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Spatial patterns of two co-occurring savanna and forest tree species in a dense fire-protected savanna fragment

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ABSTRACT

Savanna-forest transition under fire-exclusion could be explained by differential competitive performance of savanna and forest species under shading/fire-exclusion. Aiming to understand strategies related to either habitat affinity, we investigated spatial patterns of a savanna and a forest species in a fire-protected savanna. We predicted that: savanna species would have lower abundance than the forest species due to a restriction in the number of open microsites; segregation of size classes and a trend from clumping to regularity with size for forest species due to absence of microsite limitation and intra-specifc competition; and spatial association and increasing clustering with size for savanna species due to microsite limitation. To test these predictions, we described spatial patterns of plants in two size classes in three plots of 0.5 ha. We analyzed spatial patterns and associations of size classes using SADIE methodology. Different from what we expected, both species were more abundant among the studied plots and exhibited an increasing aggregation from small to large size classes. We also found a positive spatial association between size classes of both. These results suggest that both savanna and forest species produce similar spatial patterns independently of habitat affinity. We discuss the possible processes responsible for the observed patterns.

Keywords: Cerrado, competition, fire, microsite limitation, recruitment, SADIE, savanna, spatial patterns

Introduction

Plant responses to physical and biotic environments can vary depending on developmental stage (Harper & White 1974). Such developmental variation can be related to shifts in suitable sites for survival and growth throughout ontogeny, and thereby influencing spatial and size/age population structure, especially in heterogeneous environments (Schupp 1995). Details of spatial patterns throughout ontogeny can be suggestive of factors influencing demographic processes (Barot *et al.* 1999; Barot & Gignoux 2003; Schurr *et al.* 2004; Raventós *et al.* 2010). Therefore, the assessment of variation in spatial patterns throughout ontogeny is one way to verify how different demographic processes influence populations of plant species.

Different suites of processes are associated with either discordance (trend of occurrence in distinct locations) or concordance (trend to occur in close proximity) of spatial patterns of developmental stages/size classes. Discordance can be a result of microsite differences throughout ontogeny (Schupp 1995; Anderson *et al.* 2009), intraspecific competition (Stoll & Prati 2001; Raventós *et al.* 2010) and negative density dependence (Janzen 1970; Gratzer & Rai 2004); whereas concordance can be a consequence of facilitative (intra- or inter-specific) interactions (Callaway 1995; Gratzer & Rai 2004) or similarities in suitable

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probably a consequence of fire protection permitting the invasion of forest species from nearby *cerradão* fragments (the nearest is located at a distance of 4.0 km from the study fragment). The fragment has been protected from fire and human disturbances for nearly 40 years, and is beginning to be invaded by *Pinus* sp.

Study species

To understand ecological differences related to either forest or savanna affinity we choose to study one species associated with each physiognomy. The studied species were *Qualea grandiflora* and *Vochysia tucanorum* (Vochysiaceae). Information from the literature has shown habitat differences between them, with *V. tucanorum* being mainly found in forests or forest-savanna transitions (Gandolfi *et al.* 1995; Barbosa *et al.* 1999; Geiger *et al.* 2011). Gandolfi *et al.* (1995) included *V. tucanorum* in the group of early secondary species, tolerating intermediate levels of shading. *Q. grandiflora*, on the other hand, has been recorded as a typical savanna species (Felfili & Silva Júnior 1992; Geiger *et al.* 2011). Experimental studies show that light enhances this species germination (Felippe 1990), and under soil nutrient enrichment seedlings of *Q. grandiflora* invest more into underground than aboveground structures (Paulilo & Felippe 1995), suggesting that *Q. grandiflora* has better performance in more "open" conditions where light is not limiting. Although the above studies support differences in habitat preferences, *Q. grandiflora* and *V. tucanorum* can be found at the same localities (Costa & Araújo 2001; Weiser & Godoy 2001; Silva *et al.* 2002; Gomes *et al.* 2004), which makes them suitable for this comparative study.

Data collection

We collected data in three 100 x 50 m permanent plots (hereafter referred as V1, V2, V3) installed in different locations within our fragment. Each plot was divided into 200 5 x 5 m subplots. In each subplot we counted and measured the height of individuals of *Q. grandiflora* and *V. tucanorum*. Height measurements were done using a metric tape for plants up to nearly two meters tall and a clinometer for taller plants (Precision 0.01m).

