Distinct roles of savanna and forest tree species in regeneration under fire suppression in a Brazilian savanna

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Abstract

Questions: Has fire suppression relaxed barriers to the exchange of species between savanna and forest? Do all species or a subset of species participate in this exchange? Would current vegetation structure persist if fire suppression were to cease?

Location: A gallery forest edge in the Cerrado region of central Brazil that burned only once in the past 35 years.

Methods: Density of tree seedlings, saplings and adults, leaf area index (LAI), tree basal area and diameter were surveyed in 12, $10 \, \mathrm{m} \times 70 \, \mathrm{m}$ transects centred on and perpendicular to the forest–savanna boundary. Community composition was assessed using non-metric multi-dimensional scaling (NMDS).

Results: Basal area and LAI declined substantially from forest to savanna, with an associated shift in species composition. Savanna tree species were nearly absent in the forest, but accounted for the majority of stems in the savanna. In contrast, forest species comprised 14% of adults and more than one-third of juveniles in the savanna. Despite the high diversity of trees (85 species) in the forest, five species play a particularly large role in this initial phase of forest expansion. Reintroduction of fire, however, would result in widespread topkill of juveniles and the majority of adult forest trees, thereby interrupting the succession towards forest.

Conclusions: After 35 years during which the site burned only once, the savanna still remains dominated by savanna species. Nevertheless, the dominance of forest juveniles in border and savanna tree communities suggests that with a continued policy of fire suppression, the forest will continue to expand.

Introduction

Tropical savanna and closed-canopy forest are the two most extensive tropical biomes, but there is little consensus regarding factors that govern the balance between these vegetation types. While climate and/or soil nutrients are known to play important roles in determining the distribution of forest and savanna (Cole 1986; Sarmiento

1992; Ruggiero et al. 2002), fire is perhaps the most universal deterrent to forest expansion into the savanna (Hopkins 1992; Bowman 2000; Bond 2008). In areas where forest would readily occupy savanna, fire maintains abrupt transitions in structure and species composition at forest–savanna boundaries (Hopkins 1992). When fire frequency is reduced through suppression, tropical

forest frequently expands into humid savanna (Bowman & Fensham 1991; Hopkins 1992; Swaine et al. 1992; Bowman et al. 2001; Brook & Bowman 2006; Durigan & Ratter 2006). While these studies have documented changes to ecosystem structure caused by adult trees, we know little about the patterns of population and community structure leading to these changes.

The success of forest species in savanna ecosystems subject to frequent fire is limited because they have a thinner layer of protective bark and higher rates of topkill than savanna species (Hoffmann et al. 2009), and may experience higher mortality rates as juveniles (Gignoux et al. 2009) or when burned repeatedly (Fensham et al. 2003). When savannas are protected from fire, both fire-tolerant and fire-sensitive tree species experience increases in density and individual size (Fensham & Butler 2003). There are, however, many differences in growth habit between these two types of tree, and these differences can have direct implications for maintenance of the two biomes (savanna versus forest). For example, forest species colonizing savanna appear to play a particularly important role in generating the structure of forest vegetation due to their faster growth (Rossatto et al. 2009), greater adult height (Hoffmann et al. 2003) and larger and denser canopies (Hoffmann et al. 2005; Rossatto et al. 2009) than savanna trees. These species may outcompete savanna species for light and exclude grasses, which would reduce fire frequency and intensity. It is therefore important to explicitly consider species identity in attempting to understand factors that govern the distribution of savanna and forest. This is equally true when examining forest species expanding into savanna, as pioneer forest species may be more successful colonizers of high-light or exposed savanna environments and then facilitate the establishment of other forest species (Hennenberg et al. 2006).

In the Cerrado (savanna) region of central Brazil, where the current study was undertaken, most tree species are typically limited to either savanna or forest habitat (Felfili & da Silva 1992). A smaller number of species, however, are better characterized as intermediate based on their distribution across the forest–savanna boundary. Such species may occur commonly in both savanna and forest, or may be typical of mixed habitats, such as forest edges or cerradão, a dense, tall woodland physiognomy in which both savanna and forest species are present (Pinheiro & Monteiro 2006; Walter 2006). These intermediate species may play a particularly important role in early stages of forest expansion. The dynamics of forest expansion into fire-suppressed savanna, however, has not been well described for the Cerrado, in contrast to Africa (Hopkins, 1992; Swaine et al. 1992; Hennenberg et al. 2005), Australia (Bowman & Fensham

1991; Russell-Smith 2004; Banfai & Bowman 2007) and the Llanos of Venezuela (San José & Fariñas 1991). This is unfortunate, because a widespread policy of fire suppression in reserves within the Cerrado has the potential to result in succession to forest, with a loss of savanna biodiversity (Durigan & Ratter 2006).

