

Sharp differentiation on the performance of plant functional groups across natural edges

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Abstract

Aims

Gallery forests within grasslands have natural edges with open environments and offer a unique opportunity to examine how species performances vary across environmental gradients. Here, we asked if demographic rates of tree functional groups varied along the edge, if we could explain differences in plant strategies and performance through functional traits and which traits increase growth and survival in natural edges.

Methods

We examine mortality and recruitment within the first 10 m of natural edges of eight gallery forests using demographic data from five annual inventories. We defined *a priori* plant strategies using tree functional groups: light demanding, pioneer and shade tolerant.

Important Findings

The shade-tolerant group had the lowest mortality rates and basal area (BA) loss, while pioneer and light-demanding species had

similar behavior for these rates. The survival and growth of functional groups were affected differently by the distance from the edge. The pioneer group survived more near the edge, while light-demanding and shade-tolerant groups toward the forest interior. All groups had higher growth in the grassland. Those differences could be explained by functional traits since most species have an acquisitive strategy: higher specific leaf area and growth, lower leaf dry matter content, lighter stem density, deeper crowns and less slender stems. Acquisitive traits enhanced growth. However, mortality selected both strategies, but in distinct edge's zones. Our study showed that the high diversity found in natural edges can be explained by a niche and functional perspective, where differences in functional traits lead to differential performance along the environmental gradient.

Keywords: edges diversity, gradient, niche hypothesis, SLA, LDMC

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INTRODUCTION

Inside the Cerrado biome, there are narrow strips of forest alongside small streams known as gallery forests. Their structure and composition are sharply different from the surrounding savanna or grasslands and, since they are an example of old edges, they are also an amazing opportunity to study how plant populations and communities would behave in old forest edges. Besides the sharp gradient with the open grassland, gallery forests also have a strong internal gradient from the streamside toward the edge. Light, soil moisture and nutrients vary along the gradient leading to a sudden turnover of

species from the streamside toward grassland (Kellman *et al.* 1998; Rossatto *et al.* 2009; van den Berg and Oliveira-Filho 1999). Although those factors are related to the species turnover, they cannot alone explain the edges sharp feature, what is better done by the frequent fire events that take place in the grasslands, damaging the edges' plants. Moreover, most of the fires extinguish inside the edge (Rossatto *et al.* 2009; van den Berg and Oliveira-Filho 1999; van den Berg and Santos 2003).

Several aspects of these edges have been investigated along the years, as to which factors are responsible for those boundaries, how or if the forest-grassland limits change along time and the nature of the community structure and species

composition in those edges (Coelho et al. 2017; Kellman et al. 1998). On the other hand, to understand how numerous tree species can coexist in this short gradient of light and moisture, and the processes underlying the high diversity (Coelho et al. 2017), it is necessary to examine how species performance varies across those natural environmental gradients, exploring plant strategies and related functional traits associated with species success or failure in these environments.

Our knowledge regarding those questions is limited in part because the high biodiversity of these forests hinders generalization. However, approaching this complexity by using functional groups and evaluating how their responses vary across edges can possibly capture the main facets of this complex relationship between plant behavior and environmental variation (Díaz and Cabido 1997) and provide insights into the processes that determine the diversity across sharp environmental gradients, such as the one existing between grassland and gallery forest.

One of the most recognized trade-offs regarding plant strategies is the resource acquisition versus conservation (also known as fast-slow, i.e. rates of resource acquisition and processing) (Reich 2014). This trade-off is connected with the capacity to exploit habitats that are rich or poor in resources (Grime et al. 1997). The shade-tolerance or intolerance would be the consequence of this trade-off between high growth in productive (high-light) conditions and high survival in low-light conditions. Swaine and Whitmore (1988) described two extremes of a continuum of strategies in a tropical forest environment, where light is a key resource affecting ecological and physiological processes (Turton and Freiburger 1997). One group is composed of species that need direct light incidence to germinate, establish and grow, having not only fast growth but also a short lifespan. The other is made up of species that can germinate, establish and grow under a closed canopy and low-light conditions. Although classifications as this one have been considered oversimplified for a rather continuous gradient of strategies (Alvarez-Buylla and Martinez-Ramos 1992; Baker et al. 2003), their value is undeniable, allowing pooling species together in ecologically meaningful groups.

Because functional traits are related to plant strategies, differences in environmental exploration can be investigated using functional traits that are advantageous in a high-light environment versus low-light environment (Reich 2014). The specific leaf area (SLA, the ratio of leaf area to leaf dry mass) and leaf dry matter content (LDMC, the ratio between dry mass to the fresh mass of the leaf) are morphological traits measured at the leaf level that are supposed to mirror the fast-slow trade-off. Species with fast strategy have high SLA and low LDMC, and species with a slow strategy have low SLA and high LDMC (Poorter and Garnier 1999). Stem density (SD) is also related to the fast-slow trade-off. A low SD is associated with high growth and fast resource acquisition. On the other hand, a high SD is related to slow growth but high survival (Pérez-Harguindeguy et al. 2013). Allometric traits are also important in this trade-off since resource investment

in crown shape and height is linked to plant strategy (Horn 1971; Poorter et al. 2003). Shade-intolerant species are expected to have slender stems and deeper crowns as a result of their investment in vertical growth (Horn 1971; Poorter et al. 2003). Overall, shade-intolerant species, as acquisitive resource strategists, are expected to have high SLA, low LDMC, low SD, high growth rates, high mortality, slender stems and deep crowns.

Therefore, differences in functional traits reflect differences in strategies, implying that differences in functional traits lead to functional divergence and niche separation (Sterck et al. 2011), explaining species distribution and diversity within local communities (Sterck et al. 2006; Wright et al. 2004). The relationship between functional traits and plant strategies have been tested for forest environments, where gap openings are the main cause of light increase. However, forest gaps are transitory (Swaine and Whitmore 1988), unlike forest edges where high-light incidence is rather permanent and where there is a strong environmental gradient with light changing abruptly in just a few meters. Hence, natural edges are a perfect environment to test for functional and strategy divergence.

In this article, we explore the strategies of plants from a functional perspective aiming to understand if those differences in strategy contribute to the high diversity observed in natural edges. We expected that if niche processes are responsible for community assembly in natural edges, diverse functional groups will diverge regarding demographic rates. If the niche processes are overriding, we expected that acquisitive species would perform better (high survival and growth) in the immediate edge with the surrounding grassland, where light conditions are likely to be more favorable. Conservative species must be more successful toward the interior of the plots, where the canopy is more developed and shade is greater. Regarding functional traits, we expected that acquisitive species would have higher SLA, lower LDMC, lighter SD, slender stems, deeper crowns, higher growth rates and higher mortality than conservative species. We expected that the high-light and disturbed environment near the edges will act as an environmental filter selecting predominantly traits related to the acquisitive strategy. However, as natural edges have a sharp environmental gradient, with light availability changing in just a few meters, we expected environmental filters to change along the gradient resulting in conservative traits to be also important for growth and survival deeper inside the forest.