Data analysis

For all analyses we considered two size classes: plants with 0.15 m ≤ height ≤ 1.5 m, and plants with height > 1.5 m. The maximum attained height registered in studied plots was 14.08 m for *Q. grandiflora* and 13.53 m for *V. tucanorum*. The choice of the number and range of classes was a compromise between a sufficient number of plants within each class for spatial analysis (~ 20), with the similarity of classes being compared in all plots and species combinations,

and an approximation to the distinction between mature and immature trees.

To test for differences in abundance between species in different plots within the same fragment (V1, V2, V3), we performed chi-square tests for the tall size class.

We used the number of plants per subplot as a variable describing the spatial patterns of populations *of Q. grandiflora* and *V. tucanorum*. To measure and test for the presence of spatial structure we performed Spatial Analysis by Distance Indices (SADIE) (Perry 1998). This analysis allows a description of spatial patterns of count data by means of computation of an index of aggregation, Ia. Values of Ia not significantly different from 1 indicate spatially random data, whereas Ia > 1 and Ia < 1 means aggregated and regular spatial patterns, respectively. The significance of Ia was tested by means of a randomization procedure (Perry 1998). At each run, the subplot position of counts were changed randomly permitting one to build a random distribution of Ia values thereby making it possible to assign a p-value for empirically obtained values and to test for its significance on an established level (5% in this study; 5967 permutations, the maximum possible in the software used).

We tested intra-specific spatial associations between size classes of each species by SADIE methodology for spatial associations (Perry & Dixon 2002). The procedure consisted of computing local clustering indexes for each sample unit (subplots). Clustering indexes were than used for computing an X value for two sets of count data obtained in the same sample units. X values are simple correlation coefficients between the correspondent clustering indexes (obtained for each sample unit in the previous analysis) of each set of counts. The significance of X values were computed under the null hypothesis of absence of association or dissociation and tested by means of a randomization test. The randomization involved the computation of the clustering indexes obtained from permutation of observed counts amongst the sample units (subplots) in both count data sets (more details on significance tests in Perry & Dixon 2002). We performed 10000 randomizations. A significant positive value of X indicates spatial association and a negative value indicates spatial dissociation. All spatial analysis were performed in SADIEShell (measuring and testing spatial structures) and N_Ashell (spatial association) software (Conrad 2008).

Results

The abundance of the tall size class differed between species in different places of the same fragment (chi-square = 114.6, df = 2, p < 0.01), but neither species was the most abundant in all studied plots (Tab. 1). This seems mainly due to differences in abundances of species in V2 (*Q. gandiflora* more abundant than *V. tucanorum*) and V3 (*V. tucanorum* more abundant than *Q. gandiflora*) because the largest deviations from expected values computed for the chi-square tests were found in these plots.

For *V. tucanorum*, we found a predominance of aggregated spatial patterns with only one case of randomness (Tab. 2, Fig. 1). There was an increase in aggregation from small to tall height classes of *V. tucanorum*. In V1 there was a transition from randomness to clumped spatial pattern and in V2 and in V3 both size classes were clumped, with a high level of aggregation in tall size class (Tab. 2). Small and tall size classes of *V. tucanorum* were spatially associated in V2 and V3, and nearly significantly associated in V1 (Tab. 3).

For *Q. grandiflora*, we found a similar trend of increasing aggregation from small to tall size classes in all three plots (Tab. 2, Fig 2.). In V2 and V3 the trend was represented by a transition from random spatial distribution in the small size class to aggregated patterns in the tall size class, and in V1 the trend consisted of an increase in aggregation from small to tall size class (Tab. 2). In V2 both size classes of *Q. grandiflora* were spatially associated but they had no significant association or dissociation in V1 and V3 (Tab. 3).

Discussion

The studied species exhibited similar spatial patterns of increasing aggregation with increasing size class and a positive spatial association between size classes. These results were unexpected because we had hypothesized that because the studied species have different habitat affinities (savanna x forest), they should exhibit different spatial patterns suggestive of contrasting demographic responses to the same environment.