In this study, we examined vegetation structure and composition of juvenile and adult tree communities at a savanna–forest boundary where fire occurred only once in 35 years due to fire suppression. We asked the following questions: Are forest and savanna species still each restricted to their original habit or has fire suppression relaxed barriers to the exchange of species between savanna and forest? If species are expanding into neighbouring habitats, do all species participate in this exchange, or does a small subset of species play a particularly large role? Finally, has current vegetation structure reached a stage at which it is likely to resist the impacts of burning if fire suppression were to cease?

Methods

The study site is at the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE), approximately 35 km south of Brasilia (15°55′S, 47°53′W). The vegetation of IBGE is predominantly savanna (locally referred to as cerrado) interspersed with woodlands and gallery forests. Many species within these forests also occur in the Amazon and Atlantic forests (Oliveira-Filho & Ratter 1995) as well as upland mesophytic forests within the Cerrado region (Méio et al. 2003). Tree cover in savanna vegetation varies greatly, from treeless campos (fields) to 90% tree cover in savanna woodlands (known locally as cerradão) with trees 8–15-m tall (Cole 1986; Ribeiro & Walter 2008). The average annual rainfall recorded at the IBGE meteorological station from 1980 to 2008 was 1461 mm, with a distinct dry season from May to September, and a mean annual temperature of 22.5 °C. The predominant soils are deep, well-drained oxisols.

The research was carried out at the boundary between gallery (i.e. riparian) forest and savanna that had only burned once in the last 35 years due to a policy of fire suppression in the reserve. This most recent fire occurred in 1994, 13 years prior to the start of the present study. The portions of the forest included in this study occur on well-drained soils well upslope of the stream. Twelve transects were positioned perpendicularly to the forest edge and centred at the border (Fig. 1). Each transect was 10 m × 70 m and extended 30 m into forest and 30 m into savanna, with a border approximately 10-m wide. For analysis and sampling purposes, each transect was subdivided into seven 10 m × 10 m plots. Border plots were located at 0 m; plots located at 10 m, 20 m and 30 m were
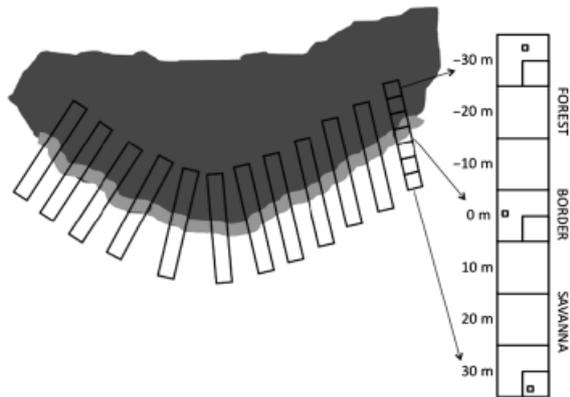
Fig. 1. Study design of the savanna–forest boundary in the Cerrado of central Brazil. Twelve 10 m × 70 m transects were placed perpendicularly to the border. The forest–savanna border was less than 10-m wide and was distinguished by an abrupt change in grass cover, leaf area index and tree density and height. Trees were sampled in 10 m × 10 m plots, saplings were sampled in 5 m × 5 m subplots, and seedlings were sampled in 1 m × 1 m subplots.