MATERIALS AND METHODS

Study sites

The study was conducted at eight sites where the gallery forests had boundaries with natural grasslands (*campo limpo*; Ribeiro and Walter 2001) in the south of Minas Gerais State, Brazil (Fig. 1). The sites are located in a disjunction of the Cerrado biome, within distribution area of seasonal semi-deciduous rainforests in southeastern Brazil (Brazilian Institute of

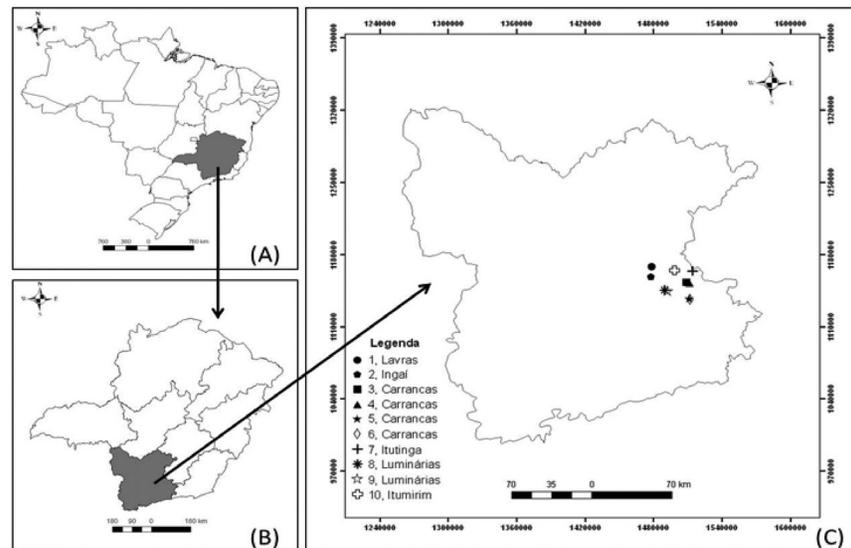


Figure 1: geographical location of the studied sites. (A) Minas Gerais State; (B) Minas Gerais macroregions; (C) Southern Minas Gerais state region, with the location of the sampled sites

Geography and Statistics–Instituto Brasileiro de Geografia e Estatística (IBGE 2004)). The climate is Cwa (humid subtropical climate) according to the Köppen climate classification, temperate and rainy (mesothermic) with dry winters and rainy summers (Dantas *et al.* 2007). Elevation varies from 850 to ~1500 m a.s.l.

We chose only sites that had natural boundaries with native grasslands and which lacked obvious anthropogenic impacts such as logging, undergrowth clearing, clear-cutting or evidence of recent fires.

Sampling

In 2009, we established three permanent plots (15 m × 20 m; 300 m²) at each of the eight sites respecting a 10-m minimum distance between plots within site. We laid out the plots with their wider side parallel to the forest edge, including 5 m of grassland and 10 m of forest (Fig. 2). Plots covered only 5 m of grassland since there was no tree beyond this point (Fig. 3). We identified, mapped and measured height and diameter at breast height (DBH) of all individuals with the DBH ≥ 1 cm (see Coelho *et al.* 2017 for more details). In the present study, we worked with all species with 50 or more sampled individuals across sites, corresponding to 30 species (Table 1).

Since 2009, we have carried out five annual inventories (2009–13). In each inventory, we measured and re-measured all living individuals and verified all dead ones. The recruits, i.e. the new individuals meeting the inclusion criterion (DBH ≥ 1 cm), were identified and mapped and had their height and DBH recorded.

Functional traits

We collected young entirely expanded and healthy leaves. We randomly selected five individuals of each species, and since SLA is strongly affected by light intensity, following the

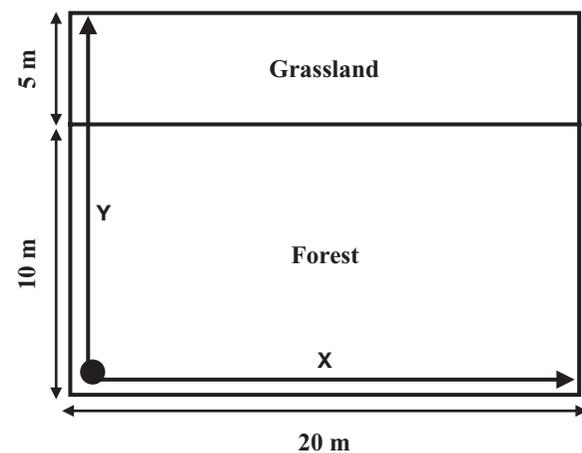


Figure 2: sketch showing how plots were assembled with 5 m of grassland and 10 m of forest's edge. X is the distance of the individual parallel to the upper limit of the plot as measured from the corner; Y is the distance of the individual from the upper limit of the plot.

recommendations of Pérez-Harguindeguy *et al.* (2013), we collected sun leaves. For species that typically grow in the overstory, we took leaves from the most exposed part. We collected five leaves from each plant and we measured leaf thickness using a digital micrometer and then weighed and scanned them. After measurements, the leaves dried for 72 h at 60°C and weighed again.

For SD analysis, we collected five samples of each species, following the recommendations of Pérez-Harguindeguy *et al.* (2013). Since individuals are very thin in the edges, we cut with a saw a ~10-cm-long section near the base of the stem. We collected branchless sections and stored them in plastic

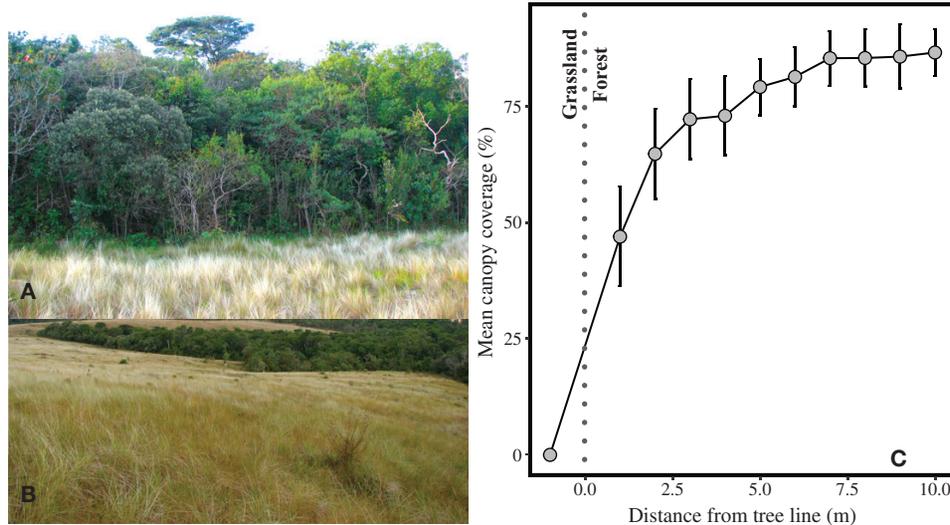


Figure 3: (A and B) Boundaries between gallery forest and the surrounding grasslands are very sharp as seen in both pictures. (C) Mean canopy coverage (%) and standard deviation in eight edges of gallery forests in Southeastern Brazil, showing how light changes abruptly from the grassland to the forest. Canopy cover was measured with a Lemmon convex spherical densitometer, facing north, south, east and west, 1 m above the ground every 1 m from the top to the bottom of the plot.

bags. We placed samples in containers with water for 30 min to ensure homogeneous distribution of water before calculating the green volume. After, volume was measured with the method of water displacement and samples were dried until constant weight and were then weighed (Pérez-Harguindeguy et al. 2013).

Based on the measurements described above, we obtained the following traits: SLA ($\text{mm}^2 \text{mg}^{-1}$), which is the one-sided area of a fresh leaf divided by its oven-dry mass; LDMC (%), which is the oven-dry mass of a leaf divided by its water-saturated fresh mass; and wood specific gravity (g cm^{-3}), which is the oven-dry mass of a section of the main stem of a plant divided by the volume of the same section when still fresh.