For *Q. grandiflora*, clumping only in tall size class in V2 and V3, an increased aggregation with size class in V1 and one case of inter-class spatial association suggest a scenario where, despite low early specificity, recruitment into maturity is only possible in some suitable locations. Clumped spatial patterns of mature size classes or stages have been documented and related to soil and topographic factors (Tsujino & Yumoto 2007; Anderson *et al.* 2009; Franklin & Santos 2011; Barbosa *et al.* 2013), and light (Dovciak *et al.* 2001; Fuchs *et al.* 2013).

We regard light as a more limiting factor to *Q. grandiflora* recruitment into maturity in the studied fragment than soil. First, because *Q. grandiflora*, being the most widespread tree species of the Cerrado (Ratter *et al.* 2003), should have high tolerance to soils with low fertility or Al toxicity, both characteristics of Cerrado soils (Motta *et al.* 2002). Second, because in the studied fragment plants have a high probability of experiencing light limitation as they grow due to the canopy openness ranging from low to moderate, rarely passing 30 %, with common values around 20% (Miranda-Melo 2004). This becomes more evident considering that Miranda-Melo *et al.* (2007) found a mean canopy openness (computed from fisheye photographs) of 19.6, 29.4 and 28.6 % in the same plots we studied here (V1, V2, V3, respectively), with V1 being the plot were light is more limiting. We found that for *Q. grandiflora* both the

Table 1. Number of individuals of tree species in two size classes in three 100 x 50 m plots (V1, V2, V3) in a Cerrado (wet savanna) fragment, São Paulo, Brazil. QG – *Qualea grandiflora*, VT – *Vochysia tucanorum*.

Plot	Height ≤ 1.5m		Height > 1.5m		Total	
	QG	VT	QG	VT	QG	VT
V1	31	47	230	229	261	276
V2	41	22	122	34	163	56
V3	19	83	32	137	51	220

Table 2. Spatial patterns of the number individuals of *Qualea grandiflora* (QG) and *Vochysia tucanorum* (VT) in two size classes (S-small, T-tall) in three 100 x 50 plots (V1, V2, V3) in a cerrado (wet savanna) fragment, São Paulo, Brazil. Ia – SADIE index of aggregation, p – significance of each Ia. Significance values smaller than the critical values (0.05) are in boldface.

Plot	Species	Class	Ia	p
v1	QG	T	2.226	**0.0002**
v1	QG	S	1.715	**0.0059**
v2	QG	T	1.789	**0.0023**
v2	QG	S	1.228	0.1156
v3	QG	T	1.858	**0.0022**
v3	QG	S	1.189	0.1483
v1	VT	T	2.224	**0.0002**
v1	VT	S	1.342	0.615
v2	VT	T	2.208	**0.0003**
v2	VT	S	1.791	**0.0032**
v3	VT	T	2.302	**0.0002**
v3	VT	S	1.872	**0.0018**

Table 3. Spatial association of the number of individuals between small and tall size classes of *Qualea grandiflora* (QG) and *Vochysia tucanorum* (VT) in three 100 x 50 plots (V1, V2, V3) in a Cerrado (wet savanna) fragment, São Paulo, Brazil. X – SADIE index of association, p – significance of each X. Significance values smaller than the critical values (0.05) are in boldface.

Plot	Species	X	p
v1	QG	-0.0336	0.664
v2	QG	0.2775	**0.0012**
v3	QG	0.0065	0.4757
v1	VT	0.1315	0.0527
v2	VT	0.2986	**0.0001**
v3	VT	0.3930	**0.0001**