in savanna, and plots located at −10 m, −20 m and −30 m were in forest. We used the change in tree structure and absence of grass to distinguish forest from savanna and to define the position of the border. Transects were spaced 10 m apart, with some variation due to curvature of the forest boundary. In 2007, all trees > 5-cm diameter in these transects were identified, mapped and stem diameter measured at 30 cm from ground level. Juveniles (seedlings and saplings) were sub-sampled in quadrats nested within the 10 m × 10 m plots located in the forest (−30 m), at the border (0 m) and in the savanna (30 m). Saplings, defined here as any woody plant > l-m tall but with stem diameter < 5 cm, were sampled in 25-m² quadrats. Seedlings, defined as woody plants < 1-m tall, were sampled in a randomly placed 1-m² quadrat, which had been set up to measure canopy cover and had been protected from trampling, within the 10 m × 10 m plot. In total, seedlings and saplings were sampled within 36 quadrats placed within savanna (30 m), forest (−30 m) and border (0 m) plots. For convenience, we refer to individuals in the largest size class as adults and to individuals in the seedling and sapling classes as juveniles, although our size classes do not necessarily correspond to sexual maturity. We classified species as typical of savannas or gallery forests according to a flora published by IBGE (2004). Species that are listed as existing in both the savanna and forest and have been commonly observed in both habitats are considered here as intermediate species, even though characteristically they are more similar to forest species, with thin bark and dense canopies. Species nomenclature follows the Flora of the Cerrado Biome (Mendonça et al. 2008).

Soil samples were collected from 0- to 15-cm depth at 10-m intervals along each transect. Soil pH was measured in 1:2.5 soil:water suspension and in 1 M KCl. Exchangeable Ca, Mg and Al were determined in extracts of 1 M KCl, and K, P, Fe, Mn, Zn and Cu in Mehlich's extract of a diacid mixture of 0.05 M HCl and 0.025 M H_2SO_4. The cations were determined with atomic absorption spectrophotometry and P by colorimetry (Allen 1989). Total N was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined using the Walkley and Black method (Allen 1989).

We determined leaf area index (LAI) for ground and tree cover in one randomly located 1-m² quadrat within each 10 m × 10 m plot using the CI-110 Plant Canopy Imager (CID Inc.). This instrument captures a digital image of overhead vegetation within a 150° field of view, from which LAI is calculated using CI-110 software. At each location, an image was captured at ground level and at 1 m. The image taken at ground level includes cover above 1 m, therefore LAI of the ground layer was calculated by subtracting the LAI measured at 1 m from the LAI measured at ground level. To estimate the LAI of the dicots and grasses within the ground layer, we visually estimated the proportion of each in the total ground cover and then multiplied these values by the LAI value for the ground layer. Images were taken in May 2007, at the end of the rainy season, under conditions of diffuse light (dawn, dusk or overcast sky).

Analyses

Analyses were performed using analysis of variance (ANOVA) in JMP 7.0 and SAS 9.1.3 (SAS Institute, Cary, NC, USA). All data were tested for normality with the Shapiro-Wilk W-statistic (Shapiro & Wilk 1965) and for homogeneous variances with O'Brien's (1981) test. When the data failed to meet these criteria, transformations were applied. Consequently, the log transformation was applied to stem diameters and most soil variables, while LAI, basal area, tree density, soil pH, K and organic carbon were left untransformed because they did not deviate significantly from the assumption of normality and homogeneity of variances. In the case of Al, Ca and Mg we used a linear mixed model (Littell et al. 2006), and the residuals did not reject the normality assumption when fitting separate residuals after the log transformation. The use of log transformation in our case is supported since the mean variance relationship is consistent (McArdle & Anderson 2004). That is, within a class (forest versus savanna), one class shows less variability, while the other shows increasing variances as the means increase for soil nutrients and stem diameter. We compared similarity of species between forest and savanna using Jaccard's

similarity index (Jaccard 1912), which has a value of 0 when the two communities share no species, and has a value of 1 when there is complete overlap of species.

Under normal conditions, the inability of forest species to resist the impacts of fire may be an important barrier to expansion of forest into savanna. Therefore to assess the impacts of a hypothetical fire on this system in which fire is currently suppressed, we estimated the proportion of existing stems that would be topkilled during a typical fire. The capability of a stem to survive fire is primarily a function of bark thickness (Hoffmann et al. 2009), which insulates a stem from fire. We first determined bark thickness of the trees based on species-specific regression equations for the relationship between stem diameter and bark thickness (Hoffmann et al. 2009). These relationships are available for 58 species, allowing us to estimate bark thickness for 78% of trees growing in the savanna. We then considered individuals with bark thickness > 6.2 mm to be resistant to topkill, based on a previous study that estimated that this thickness is sufficient to ensure that a stem has at least a 50% chance of resisting topkill (Hoffmann et al. 2009). Fire intensity influences this relationship, so this analysis is meant only to assess the relative impacts of a moderate-intensity fire on stems of savanna and forest species.