Allometric traits

For allometric measurements, we randomly selected 25 trees of each species within plots. We measured total height, height of the first bifurcation, height of the first leaves from the ground, crown diameter in two perpendicular directions, stem DBH (at 1.3 m from the ground) and stem diameter at 10% of the height. Using these measures, we calculated the following indices: relative crown width (RCW), calculated as the ratio of tree crown width to crown depth (crown depth was calculated as the difference between tree height and height of the first lower leaves), and stem slenderness (RTH), calculated as the ratio of tree height to tree CBH (circumference at breast height).

Plant strategies

Functional groups can be defined as a group of different species that respond in a similar way to a set of environmental factors (Gourlet-Fleury et al. 2005), in other words, a group

of species with a similar strategy. We defined *a priori* plant strategies using functional group classification based on light requirements for germination and establishment: pioneer (fast growth-acquisitive strategy) and non-pioneer (slow growth-conservative strategy) (Swaine and Whitmore 1988). Pioneers (P) were those species whose seeds only germinate in sites with direct light at the ground level for at least part of the day. Their germination is triggered by an increase in red light or soil temperature fluctuation, and their seedlings also require direct light for establishment and growth. On the other hand, non-pioneers germinate, and their seedlings establish under the canopy without direct light (Swaine and Whitmore 1988). We subdivided this last group into two others: light-demanding species (L), which demand more solar radiation for growth and have faster growth, and shade-tolerant species (S), which require very little light and grow slowly (Swaine and Whitmore 1988). We based our classification on studies developed in the same region. We recognize the existence of other classifications and approaches to classify functional groups; however, we believe that the classification proposed by Swaine and Whitmore is suitable for our analysis since it is based on light requirements, which is a major defining environmental condition for natural edges.

We used the Kruskal–Wallis test to seek for differences in functional and allometric traits between groups.

Demographic rates

We calculated annual mortality rates (M), recruitment (R) and net change (Ch_N) rates regarding individuals, and loss (L), gain (G) and net change (Ch_{BA}) of basal area (BA) for each site and species. We calculated M , R , L and G following Sheil et al. (2000):

$$M = \left\{ 1 - \left[\frac{N_0 - N_m}{N_0} \right]^{\frac{1}{t}} \right\} \times 100 \quad (1)$$

$$R = \left\{ 1 - \left[1 - \frac{N_t}{N_t} \right]^{\frac{1}{t}} \right\} \times 100 \quad (2)$$

$$P = \left\{ 1 - \left[\frac{(BA_0 - BA_m - BA_d)}{BA_0} \right]^{\frac{1}{t}} \right\} \times 100 \quad (3)$$

$$G = \left\{ 1 - \left[1 - \left(\frac{BA_r + BA_g}{BA_t} \right)^{\frac{1}{t}} \right] \right\} \times 100 \quad (4)$$

where t is the time between censuses in years (precisely 1 year in the present case); N_0 and N_t are the initial and final individual tree counts, respectively; N_m and N_r are the number of dead trees and recruits, respectively; BA_0 and BA_t are the initial and final tree BAs, respectively; BA_m is the BA of dead trees; BA_r is the BA of recruits; and BA_d and BA_g are the decrease (due to trunk break or partial loss) and increase in the BA of surviving trees, respectively.

We calculated Ch_N and Ch_{BA} using the following equations (Korning and Balslev 1994):

$$Ch_N = \left[\left(\frac{N_t}{N_0} \right)^{\frac{1}{t}} \right] \times 100 \quad (5)$$

$$Ch_{BA} = \left[\left(\frac{BA_t}{BA_0} \right)^{\frac{1}{t}} \right] \times 100 \quad (6)$$

Finally, we calculated those rates for each functional group separately within each site.

Effect of environmental gradient and size on survival and growth

To examine how annual growth (Gr , % year⁻¹) and survival (S) change with distance from the edge and with the size of individuals we fitted Bayesian models, in which the growth and survival probability were a function of the size of the individual and distance Y (Fig. 2). The growth model takes the form:

$$Gr_j = \rho + \partial_i * dist_j + \sigma_i * size_j \quad (7)$$

Growth was calculated as:

$$Gr = \left(\frac{DBH_t - DBH_i}{DBH_i} \right)^{\frac{1}{2}} \quad (8)$$

Table 1: species with more than 50 individuals in the edges of studied gallery forest ordered by their numbers (N) followed by their functional group (FG): P, pioneer; L, light demanding; S, shade tolerant

| Species | N | FG |
|---|-----|----|
| <i>Myrsine umbellata</i> Mart. | 652 | L |
| <i>Eremanthus erythropappus</i> (DC.) MacLeish | 619 | P |
| <i>Myrcia splendens</i> (Sw.) DC. | 498 | L |
| <i>Psychotria vellosiana</i> Benth. | 397 | L |
| <i>Miconia chartacea</i> Triana | 223 | L |
| <i>Vismia guianensis</i> (Aubl.) Pers. | 214 | P |
| <i>Hyptidendron asperinum</i> (Epling) Harley | 211 | L |
| <i>Leandra scabra</i> DC. | 209 | P |
| <i>Protium spruceanum</i> (Benth.) Engl. | 207 | L |
| <i>Pera glabrata</i> (Schott) Poepp. ex Baill. | 179 | L |
| <i>Casearia sylvestris</i> Sw. | 175 | P |
| <i>Vochysia tucanorum</i> Mart. | 164 | L |
| <i>Calyptanthes brasiliensis</i> Spreng. | 150 | S |
| <i>Clethra scabra</i> Pers. | 143 | L |
| <i>Daphnopsis fasciculata</i> (Meisn.) Nevlng | 134 | L |
| <i>Miconia pepericarpa</i> DC. | 121 | P |
| <i>Tapirira obtusa</i> (Benth.) J.D.Mitch. | 107 | L |
| <i>Myrcia venulosa</i> DC. | 99 | L |
| <i>Faramea latifolia</i> (Cham. & Schldl.) DC. | 91 | L |
| <i>Miconia paulensis</i> Naudin | 90 | P |
| <i>Protium widgrenii</i> Engl. | 85 | L |
| <i>Casearia decandra</i> Jacq. | 82 | S |
| <i>Calyptanthes clusiifolia</i> O.Berg | 78 | S |
| <i>Miconia theaezans</i> (Bonpl.) Cogn. | 77 | L |
| <i>Myrsine guianensis</i> (Aubl.) Kuntze | 70 | P |
| <i>Alchornea triplinervia</i> (Spreng.) Müll.Arg. | 65 | L |
| <i>Siphoneugena reitzii</i> D.Legrand | 63 | L |
| <i>Copaifera langsdorffii</i> Desf. | 57 | S |
| <i>Myrcia tomentosa</i> (Aubl.) DC. | 51 | L |

Survival was modeled as a logistic:

$$\text{Logit}(S_j) = \alpha + \beta_i * dist_j + \theta_i * size_j \quad (9)$$

Rather than fit separate models for each functional group, we included a second level (parameter β) in the hierarchical model for each parameter in Equations 1 and 2. For instance, Parameter β for functional group i in Equation 9 is modeled as follows:

$$\beta_i = \text{normal}(\mu_i, T_i) \quad (10)$$

For each model, we calculated the predicted values and the credible intervals for the four following distances: in grassland (upper limit of the plot), edge (5 m from upper limit), 5 m from edge (10 m from upper limit) and 10 m from edge (15 m from upper limit).