highest index of aggregation (Ia) of tall size class and the only significant positive association between small and tall size classes occurred in V1. The results of Miranda-Melo *et al.* (2007) and ours suggest that individuals of *Q. grandiflora* tend to be more aggregated were light is more limiting. Preceding studies have also found results suggesting that *Q. grandiflora* has better performance in
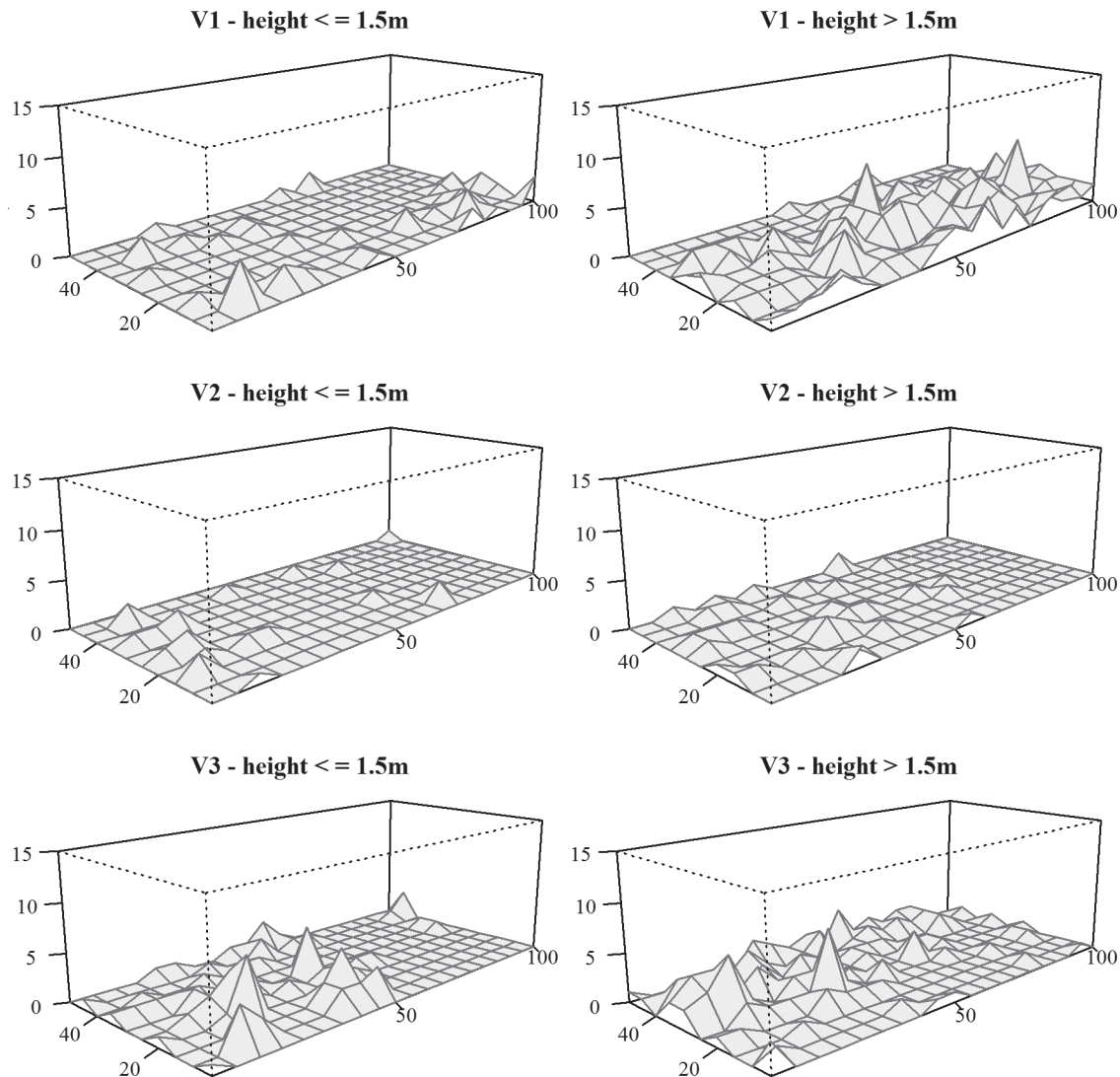
Figure 1. Perspective plots of the number of *Vochysia tucanorum* trees per 5 x 5 m subplots (vertical axis) in 100 x 50 m plots located in a Cerrado fragment, Itirapina, São Paulo. Plots for small and large size classes are on the left and right columns, respectively.

more "open" conditions where light is not limiting (Felippe 1990; Paulilo & Felippe 1995). Taken together, these results are evidence that *Q. grandiflora* has better performance in more "open" conditions where light is not limiting, hence its recruitment into maturity should be restricted to less shaded microsites in savanna-to-forest transitions generating the observed spatial patterns.

The spatial patterns of *Q. grandiflora* could also be explained by a fire effect. In savannas, tree clumping can be generated by the influence of fire, either by enhanced survival due to crowd protection against fire damage or by fire induced re-sprouting in species with the ability to spread clonally (Kennedy & Potgieter 2003). The studied fragment has been fire protected for 30-40 years and fire could explain tree clumping in this case only as a "memory" of spatial patterns left by a past of more frequent fire events.