To analyse changes in species composition in relation to size class and distance from the forest–savanna border we performed non-metric multi-dimensional scaling (NMDS) using PC-Ord software v4.0 (MjM Software, Gleneden Beach, OR, USA). NMDS is a preferred ordination method for analysing community data (McCune & Grace 2002). We analysed density of individuals from three size classes (seedling, sapling, tree) and from three habitats (forest, border, savanna). Data were log transformed prior to analysis. To determine the appropriate number of axes (dimensions), we conducted a preliminary run using the Sørensen (Bray-Curtis) distance measure and selected a step-down from six dimensions to one with a maximum of 200 iterations, 30 runs of real data, 30 randomized runs, and a stability criterion of 0.0001. We selected a Monte Carlo test of 30 runs for each preliminary ordination. Our final ordination was based on a starting configuration file from the preliminary run that balanced low stress with minimum number of axes. The final stress was 19.28 (between 10 and 20 is considered normal for ecological data), final instability of 0.0001, and 156 iterations for a three-dimensional solution. To determine the proportion of variance represented by each of the final three axes, we calculated the r^2 between distance in ordination space and distance in the original space. We added a joint plot with an r^2 cutoff set to 0.25 to show strength and direction of the relationship between soil nutrients and ordination scores.

Results

There was an abrupt transition in vegetation structure across the savanna–forest boundary. Although there was not a significant difference in total number of adult stems > 5 cm between forest and savanna (Fig. 2a, $F_{1,22} = 0.03$, $P = 0.87$), tree basal area in the forest was twice that in the savanna (Fig. 2b, $F_{1,22} = 35.4$, $P < 0.0001$). Correspondingly, average adult diameter was greater in forest than in savanna (Fig. 2c, $F_{1,21} > 22.5$, $P < 0.0001$), and tree LAI declined from 3.4 in forest to 1.8 in savanna (Fig. 2d, $F_{1,22} = 25.4$, $P < 0.0001$). These differences were associated with changes in soil nutrients across the savanna–forest boundary (supporting information, Fig. S2). Savanna sites had lower quantities of organic carbon, total N, K, Ca, Mg, Mn and Zn ($P < 0.008$), but higher levels of Cu ($P = 0.0002$) than forest sites.

There was a corresponding transition in species composition across the boundary. Among individuals with stem diameter > 5 cm, there was a nearly complete turnover of species between forest and savanna (0.11 ± 0.02; Jaccard similarity index). Of the savanna species found in the forest, the majority of individuals occurred within 10 m of the border; savanna species comprised only 0.9% of stems at distances of 20 m or more into the forest. One species, *Eriotheca pubescens*, accounted for more than half of the adults of savanna species in the forest. In contrast, while forest and intermediate species dominated forest environments, they each contributed about 10% and 4% of adult stems in savanna plots, respectively, and did not show a decline at distances greater than 10 m from the border (Fig. 2a).

At the border and in the savanna, forest and intermediate species also comprised a substantial fraction of individuals in juvenile size classes. Notably, this presence was dominated by a small group of forest (*Guapira areolata, Myrcia rostrata, Tapirira guianensis*) and intermediate (*Ocotea spixiana, Styrax camporum*) species, which accounted for the majority of stems of these species types in all three size classes (Fig. 3). These five species comprised more than half of the total number of forest and intermediate individuals in the savanna, despite relatively low densities in forest plots. In contrast, savanna species accounted for half of adults at the boundary but only 20% of saplings and 30% of seedlings. As a result of the patterns described above, there were marked differences in the size distributions of these three groups of species. For forest and intermediate species, the ratio of seedling and sapling density to adult density was higher in savanna than in forest and was higher overall than the ratio for savanna species (supporting information, Fig. S3).