Functional traits and survival

To answer which functional and allometric traits affected growth (annual growth rate, % year⁻¹) and survival at edges we fitted Bayesian models and we modeled mortality as a Binomial process and growth as a Gaussian process.

$$\text{Logit}(S) = \varepsilon + \varphi_1 x_1 + \dots + \varphi_n x_n \quad (11)$$

$$\text{Gr} = \psi + \omega_1 x_1 + \dots + \omega_n x_n \quad (12)$$

We used the predictors SLA, LDMC, stem slenderness, RCW and relative growth rate (RGR) for survival and the predictors SLA, LDMC, stem slenderness and RCW for growth. RGR was calculated as follows:

$$\text{RGR} = \frac{\ln\left(\frac{\text{DBH}_i}{\text{DBH}_f}\right)}{(t_f - t_i) (\text{DBH}_i)} \quad (13)$$

where DBH_i and DBH_f are the initial and final DBH, respectively, and t_i and t_f are the initial and final years, respectively.

We obtained posterior distributions of parameters of both models using the Markov chain Monte Carlo method. We monitored convergence by running three different chains with different start values. From the posterior distribution, we computed the mean and Bayesian credible intervals (BCI) for all parameters and the significance of parameters was assessed by a 95% BCI, and for evaluating discrepancy, we calculated a Bayesian *P*-value (Gelman et al. 1996).

For all analyses, we used the R software, version 3.1.1. For the Bayesian models, we used the RJAGS package (Plummer 2016). For the Kruskal–Wallis tests, we used the Agricolae package (Mendiburu 2014).

RESULTS

Demographic rates and functional groups

Overall, recruitment and BA gain rates were equal for all groups, but mortality and BA loss were lower for the shade-tolerant group (Tables 2 and 3).

During the evaluation period (2009–13), the recruitment was higher than mortality, leading to a positive net change rate (Table 2). When considering the rates of gain and loss of BA, gain was higher than loss for all the functional groups, also leading to positive net change values. The recruitment rates were higher than mortality rates for 2011–12 and 2013–14 and lower than mortality for 2010–11 and 2012–13 (Table 2). Despite the two periods with negative net change rate regarding individuals, the net change in BA was negative only in 2012–13 (Table 3). In 2010–11, the surviving individuals gained enough BA to compensate for the loss regarding BA related to mortality.

Since negative rates could be a consequence of fires that took place during both periods, we recalculated the rates, removing sites that were burned: Site 9 (2010–11) and Site

8 (2012–13). The exclusion of Site 9 for the 2010–11 period did not lead to recruitment higher than mortality or a positive net rate change in number of individuals, but there was a decrease in mortality (from 4.79 to 3.67 % year⁻¹) and an increase in the net change rate for number of individuals (from -1.56 to 0.00 % year⁻¹). However, the BA loss rate (11.09 % year⁻¹) continued to be higher than the gain rate (7.75 % year⁻¹) and the net change rate continued to be negative (-1.34 % year⁻¹). For the 2012–13 period, the exclusion of Site 8 led to higher recruitment than mortality ($M = 3.21$ % year⁻¹; $R = 5.71$ % year⁻¹) and to a positive net change rate in number of individuals (2.66 % year⁻¹). For BA, all rates continued positive ($L = 6.10$ year⁻¹; $G = 10.93$ year⁻¹; $\text{Ch}_{\text{BA}} = 5.35$ year⁻¹).

Growth, environmental gradient and size

The Gaussian model for growth based on size and distance had a good fit for all groups since *P*-values were close to 0.50 (*P*-value (P) = 0.50; *P*-value (L) = 0.49; *P*-value (S) = 0.50). Size and distance had a negative effect on growth of all groups (Fig. 4). Pioneer groups had the highest growth, and shade-tolerant groups had the lowest growth (Fig. 5). There was a decline in growth from grassland toward the interior for all groups (Fig. 5).

Probability of survival, environmental gradient and size

The binomial model for survival had a good fit with Bayesian *P*-value of 0.49. Size had a positive effect on survival of pioneer and light-demanding groups but had no effect on survival of shade-tolerant species. Distance had a positive effect on survival of light-demanding and shade-tolerant species, but a negative effect on the pioneer group (Fig. 4). In grasslands and in the first 5 m of forest, the pioneer group had highest survival regardless of size; however, deeper inside the forest (10 m), light-demanding and shade-tolerant species had higher survival (Fig. 6).

Differences in strategies between functional groups

The functional groups had different strategies to survive at the edges (Table 4). Pioneers had higher rates of growth, higher SLA, intermediate LDMC and lower stem slenderness than light-demanding and shade-tolerant species. Light-demanding species had lower LDMC than the other groups and did not differ from shade-tolerant species in SLA and stem slenderness. RCW and SD did not differ among the groups.

Effect of functional traits on growth and survival

Both the binomial and Gaussian models had a good fit with *P*-value of 0.51 and 0.50, respectively. LDMC, RCW and stem slenderness affected growth (Fig. 7). Species with smaller LDMC, deeper crown and slimmer stem showed higher growth. RGR, SLA and LDMC affected on survival (Fig. 7). Species with higher RGR and LDMC and lower SLA and SD had a higher survival probability.

Table 2: number of dead individuals and recruits, as well as their initial and final number of individuals and rates of mortality, recruitment and net change for light-demanding, pioneer and shade-tolerant groups in the edges of studied gallery forests, from 2009 to 2013