If this is true, in fire protected fragments an expansion of establishment further from parent plants since fire exclusion is expected because recruitment would be "free" from the aggregative effects of fire. In this case, when comparing fire protected and unprotected fragments, spatial aggregation should be lower in intensity and larger in scale of aggregation (size of clumps) in fire protected fragments. In a study of spatial patterns of *Q. grandiflora* in fire-protected and unprotected Cerrado fragments, Costa & Santos (2011) found results contrary to this expectation: in fire-prone fragments the intensity was equal to or lower than, and the scale of aggregation was similar to, that found in fire-protected fragments.

Spatial patterns of *V. tucanorum* were similar to that found for *Q. grandiflora*. This is an unexpected result because we expected forest species would not be microsite limited

Figure 2. Perspective plots of the number of *Qualea grandiflora* trees per 5 x 5 m subplots (vertical axis) in 100 x 50 m plots located in a Cerrado fragment, Itirapina, São Paulo. Plots for small and large size classes are on the left and right columns, respectively.
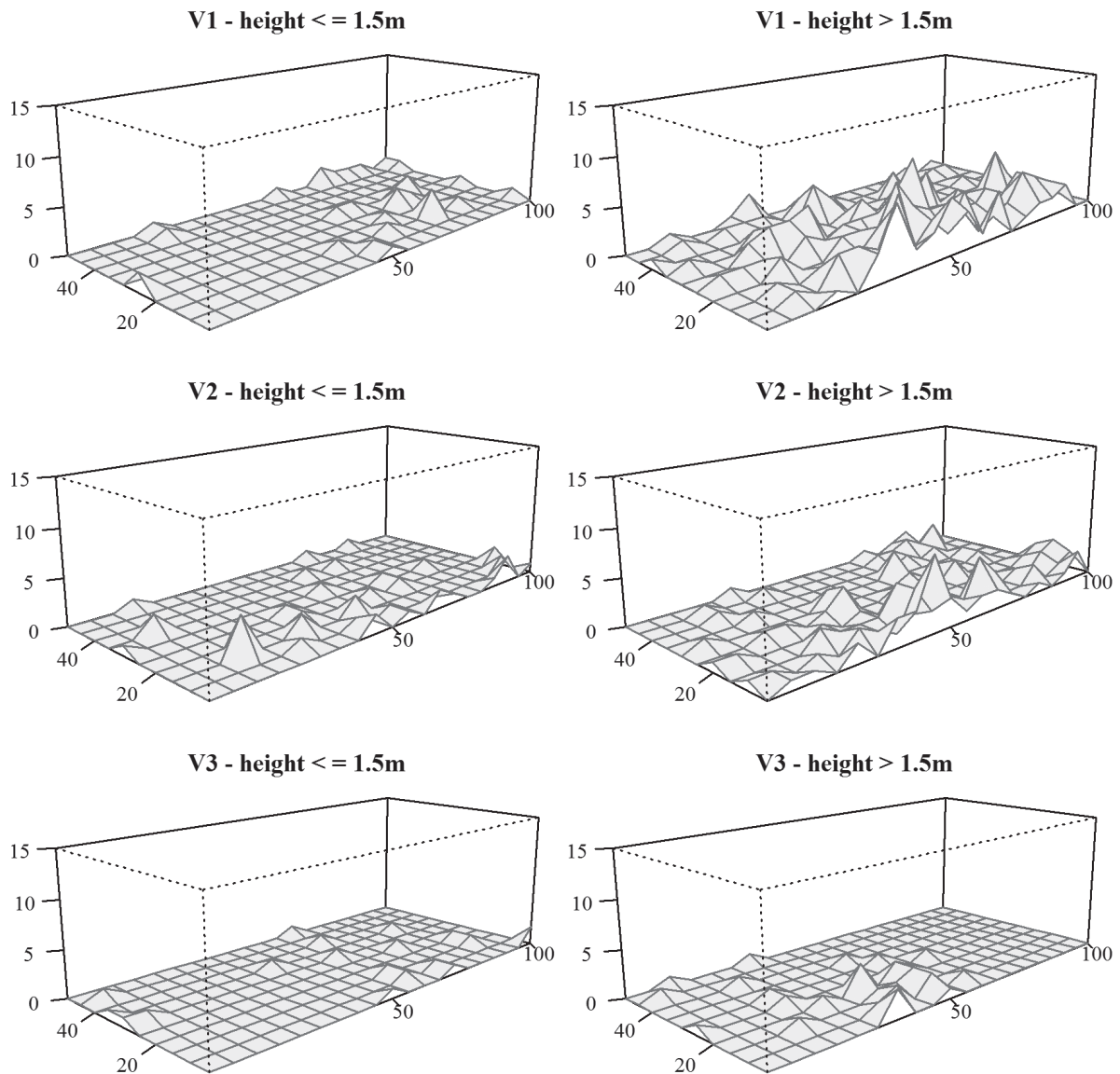
in more shaded conditions of fire-protected dense Cerrado vegetation. Experimental evidence shows that, although *V. tucanorum* germination is favored by light at some temperatures, its seeds are able to germinate both under light or dark conditions (Barbosa *et al*. 1999), showing that light is not important for germination. Additionally, even with the variation in mean canopy openness (19.6 – 28.6 %) among the studied plots (Miranda-Melo *et al*. 2007), the index of aggregation (Ia) for tall size class of *V. tucanorum* had very similar values among plots (2.224, 2.208, 2.302) and spatial association was positively significant in two of them, suggesting that individuals of *V. tucanorum* do not tend to be more aggregated where light is more limiting, as for *Q. grandiflora*. Microsite limitation could be the process responsible for the spatial patterns of *V. tucanorum* due to a

