al. 2005), and forest fragmentation (Schnitzer and Bongers 2002; Barry et al. 2015). Our study demonstrates for the first time that liana population dynamics can be directly related to local tree community characteristics that are similar to those associated with forest fragmentation. Studies on liana dynamics are key to understand and predict changes in liana abundance in tropical forests and the associated impacts on forest dynamics and structure.

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608

Table 1. Characteristics of the stages and number of individuals (N) of *Mansoa difficilis* over the study period, 2012-2014.

Ontogenetic stage	Characteristics				2012	2013	2014
	Upright	Lies on the ground	Climbing	Forest stratum	N	N	N
Free-standing	yes	no	no	understory	44	62	40
Searcher	no	yes	no	understory	55	39	35
Small climber	no	no	yes	understory	276	243	207
Large climber	no	no	yes	canopy	286	292	281

Table 2. Subsets of environmental variables measured and the models in which they were used. In the “Model used” column X stands for stages F (free-standing), S (searcher), SC (small climber) and LC (large climber) (see Table A2 in Appendix for more details on the models).

Subset	Measured variables	Model used
(i) Nutrients	P, K, Ca	X01, X02, X06, X07, X08, X09, X10
(ii) Water related	clay, silt, fine sand, organic matter, available water content, distance from the river, soil depth	X01, X03, X06, X07, X08, X11, X12, X13
(iii) Light availability	canopy openness	X01, X04, X06, X09, X11, X12, X14
(iv) Tree community structure	above ground biomass, number of trees, maximum canopy height	X01, X05, X07, X10, X11, X13, X14

Table 3. Transition matrices for *Mansoa difficilis* in the periods 2012-2013 and 2013-2014.

Life class	Life class			
	Free-standing	Searcher	Small climber	Large climber
2012-2013				
Free-standing	0.409	0.056	0.004	0.145
Searcher	0.159	0.509	0.014	0.000
Small climber	0.068	0.073	0.764	0.087
Large climber	0.000	0.000	0.153	0.874
2013-2014				
Free-standing	0.327	0.065	0.003	0.025
Searcher	0.127	0.608	0.014	0.000
Small climber	0.055	0.087	0.727	0.088
Large climber	0.000	0.000	0.145	0.877

Table 4. Elasticity matrices of a population of *Mansoa difficilis* for the periods 2012-2013 and 2013-2014.

Life class	Life class			
	Free-standing	Searcher	Small climber	Large climber
2012-2013				
Free-standing	0.011	0.001	0.000	0.014
Searcher	0.004	0.006	0.001	0.000
Small climber	0.010	0.004	0.239	0.047
Large climber	0.000	0.000	0.061	0.602
2013-2014				
Free-standing	0.001	0.000	0.000	0.002
Searcher	0.001	0.003	0.001	0.000
Small climber	0.001	0.002	0.179	0.049
Large climber	0.000	0.000	0.051	0.708

Table 5. Mean elasticity matrices (mean $\pm$ standard deviation) for a population of *Mansoa difficilis* across 100 plots in a Seasonal Semideciduous Tropical Forest (Brazil) for the periods 2012-2013 and 2013-2014.

Life class	Life class			
	Free-standing	Searcher	Small climber	Large climber
2012-2013				
Free-standing	0.030 ± 0.157	0	0	0.004 ± 0.010
Searcher	0	0.001 ± 0.002	0	0
Small climber	0.004 ± 0.010	0	0.288 ± 0.278	0.036 ± 0.026
Large climber	0	0	0.040 ± 0.028	0.597 ± 0.314
2013-2014				
Free-standing	0	0	0	0
Searcher	0	0.076 ± 0.267	0	0
Small climber	0	0	0.103 ± 0.303	0
Large climber	0	0	0	0.820 ± 0.383

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Fig. 1. Life-cycle diagram (a) and transition matrix (b) for a population of *Mansoa difficilis*. Edges represent potential transitions between life stages: growth (G), stasis (S), regression (R) and fertility (F).

Fig. 2 Maps of predicted population growth rate (λ) per plot for a population of *Mansoa difficilis* in the periods 2012-2013 (a) and 2013-2014 (b). Isoclines are altitude (m) relative to the river (0 m), squares are the 10 m $\times$ 10 m plots and colors indicate range values of λ .

Fig. 3 Autocorrelation population growth rate (λ) per plot for a population of *Mansoa difficilis* in the periods 2012-2013 (a) and 2013-2014 (b). Squares indicate Moran's I to each distance class. Lines indicate critical Moran's I to alpha (0.05).