| Year | Group | Number of dead | Number of recruits | Number of survival | Initial number | Final number | Mortality (%) | | Recruitment (%) | | Change (%) | |
|---------|---------|----------------|--------------------|--------------------|----------------|--------------|----------------------------|-------|---------------------------|-------|---------------------------|-------|
| | | | | | | | Mean | SD | Mean | SD | Mean | SD |
| 2009–10 | Light | 79 | 336 | 3200 | 3279 | 3536 | 2.41^a | 1.80 | 9.50^a | 10.67 | 7.84^a | 18.78 |
| 2009–10 | Pioneer | 19 | 113 | 1377 | 1396 | 1490 | 1.36^{ab} | 1.43 | 7.58^a | 11.75 | 6.73^a | 19.21 |
| 2009–10 | Shade | 4 | 27 | 337 | 341 | 364 | 1.17^b | 1.82 | 7.42^a | 31.69 | 6.74^a | 4.88 |
| | | | | | | | $\chi^2 = 5.90; P = 0.05$ | | $\chi^2 = 0.87; P = 0.64$ | | $\chi^2 = 0.82; P = 0.66$ | |
| 2009–10 | Overall | 102 | 476 | 4914 | 5016 | 5390 | 2.03 | | 8.83 | | 7.46 | |
| 2010–11 | Light | 182 | 92 | 3354 | 3536 | 3446 | 5.15^a | 8.26 | 2.67^a | 1.33 | -2.55^a | 9.10 |
| 2010–11 | Pioneer | 68 | 72 | 1422 | 1490 | 1494 | 4.56^a | 9.71 | 4.82^a | 3.42 | 0.27^a | 12.14 |
| 2010–11 | Shade | 8 | 10 | 356 | 364 | 366 | 2.20^b | 8.70 | 2.73^a | 10.73 | 0.55^a | 19.76 |
| | | | | | | | $\chi^2 = 10.01; P = 0.01$ | | $\chi^2 = 3.10; P = 0.21$ | | $\chi^2 = 3.22; P = 0.19$ | |
| 2010–11 | Overall | 258 | 174 | 5132 | 5390 | 5306 | 4.79 | | 3.28 | | -1.56 | |
| 2011–12 | Light | 190 | 292 | 3283 | 3473 | 3575 | 5.47^a | 3.10 | 8.17^a | 3.75 | 2.94^a | 5.80 |
| 2011–12 | Pioneer | 81 | 129 | 1420 | 1501 | 1549 | 5.40^a | 6.48 | 8.33^a | 5.15 | 3.20^a | 9.90 |
| 2011–12 | Shade | 8 | 39 | 362 | 370 | 401 | 2.16^b | 11.77 | 9.73^a | 15.45 | 8.38^a | 35.49 |
| | | | | | | | $\chi^2 = 0.92; P = 0.01$ | | $\chi^2 = 0.05; P = 0.97$ | | $\chi^2 = 2.16; P = 0.33$ | |
| 2011–12 | Overall | 279 | 460 | 5065 | 5344 | 5525 | 5.22 | | 8.33 | | 3.39 | |
| 2012–13 | Light | 260 | 216 | 3336 | 3596 | 3552 | 7.23^a | 7.93 | 6.08^a | 3.08 | -1.22^a | 9.54 |
| 2012–13 | Pioneer | 74 | 65 | 1482 | 1556 | 1547 | 4.76^a | 8.31 | 4.20^a | 4.28 | -0.58^a | 10.60 |
| 2012–13 | Shade | 10 | 27 | 391 | 401 | 418 | 2.49^b | 7.40 | 6.46^a | 6.30 | 4.24^a | 12.73 |
| | | | | | | | $\chi^2 = 5.41; P = 0.06$ | | $\chi^2 = 0.76; P = 0.68$ | | $\chi^2 = 0.94; P = 0.62$ | |
| 2012–13 | Overall | 344 | 308 | 5209 | 5553 | 5517 | 6.19 | | 5.58 | | -0.65 | |
| 2009–13 | Light | 616 | 861 | 2739 | 3355 | 3600 | 3.98^a | 2.96 | 5.32^a | 3.49 | 1.42^a | 5.72 |
| 2009–13 | Pioneer | 209 | 354 | 1212 | 1421 | 1566 | 3.13^a | 3.71 | 5.00^a | 4.29 | 1.96^a | 6.33 |
| 2009–13 | Shade | 26 | 100 | 318 | 344 | 418 | 1.56^b | 5.89 | 5.32^a | 31.62 | 3.97^a | 7.87 |
| | | | | | | | $\chi^2 = 8.33; P = 0.01$ | | $\chi^2 = 0.26; P = 0.87$ | | $\chi^2 = 0.66; P = 0.71$ | |
| 2009–13 | Overall | 851 | 1315 | 4269 | 5120 | 5584 | 3.57 | | 5.23 | | 1.75 | |

Values followed by the same letter are not significantly different according to an least square difference test. Bold values indicate dynamic rates.

DISCUSSION

We explored how different are plant's strategies from a functional perspective aiming to understand if those differences could explain the high diversity observed in natural edges of gallery forest. We found differences in demographic rates among the groups, with shade-tolerant species having the lowest rates of mortality. Thus, they seem to be thriving well in the gallery forest edges, even increasing in number and biomass despite the proximity of the grassland. We also investigated how different plant strategies, evaluated by functional traits, lead to different performances in natural edges, finding that shade-intolerant species were favored by grassland proximity and shade-tolerant species were favored by canopy closure. Functional traits explained differences in behavior among the groups under different resource availability. The largest

part of the studied species in natural edges had an acquisitive strategy and growth was enhanced by those traits. However, mortality selected both strategies, but in distinct zones of the edges, i.e. groups with an acquisitive strategy have a higher survival by the edge, while groups with a conservative strategy survive more toward the interior. We believe that those differences in strategies, due different functional traits, leads to the high diversity observed in those edges since different species with different strategies can perform well in the edge thanks to its sharp changes regarding light availability.

Differences in demographic rates

We expected shade-tolerant species to have the lowest mortality, recruitment and BA gain among the functional groups. However, they only had the lowest mortality leading to the lowest BA loss. This is strong evidence that despite the high

Table 3: BA of dead individuals, recruits, as well as their initial and final BA and rates of loss, gain and net change in terms of BA for light-demanding, pioneer and shade-tolerant groups in the edges of studied gallery forests, from 2009 to 2013

| Year | Group | Dead | Recruit | Survivor | Increment | Decrement | Initial BA | Final BA | Loss (%) | | Gain (%) | | Change (%) | |
|---------|---------|------|---------|----------|-----------|-----------|------------|----------|---------------------------|--------|---------------------------|--------|---------------------------|--------|
| | | | | | | | | | Mean | SD | Mean | SD | Mean | SD |
| 2009–10 | Light | 0.04 | 0.05 | 5.34 | 0.53 | -0.10 | 4.96 | 5.39 | 2.85^a | 1.39 | 10.88^a | 4.56 | 8.61^a | 7.65 |
| 2009–10 | Pioneer | 0.01 | 0.02 | 4.49 | 0.50 | -0.08 | 4.10 | 4.51 | 2.35^a | 3.10 | 11.51^a | 6.17 | 10.12^a | 10.400 |
| 2009–10 | Shade | 0.01 | 0.01 | 0.61 | 0.06 | -0.01 | 0.57 | 0.62 | 3.65^a | 8.82 | 10.70^a | 62.61 | 7.83^a | 3.58 |
| | | | | | | | | | $\chi^2 = 2.38; P = 0.30$ | | $\chi^2 = 0.81; P = 0.66$ | | $\chi^2 = 0.23; P = 0.88$ | |
| 2009–10 | Overall | 0.06 | 0.09 | 10.44 | 1.09 | -0.20 | 9.64 | 10.52 | 2.68 | | 11.14 | | 9.21 | |
| 2010–11 | Light | 0.13 | 0.02 | 5.22 | 0.34 | -0.48 | 5.39 | 5.25 | 11.41^a | 5.94 | 6.94^a | 2.93 | -2.60^a | 6.69 |
| 2010–11 | Pioneer | 0.09 | 0.02 | 4.44 | 0.37 | -0.41 | 4.51 | 4.47 | 11.12^a | 13.599 | 8.86^a | 6.36 | -0.95^a | 12.06 |
| 2010–11 | Shade | 0.01 | 0.00 | 0.61 | 0.04 | -0.04 | 0.62 | 0.62 | 8.08^a | 13.37 | 6.67^a | 6.81 | -0.29^a | 10.06 |
| | | | | | | | | | $\chi^2 = 2.66; P = 0.26$ | | $\chi^2 = 0.73; P = 0.69$ | | $\chi^2 = 0.71; P = 0.70$ | |
| 2010–11 | Overall | 0.23 | 0.05 | 10.26 | 0.75 | -0.94 | 10.52 | 10.34 | 11.09 | | 7.75 | | -1.76 | |
| 2011–12 | Light | 0.09 | 0.04 | 5.40 | 0.48 | -0.28 | 5.25 | 5.45 | 7.03^a | 3.94 | 9.58^a | 3.82 | 3.82^a | 5.73 |
| 2011–12 | Pioneer | 0.06 | 0.02 | 4.58 | 0.36 | -0.22 | 4.47 | 4.61 | 6.37^a | 6.87 | 8.35^a | 3.93 | 3.06^a | 6.14 |
| 2011–12 | Shade | 0.00 | 0.01 | 0.63 | 0.04 | -0.02 | 0.62 | 0.63 | 4.67^a | 37.96 | 6.98^a | 27.10 | 2.43^a | 43.66 |
| | | | | | | | | | $\chi^2 = 4.23; P = 0.12$ | | $\chi^2 = 0.39; P = 0.82$ | | $\chi^2 = 0.42; P = 0.81$ | |
| 2011–12 | Overall | 0.15 | 0.07 | 10.61 | 0.88 | -0.53 | 10.34 | 10.69 | 6.60 | | 8.90 | | 3.41 | |
| 2012–13 | Light | 0.03 | 0.03 | 5.64 | 0.57 | -0.34 | 5.45 | 5.68 | 6.75^a | 7.65 | 10.50^a | 4.93 | 4.12^a | 11.24 |
| 2012–13 | Pioneer | 0.01 | 0.01 | 4.81 | 0.57 | -0.33 | 4.61 | 4.84 | 7.35^a | 7.71 | 11.94^a | 9.74 | 5.10^a | 15.78 |
| 2012–13 | Shade | 0.00 | 0.00 | 0.67 | 0.05 | -0.01 | 0.63 | 0.67 | 1.87^a | 8.98 | 7.81^a | 12.088 | 6.44^a | 19.07 |
| | | | | | | | | | $\chi^2 = 3.46; P = 0.17$ | | $\chi^2 = 2.58; P = 0.27$ | | $\chi^2 = 1.65; P = 0.43$ | |
| 2012–13 | Overall | 0.04 | 0.04 | 11.12 | 1.18 | -0.68 | 10.69 | 11.19 | 6.72 | | 10.96 | | 4.68 | |
| 2009–13 | Light | 0.37 | 0.18 | 5.68 | 1.27 | -0.56 | 4.96 | 5.68 | 4.07^a | 4.65 | 5.74^a | 2.49 | 2.72^a | 18.71 |
| 2009–13 | Pioneer | 0.33 | 0.12 | 4.85 | 1.22 | -0.48 | 4.10 | 4.84 | 4.28^a | 8.88 | 6.28^a | 4.53 | 3.39^a | 34.56 |
| 2009–13 | Shade | 0.01 | 0.01 | 0.67 | 0.12 | -0.02 | 0.57 | 0.67 | 1.22^b | 61.51 | 4.33^a | 64.78 | 3.23^a | 32.60 |
| | | | | | | | | | $\chi^2 = 6.96; P = 0.03$ | | $\chi^2 = 0.49; P = 0.78$ | | $\chi^2 = 2.47; P = 0.28$ | |
| 2009–13 | Overall | 0.72 | 0.31 | 11.20 | 2.62 | -1.05 | 9.64 | 11.19 | 3.98 | | 5.88 | | 3.04 | |