Of the adults present in savanna, we estimate that 90% of stems of the savannas species have a bark thickness
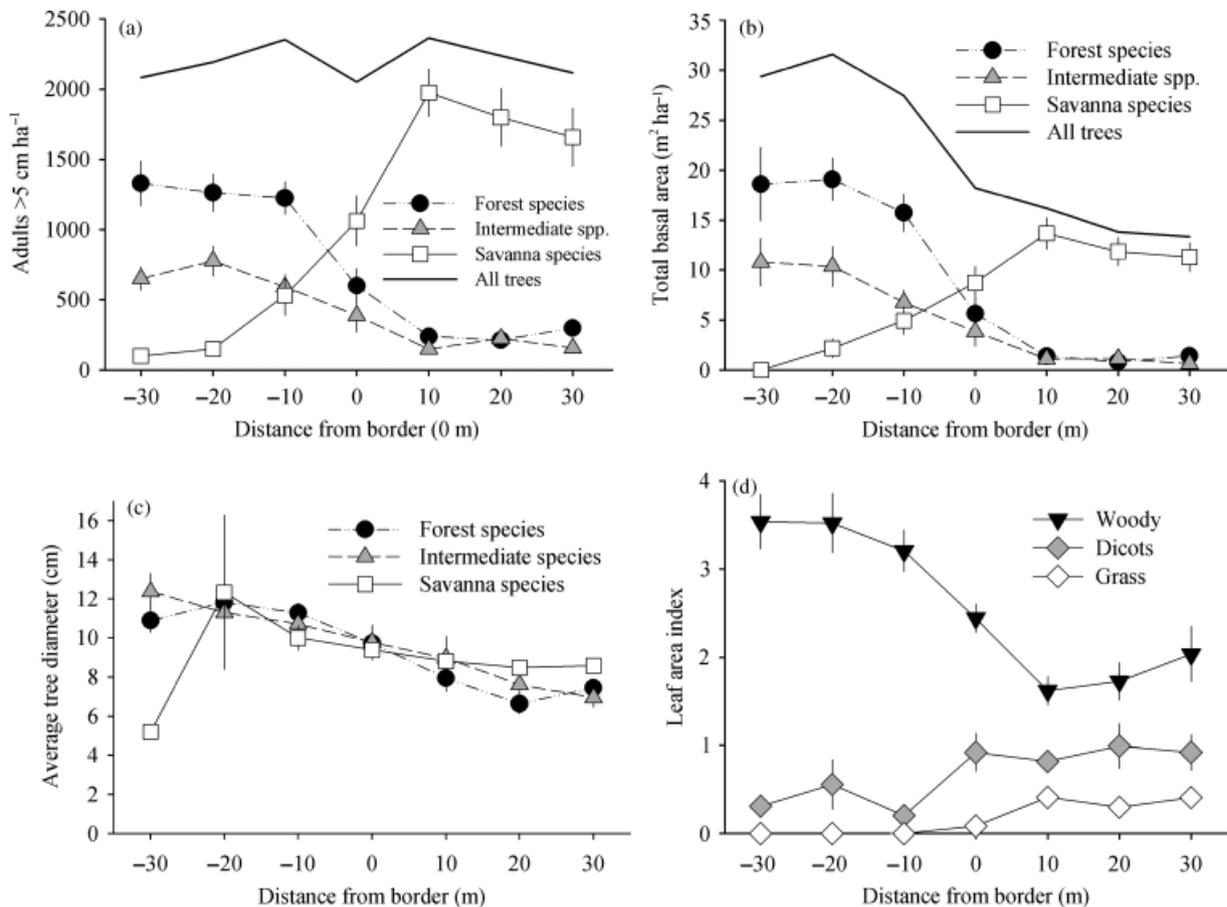
Fig. 2. Vegetation structure across a forest–savanna boundary in central Brazil (negative numbers indicate forest, positive numbers indicate savanna, and border areas occur around zero). Average (mean ± SE of 12 transects) adult tree density (a), total basal area (b), tree diameter (c) of forest, intermediate or savanna groups, and leaf area index (d) for woody plants, herbaceous dicots and grasses. In graphs a, b and c, mean values for savanna species at −20 m and −30 m are represented by very few individuals.

> 6.2 mm and therefore are not likely to be topkilled in the event of a fire. In contrast, only 42% of stems of intermediate species and 48% of stems of forest species had bark exceeding 6.2 mm, so the majority of stems of these species are vulnerable to topkill.