limited ability of forest species to reach deep water-reserves. Hoffmann & Franco (2003), in a comparative growth analysis of pairs of congener woody species of savanna and forest found that while Cerrado species allocated more biomass to coarse roots, forest species allocated more to stem growth. Cerrado exhibits floristic/physiognomic gradients due to variation in soil fertility (mainly P, N and K; Goodland & Pollard 1973) and fluctuations in water table level (Oliveira-Filho *et al*. 1989; Oliveira *et al*. 2005). Therefore, species with a limited ability to reach deep soil layers should be spatially associated with patches of soil with better fertility or a shallower water table. We failed to find any literature information on relative biomass investment in roots and aerial parts for *V. tucanorum* and, therefore, spatial dependence on patches of fertility or shallow water

table by this species deserves further investigation.

An alternative for the microsite hypothesis could be that the spatial patterns of *V. tucanorum* are the result of spatial expansion of its population since initial colonization following fire-protection. Although not being microsite limited, the establishment of forest species into savannas could generate increasing aggregation with ontogeny and positive association of size classes because it should start with a low number of seeds that successfully establish and becomes mature trees acting as nuclei for further spreading of the invasion. For example, in a forest–savanna boundary in a Cerrado region near Brasilia, Brazil, 35 years of fire-protection (similar to our study) allowed the establishment of forest tree species that, although comprising a minority of the mature stems in savanna plots, corresponded to one-third of the juveniles (Geiger *et al.* 2011). Some of these juveniles were likely produced by early colonizers that probably acted as nuclei of invasion spreading. Some of our results give evidence for the importance of this process on *V. tucanorum* dynamics. When comparing maps of *V. tucanorum,* subplots of high density of small individuals surrounding plots of high density of larger individuals can be seen (in V1 and V2), suggesting expansion of establishment from an initial nucleus. Furthermore, we found evidence of a stronger positive spatial association among size classes for *V. tucanorum* than for *Q. grandiflora*. This consistent positive association could be the result of the importance of a few starting nuclei as a source of seeds for establishment of new cohorts and spatial expansion of populations.

The fact that both species were able to be more abundant relative to each other in different places (plots) of the same fragment is further evidence that *Q. grandiflora* should have its abundance restricted by the limitation of suitable places for survival until maturity. This species should be rare in locations with low availability of light microsites. Limitation of microsites defined by soil fertility or water table level remains a possible generating mechanism for the observed *V. tucanorum* spatial patterns, but we also find evidence that population expansion following fire-suppression could generate the observed patterns. Taken together, our results suggest that even having different affinities (forest x savanna), both species exhibited similar spatial patterns. To what extent this similarity can be the result of the same process (microsite limitation) deserves future study associating light and soil variables to survival of plants in different developmental stages of forest and savanna species and documenting spatial patterns, recruitment and survival of forest species invading savanna sites following fire-protection.

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