Values followed by the same letter are not significantly different according to an least square difference test.

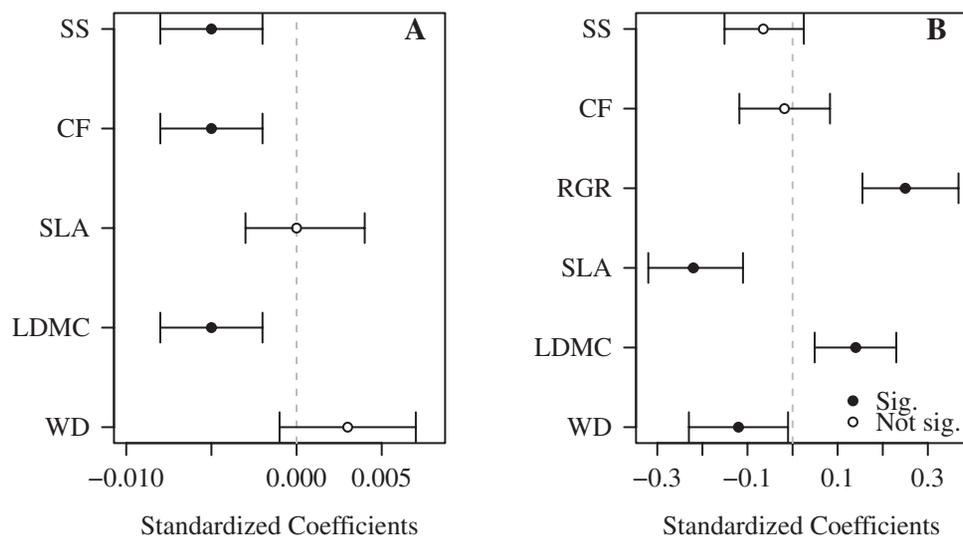


Figure 4: Bayesian credible interval (95%) for growth model parameters (A) and survival model parameters (B). Values that do not overlap zero are significant. P, pioneer; L, light demanding; S, shade tolerant; Dist., distance.

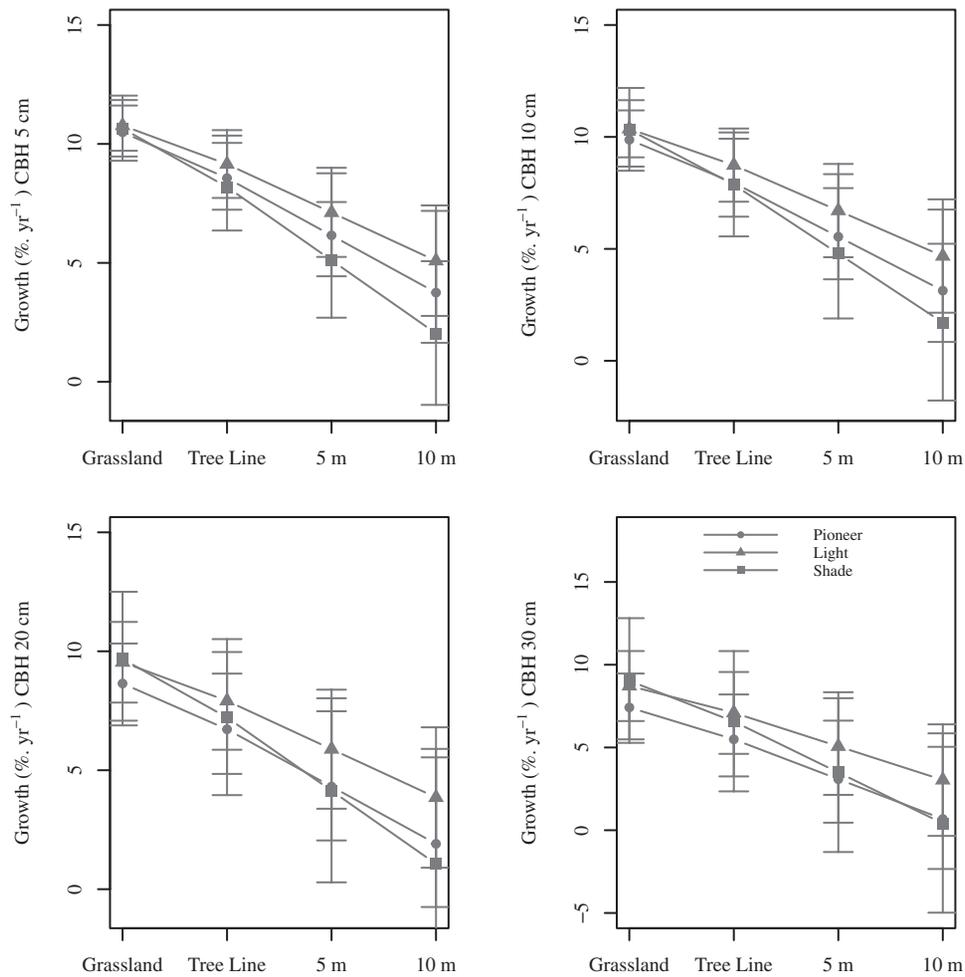


Figure 5: predicted growth values for trees of different sizes and Bayesian credible intervals (95%) for each functional group in four distances: grassland (upper limit of plot), edge (5 m from upper limit), 5 m from edge (10 m from upper limit) and 10 m from edge (15 m from upper limit).

levels of light in the edges due to vertical and lateral gaps (van den Berg and Santos 2003), the light gradient is very sharp, allowing coexistence of light-demanding and shade-tolerant species in these 10-m narrow strip of forest edge. Actually, we found that although the shade-tolerant species have a lower number of individuals than the pioneer and light-demanding groups, their number of individuals and BA increased, and they even had a lower mortality and BA loss than both other groups. Therefore, regardless of all disturbances that take place at natural edges and their environmental conditions, shade-tolerant species are thriving well in the gallery forest edges, even increasing in number and biomass despite the proximity to the grassland.