Non-metric multi-dimensional scaling (NMDS, Fig. 4) revealed a clear division between savanna and forest communities along axis 1; this axis was stable ($P < 0.0001$). As an increasing number of forest and intermediate species occupy the sapling and seedling communities in the savanna, the plots show a shift in ordination space in the direction of forest plots. The axes explained more than 50% of the overall variation and were associated with soil nutrients ($P < 0.03$, Fig. 4). Species scores from NMDS revealed many forest species were widespread across communities, while intermediate and savanna species showed more limited distributions (Fig. 4).

Discussion

After a period of 35 years with only one fire, what was once an open savanna with abundant grass cover and sparse trees has shifted drastically in tree density and composition. Basal area in the savanna averages 15 m^2 ha^{-1} and density averages 1800 trees ha^{-1}, exceeding values typical for one of the densest cerrado formations, cerrado *denso* (Andrade et al. 2002). While this basal area is more than half of the basal area found in the neighbouring forest (28 m^2 ha^{-1}), the two vegetation types have nearly the same density of trees (2000 trees ha^{-1}). In the absence of fire, tree density may continue to increase until the cerrado shifts from savanna to a type of woodland known as cerradão, which is characterized by the presence of taller trees, increases in forest and intermediate species and further declines in herbaceous cover (Veloso 1992). Estimates of canopy cover using the leaf
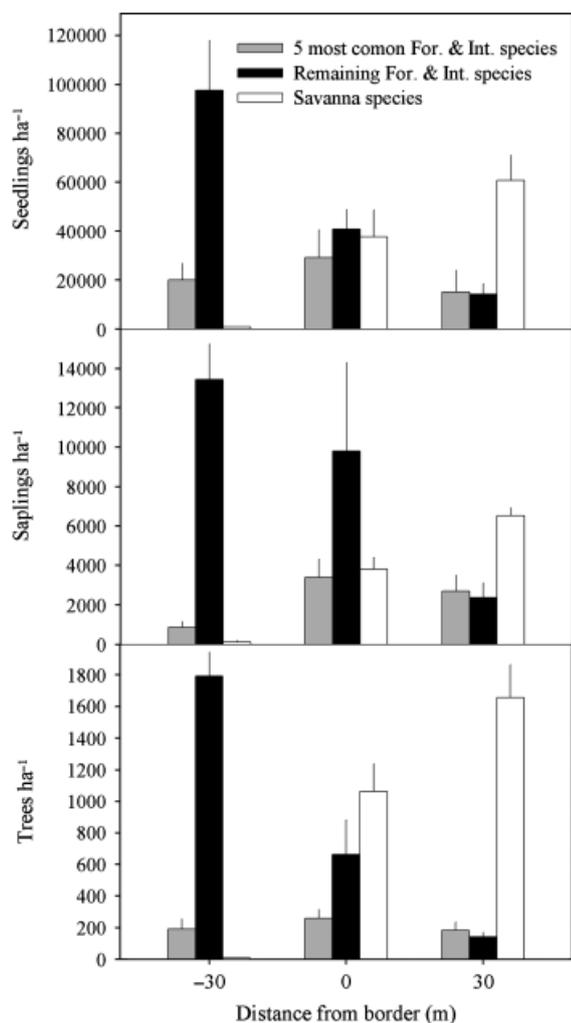
Fig. 3. Average (mean ± SE of 12 transects) number of seedlings, saplings and adult trees per hectare in the forest (− 30 m), at the border (0 m) and in the savanna (30 m). Bars represent abundance of the five most abundant forest and intermediate species, the remaining forest and intermediate trees, and savanna trees.

area index (LAI) indicate that the savanna plots at our study site have high woody and low grass LAI values, approaching values found in cerradão (Hoffmann et al. 2005). High woody plant cover or density is often associated with low grass production, particularly in savannas receiving > 800 mm yr^{-1} of precipitation (Mordelet & Menaut 1995), resulting in a more forest-like and less savanna-like structure (Scholes & Archer 1997; Hoffmann et al. 2005).