For all groups, we found mortality rates lower than recruitment and a positive net change rate regarding number of individuals. We also found a higher gain than loss and positive net change of BA, although, for the intervals when there were fires, we found higher mortality and BA losses. The increase in the number of individuals and BA in forest edges confirms the expansion of the forests toward the

surrounding natural grasslands, a trend found by several authors. However, after a fire event, the number of individuals in Site 8 grassland reduced and some studies have shown that in the savanna-forest boundary, the forest can expand and retreat as a consequence of disturbances (Hopkins 1992). Therefore, forest expansion seems to be hindered by fire events taking place in the grassland (Hoffmann *et al.* 2009).

Differences in the effect of the environmental gradient on survival and growth

Pioneer species had a higher survival probability closer to the edge, whereas the survival of climax species (whether shade tolerant or not) increased toward the forest interior. Also, the survival of pioneer and light-demanding species varied with their sizes, whereas survival of shade-tolerant species was only affected by the distance to the edge. The height of shade-tolerant species was less variable than the height of the other groups since they are species commonly restricted to the understory of gallery forests. This particularity possibly contributed to the non-detection of

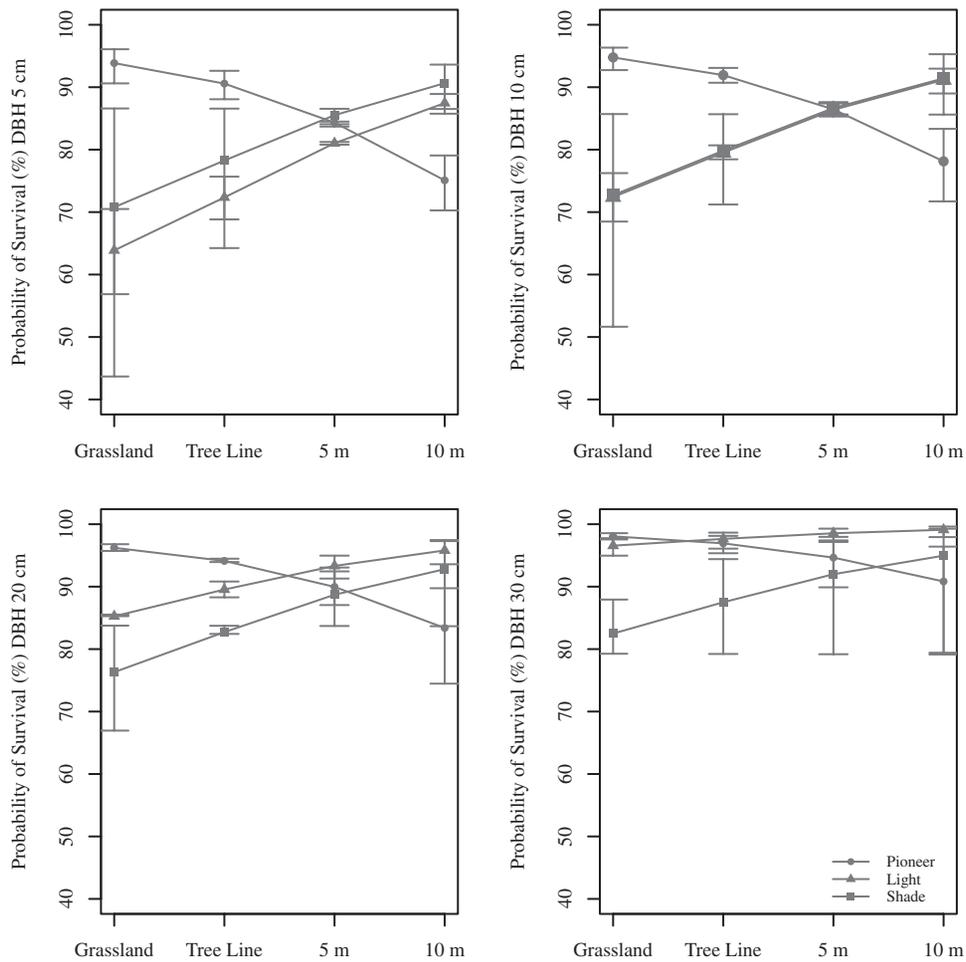


Figure 6: predicted survival probability values for trees of different sizes and their Bayesian credible intervals (95%) for each functional group in four distances: grassland (upper limit of plot), edge (5 m from upper limit), 5 m from edge (10 m from upper limit) and 10 m from edge (15 m from upper limit).

Table 4: differences in functional and allometric traits for tree functional groups in the edges of studied gallery forests

| | SLA | LDMC | SS | CRW | SD |
|---------|--------------------|-------------------|-------------------|-------------------|-------------------|
| Pioneer | 4.35 ^a | 0.37 ^b | 0.36 ^b | 0.86 ^a | 0.25 ^a |
| Light | 3.99 ^b | 0.35 ^c | 0.42 ^a | 0.85 ^a | 0.25 ^a |
| Shade | 3.24 ^{ab} | 0.44 ^a | 0.43 ^a | 0.76 ^a | 0.35 ^a |
| | $\chi^2 = 10.67$ | $\chi^2 = 65.28$ | $\chi^2 = 18.79$ | $\chi^2 = 1.75$ | $\chi^2 = 4.37$ |
| | $P < 0.001$ | $P < 0.001$ | $P < 0.001$ | $P = 0.41$ | $P = 0.11$ |

CBH, circumference at breast height; LDMC, leaf dry matter content (%); RCW, relative crown width (crown width/crown depth); SD, stem density; SLA, specific leaf area ($\text{mm}^2 \text{mg}^{-1}$); SS, stem slenderness (tree height/CBH).

a plant-size effect on their survival, if any effect actually exists.

All groups grew faster in the grasslands. Pioneer species need light to germinate and grow so they obviously benefit from the permanent gap condition found in the edge.

However, this permanent gap condition only exists in the first few meters, leading to a higher mortality risk and lower number of individuals toward the interior probably due to shading. For the pioneer species, light is, therefore, the most important factor for their survival, regardless of the disturbances and harsh microclimatic environments occurring at the forest edge. On the other hand, although climax species also benefit from the higher luminosity leading to higher growth toward the grassland, the harsher conditions there have a price on survival. In addition to the higher light conditions in the immediate edge, there are also microclimatic differences, such as lower soil and air moisture and higher temperature variations (Murcia 1995; van den Berg and Santos 2003). These environmental conditions handicap climax species (Laurance and Peres 2006), increasing mortality and reducing the number of individuals in grassland and first meters of edge. Therefore, for climax species, the unsuitable microclimatic condition in the exposed edge is the most important factor for their survival, although, for

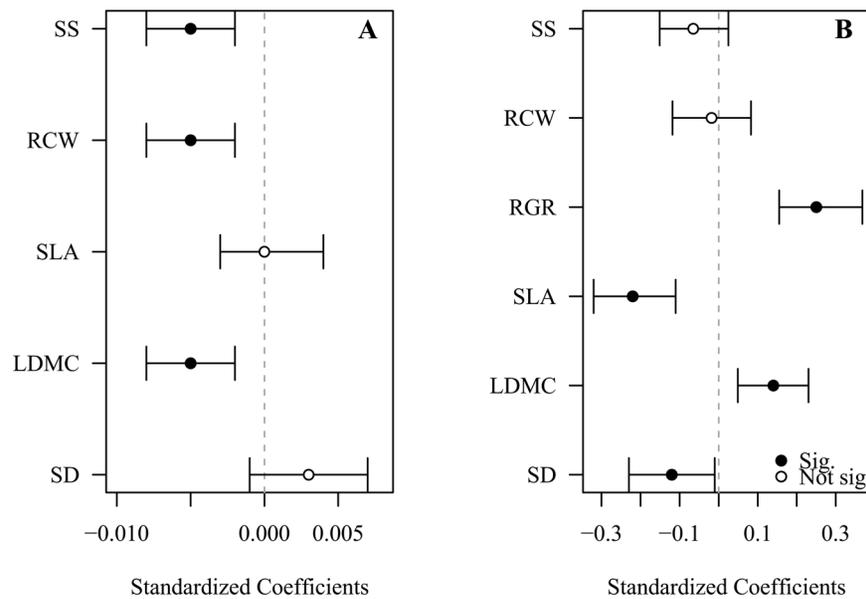


Figure 7: Bayesian credible intervals (95%) for growth model parameters (**A**) and survival model parameters (**B**). Values that do not overlap zero are significant. SS, stem slenderness; RCW, relative crown width; SLA, specific leaf area; LDMC, leaf dry matter content; SD, stem density; RGR, relative growth rate.

the surviving trees, the growth is favored by higher light availability.

Differences in strategies between functional groups

Even though we worked with subjective groups, we found similarities for the species within groups and differences in strategies among the groups. SLA and LDMC are markers of position in the fundamental trade-off between acquiring or conserving resources (Garnier *et al.* 2001), and we found differences between groups, with pioneer species with higher SLA and lower LDMC (acquiring strategy) and shade-tolerant species with lower SLA and higher LDMC (conservative strategy).

The groups had different spatial distribution at the edges and are affected by the edge in different ways. Pioneer species were favored in the most exposed section of the edge, while shade-tolerant species were favored in the opposite side deeper inside the forest, with the light-demanding group in an intermediary situation. Those differences in behavior can be explained by functional traits. Pioneer species are favored in the most exposed section of the edge because they have a strategy focused on acquiring resources, resulting in low investment in traits related to endurance and longevity (Alvarez-Buylla and Martinez-Ramos 1992). Their leaves with high SLA and low LDMC are productive (Poorter and van der Werf 1998; van der Werf *et al.* 1998), allowing them to have higher growth than climax species in a productive environment, such as the immediate edge. On the other hand, shade-tolerant species have low SLA and higher LDMC, features that favor efficiency in resource use and, consequently,

survival and longevity, being more advantageous toward the forest interior, where light is scarce. Their investment in resource conservation mirrors their lower growth rates in comparison to pioneer species. Light-demanding species, in turn, have intermediate traits that reflect in their intermediate growth and intermediate response to the edge.

Frequently, pioneer species are associated with investment in height, having slender stems (Poorter *et al.* 2003). On the contrary, we found pioneer species to be the less slender group. This is probably a consequence of environmental conditions at the front of the edge, where pioneers are preferentially found. In a closed forest condition, pioneer species colonize gaps (Swaine and Whitmore 1988), and although those gaps receive high levels of light, they are more enclosed than natural edges, with light coming predominantly from the top. Under this condition, investment in height improves survival and further growth. However, in natural edges, the lateral light incidence is permanent implying no need for height growth. Besides this, the higher wind exposure of the edges could lead to higher damage to taller trees. Therefore, we hypothesize that in natural edges, due to their permanent high-light conditions and harsher wind exposition, pioneers have a less slender trunk than climax species.

Effect of functional traits on growth

We found that some functional and allometric traits enhance growth. In the edges, species with deeper crowns, instead of wider, grew more. A crown shape that can boost light interception is crucial and, given that in edges light reaches the forest not only vertically but also laterally, deeper crowns

allows a better interception of lateral light promoting higher growth. The crown shape is also linked with successional position (Horn 1971), and because early-successional species (thus pioneer and light-demanding groups) are fast-growing species with low investment in wood, they cannot bear wide crowns. Shade-intolerant species are multilayered, with narrow crowns and several branches disposed along those layers (Horn 1971). However, self-shading in deeper crown pays off only in high-light environments or when light comes laterally, such as the case of these studied natural edges.

Our results support the acquisitive–conservative trade-off, where it is expected that species with the strategy of a rapid production of biomass, i.e. high growth rates, will have low LDMC. In natural edges, species with low LDMC grow faster. LDMC is a functional marker of plant strategy and low LDMC is linked to shade-intolerant species and it is also linked to productive and often highly disturbed environments (Pérez-Harguindeguy et al. 2013), such as natural edges. In edges, temperatures are higher and more variable, there are more light and wind, which leads to a decrease in air and soil moisture and consequently more fires, creating an environment comparatively more disturbed than interior (Murcia 1995).

We expected that growth would have a positive relationship with stem slenderness, but we found the opposite, less slender stems grew more. This could be a consequence of how RGR is measured since it is based on the trunk diameter increment. However, we also found that pioneer species have less slender trunks and also have higher growth. Therefore, having a less slender stem can be an advantageous trait in natural edges for the reasons put forth previously.

Effect of functional traits on survival

Climate, disturbance and site productivity act as consecutive environmental filters that select certain traits (Woodward and Diament 1991). In natural edges, where there is a short and sharp environmental gradient, we expected environmental filters to change along the gradient resulting in different performances of the groups along the gradient. If this hypothesis is true, we expected to find survival to be enhanced by functional traits of both strategies. We did find species with traits of both strategies, acquisitive and conservative. Survival is enhanced by lower SLA and higher LDMC, both features of shade-tolerant species and features of conservation strategy. Survival is also enhanced by higher growth and lower SD, features of shade-intolerant species and an acquisitive strategy. We found that probability of survival varies with distance from the edge and among the functional groups. As mentioned before, pioneer species have a higher survival probability closer to the edge, whereas the survival of climax species (whether shade tolerant or not) increased with increasing distance from the edge. So, in this short gradient, both strategies are selected but in distinct zones of the edge. The same effect was not observed for growth because all groups grow less toward the interior; thus, the effect of the gradient on growth did not change with the functional group.

CONCLUSIONS

Our study showed that the high diversity found in natural edges can be explained by a niche and functional perspective, where differences in functional traits lead to differential performance along the environmental gradient. Therefore, growth and survival of diverse functional groups differed strongly along the sharp gradient of only 10 m studied here. Shade-intolerant species were favored by grassland proximity, and shade-tolerant species were favored by canopy closure. Those differences in behavior were explained by differences regarding functional traits. Growth was enhanced by acquisitive traits. However, mortality selected both strategies, but in distinct zones of the edge, i.e. groups with an acquisitive strategy have a higher survival by the edge, while groups with a conservative strategy survive more toward the interior. We believe that those differences in strategies evidenced by functional traits lead to the high diversity observed in those edges since species with diverse strategies can perform well in zones of the sharp light gradient present in the edges. We encourage further studies focusing on the mechanisms behind forest expansion as to if/how pioneer species facilitate non-pioneer establishment, and the long-term effect of fire as a forest expansion suppressor.

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