While savanna species still account for the majority of the total basal area in the savanna (Fig. 2b), forest species are playing an increasingly greater role in savanna structure (Figs 3 and 4, supporting information, Fig. S3). Forest and intermediate species together make up 14% of stems in the savanna despite the striking decreases in soil
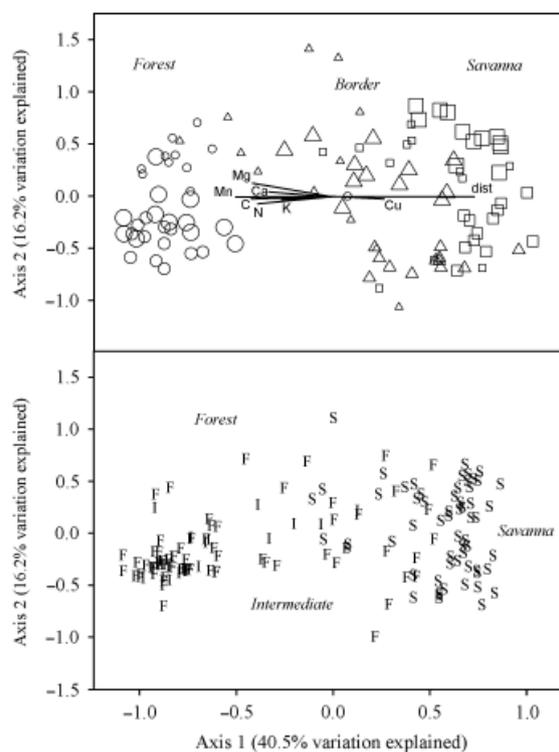

Fig. 4. Comparison of tree (> 5-cm diameter), sapling (> 1-m tall and < 5-cm diameter) and seedling (< 1-m tall) communities along the savanna–forest boundary in the Cerrado of central Brazil using non-metric multi-dimensional scaling (NMDS). Above, forest (circles), border (triangles) and savanna (squares) sites are shown for each size class that was used to describe their species composition: seedlings (small symbols), saplings (medium symbols) and trees (large symbols). A joint plot shows the influence of organic carbon (C), nitrogen (N), magnesium (Mg), manganese (Mn), calcium (Ca), potassium (K), copper (Cu) and distance from the forest–savanna boundary (dist). Below, scores for forest (F), intermediate (I) and savanna (S) species are shown.

nutrients across the forest–savanna boundary (supporting information, Fig. S2). The average tree diameter of forest trees in the savanna is 55% less than individuals of the same species growing in the forest (Fig. 2c). However, these differences are more likely the result of tree age than environmental limitations, as forest tree species grow faster when growing in the savanna than do co-occurring savanna species (Rossatto et al. 2009). Additionally, in the savanna, the ratio of juveniles to adults is high for forest and intermediate species, suggesting an actively increasing population. Forest and forest intermediates comprised more than one-third of juveniles in the savanna. Compositionally, the juvenile communities in savanna are becoming more forest-like (Fig. 3). The ratio of juveniles to adults of forest and savanna species indicates that with continued fire suppression, conversion of savanna to dense woodland and forest types is likely to occur. In the savanna there were 2.5-times more

seedlings and four-times more saplings per adult tree for forest/intermediate species than for cerrado species (supporting information, Fig. S3). Moreover, the ratio of juvenile to adult forest and intermediate species was greater in the savanna as compared to forest sites.

Despite initial increases in savanna tree density resulting from fire suppression in these systems (Pinheiro & Durigan 2009), savanna species appear likely to undergo future declines. The ratio of juveniles to adults is very low, especially in comparison with forest species. Savanna species are shade intolerant, as evidenced by their near absence in the forest and their lower ability to establish and survive in shaded conditions in comparison with forest species (Hoffmann 2000). Their extremely low abundance suggests that successful recruitment of savanna species is rare in the forest and that these do not represent self-sustaining populations. The adult trees can be relicts of a former savanna community (e.g. Banfai & Bowman 2007) and suggest that forest expansion has already occurred. The majority of savanna adults present in the forest were limited to the edge (< 10 m of the border; Fig. 2a) and tended to be large (Fig. 2c). Only one adult and very few juveniles (< 1%) were found more than 20 m into the forest. The only savanna species present in both the adult and juvenile size classes in this forest was *Qualea multiflora*, which though typical of savanna, is also commonly found in cerradão woodlands (Felfili 1997). Isotopic composition at a nearby savanna--forest boundary has shown that forest expansion into savannas in this area occurred as recently as 390 BP to 3100 BP (Silva et al. 2008), although this trend may be unique to gallery forests (Silva et al. 2010).

Not all forest species participate equally in expansion. This forest expansion seems to be driven primarily by a small group of forest and intermediate species (Fig. 3). Five species made up more than 50% of the individuals of forest and intermediate species types in the savanna, yet accounted for only 11% of adult stems in the forest. Interestingly, only one of these five savanna colonizers (*T. guianensis*) is characterized as a pioneer species (Lorenzi 1998), while the others do not exhibit traits considered typical of forest pioneers, such as thin leaves, extremely fast growth and low wood density. The same species have been found in other areas of cerrado (Teixeira & Rodrigues 2006) and are common in cerradão (Felfili & da Silva 1992; Felfili 1997), suggesting greater capability to cope with savanna conditions. The encroachment by forest species is evident over much of the IBGE reserve, not only in the immediate vicinity of the forest. While the general patterns documented here appear representative of much of the reserve, there is considerable variation in the amount of encroachment by forest species and in the species that have participated in this

encroachment. Elsewhere, other species such as *Miconia cuspidata*, *Vochysia tucanorum* and *Symplocos mosenii* have played a dominant role. These savanna colonizers may facilitate establishment of other forest species that may be less tolerant of open savanna conditions, as has been suggested for *Anogeissus leiocarpus*, a forest tree that dominates early stages of forest expansion in the Ivory Coast (Hennenberg et al. 2005). Indeed, some common forest species (e.g. *Copaiba langsdorfii* and *Matayba guianensis*) are absent as adults in the savanna but are now appearing in the seedling size class.

Forest species can have a transformative effect on savanna dynamics owing to the suite of traits they possess. Forest trees, in comparison with savanna species, have taller, larger and denser canopies and faster growth (Hoffmann et al. 2005; Rossatto et al. 2009). Therefore, when present, they can result in more rapid and complete canopy closure, further limiting juveniles of savanna species and favouring exclusion of grasses. In contrast, the slow growth and open crowns of savanna species appear much less effective at shading the understorey and excluding grasses. These environmental effects of forest trees (i.e. greater shade and suppression of grasses) likely facilitate the establishment of forest species that are otherwise poor colonizers of savanna.

Although the savanna plots are becoming more forest-like in structure and composition, this change has been slow. The site had burned only once in 35 years, yet the savanna still appears far from reaching a forest physiognomy. Such a low frequency of fire would probably have been very uncommon under traditional grazing management (Coutinho 1990) or indigenous occupation (Mistry et al. 2005), so historically it may be atypical for a cerrado savanna to attain this advanced stage of succession. Even so, the savanna is far from attaining a forest physiognomy that would be stable if fire were to return. In fact, if regular burning were now reintroduced into this site, few of the forest trees in the savanna would be of sufficient size to reliably escape topkill (i.e. death of the aerial stem), owing to their smaller size and lower bark thickness. Although the forest species invading savanna are able to resprout vigorously following topkill (Hoffmann et al. 2009), it does cause a substantial reduction in size, making them more susceptible to topkill in subsequent fires. Even if forest species are able to persist as suppressed individuals under frequent burning, their contribution to savanna structure would be negligible. This emphasizes the slow rate of forest succession in these savannas.

Conclusions

Changes in tree density and species composition are occurring at a forest–savanna boundary in a cerrado

region near Brasília, Brazil. After 35 years of active suppression, with only one fire, forest and intermediate species are expanding into neighbouring savanna, despite lower soil nutrient levels. Forest and intermediate tree species together contribute more than one-third of the juveniles in savanna plots, despite comprising a minority of adult stems. Moreover, the species composition of this sapling and seedling community differs from the adult forest and forest intermediate trees, which indicates that a small subset of forest and intermediate species have colonized the adjacent savanna. In contrast, there is little evidence of such broad shifts in species composition in the forest; savanna species are virtually absent from forest plots for all size classes. Increased density of forest species with their denser crowns may facilitate expansion of other forest species. Reintroduction of fire, however, would result in widespread topkill of juveniles and the majority of adult forest trees present in the savanna.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of species in plots at RECOR-IBGE in central Brazil. Names with '*' indicate forest species,

names with '^' indicate intermediate species, remaining names are savanna species.

Figure S1. Change in soil nutrients in 10×70 m transects across a forest–savanna boundary at RECOR-IBGE in central Brazil.

Figure S2. Ratio of number of seedlings (a) and saplings (b) to adult trees in the forest (-30 m), at the border (0 m) and in the savanna (30 m). Data for savanna species in the forest not shown because of the low sample size.

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