Word count: 5966

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Title: The role of edge contrast and forest structure in edge influence: vegetation and microclimate at edges in the Brazilian cerrado

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Abstract

The effect of the adjacent non-forested environment on the forest near the edge, edge influence (EI), is an important impact in fragmented landscapes and is believed to vary with factors such as forest structure and edge contrast. In order to improve our understanding of the factors governing the variability in EI, we studied microclimate and vegetation at *cerrado* edges surrounded by variable land uses in southeastern Brazil, a system with both forest and savanna fragments. We determined the significance, magnitude and distance of EI on microclimate, vegetation structure and grass biomass which we measured along five transects perpendicular to fourteen edges in forest or savanna next to different land uses. We introduce a quantitative measure of edge contrast that considers land uses at different distances from the same edge (e.g., a firebreak between a forest edge and a plantation) and verified whether edge contrast is correlated with EI in this system. Notwithstanding the large variation in EI among variables and study sites, there were some similarities in the patterns of EI between forest and savanna edges. Edge contrast was successfully quantified by our measure but was only correlated with EI on moisture and grass biomass. Our results point to the high variability in EI within a region. Our quantitative measure of edge contrast may be useful in explaining variability in EI. However, much unexplained variation remains in the highly fragmented *cerrado* system which is affected by EI in both forest and savanna fragments.

Keywords: Edge effects; exotic grasses; moisture; savanna; temperature; vegetation height.

Introduction

Edge influence (EI) has important impacts on habitat fragments, and its assessment is important for the conservation of fragmented ecosystems (Fahrig 2003; Harper et al. 2005). In general terms, EI may be understood as differences in structure, composition and/or function between the forest edge and the forest interior (Harper et al. 2005). Edge influence varies among ecosystems and forest types (Delgado et al. 2007) and also within the same ecosystem, mostly due to variability in adjacent land use (Wright et al. 2012; Cilliers et al. 2008), fragment size (Didham and Lawton 1999), edge orientation (Gehlhausen et al. 2000; Honnay et al. 2002), edge age (Chabrerie et al. 2013), and vegetation structure (Didham and Lawton 1999; Cadenasso and Pickett 2000).

An important edge characteristic is edge contrast, a measure of the difference in ecosystem structure, function or composition between the forest and the adjacent land use (Cadenasso et al. 2003). Higher edge contrast is usually associated with greater material and energy flow across the edge, resulting in greater EI (Ries et al. 2004, Harper et al. 2005), as observed in some studies (Reino et al. 2009, Noreika and Kotze 2012); however, this relationship is not universal (Delgado et al. 2007; Alignier and Deconchat 2011). Some studies (e.g. Noreika and Kotze 2012) quantify edge contrast with categories such as low, intermediate and high contrast, whereas other use a proxy variable such as management intensity (Chabrerie et al. 2013) or vegetation height and density (Reino et al. 2009). However, the existence of different land uses near the edge, e.g. a firebreak separating the forest from an agricultural field, is not always considered. We address this issue by proposing a form of quantifying edge contrast that considers different land uses at different distances from the edge.

Although EI has been studied extensively in forest vegetation (e.g. Didham and Lawton 1999; Delgado et al. 2007), less attention has been paid to grasslands and savannas which are very fragmented, threatened ecosystems with lots of edges (Riiters et al. 2012) (but see Morgan 1999; Pivello et al. 1991; Cilliers et al. 2008; Smit and Asner 2012). Savannas differ from forests in having an open woody layer and a ground layer occupied by shade-intolerant grasses (Gottsberger and Silberbauer-Gottsberger 2006; Ribeiro and Walter 2008). Sparse and dense forests may show similar patterns of EI (Wright et al. 2010), and an assessment of EI on different variables in forest and savanna areas located in the same region may help to understand regional variability in EI.

We studied EI on vegetation and microclimate in forest and savanna fragments in São Paulo state, South-Eastern Brazil, and related it to edge contrast. Multiple land uses adjacent to the fragments of natural vegetation and the existence of forest and savanna fragments that are part of the *cerrado* domain make it a good model to study the factors influencing EI variability. The high level of fragmentation also adds to the importance of understanding EI in this system (Klink and Machado 2005; Durigan et al. 2007). Our specific objectives were: (1) to determine EI on microclimate, vegetation structure and abundance of grasses at forest and savanna edges, (2) to introduce a new, quantitative measure of edge contrast which accounts for the existence of different land uses near the edge, and (3) to test whether higher contrast is associated with greater EI in forest fragments.

Methods

Study area

We studied *cerrado* fragments in São Paulo state, southeastern Brazil, between November 2009 and November 2010. The climate is seasonal with dry winters and wet summers. Average temperature in the study areas varied between 15 and 30°C during the sampling period, with annual precipitation between 1300 and 1600 mm (CIIAGRO 2011). We sampled four *cerrado* vegetation types: *campo cerrado*, *cerrado sensu stricto*, dense *cerrado* and *cerradão* (Coutinho 1978; Ribeiro and Walter 2008), commonly found on dystrophic aluminium-rich soils (Gottsberger and Silberbauer-Gottsberger 2006). *Campo cerrado* is an open savanna with arboreal cover of 5-20%, dominated by trees and shrubs 2-3 m high; *cerrado sensu stricto* is a savanna with arboreal cover of 20-50% and average tree height of 3-6 m; dense *cerrado* is a woodland with arboreal cover of 50-70% and a canopy 5-8 m high; and *cerradão* is a woodland or dry forest with a continuous canopy 8-15 m high (Gottsberger and Silberbauer-Gottsberger 2006; Ribeiro and Walter 2008). Hereafter, we refer to *campo cerrado* and cerrado *sensu stricto* as "savanna" and to dense *cerrado* and *cerradão* as "forest".

Sampling design

We sampled three savanna and eleven forest edges distributed among seven fragments adjacent to different land uses (Figure 1, Table 1). All edges had been maintained for at least 20 years. We are aware that the different number of forest and savanna edges makes comparisons more difficult; however, site selection was limited by the need to encompass a variety of land uses only found at the forest edges. We established five 180 m-long transects perpendicular to each edge with a random distance of 20 to 40 m between adjacent transects. Only the forest or savanna side of the edge was sampled to focus on the edge-related changes in the natural vegetation. Each edge site (set of five transects) was at least 300 m from all other edges. Along each transect we sampled 15 distances from the edge, at 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 120, 150, and 180 m. The edge at 0 m was located on an embankment that represented the edge creation line or, when no embankment was present, by an abrupt change in the vegetation. Edge F3 represented a common situation in the study region, namely *cerrado* vegetation regenerating after eucalypt plantation, but was sampled only up to 100 m because the *cerrado* beyond 100 m had smaller trees, indicating that it had been regenerating for less time.

Data collection and treatment

At each sampling point, we measured two microclimatic variables (air temperature and moisture), two structural variables (maximum tree height and canopy closure), and graminoid biomass (total, exotic and native). We measured air temperature and moisture once at 1.3 m directly above each sampling point, on clear or slightly overcast days, with an Instrutherm's THAL 300 hygro-thermo-anemometer. The thermometer was not protected from wind or direct solar radiation but this did not seem to affect the measurement values except at one savanna edge where it led to measurement errors by overheating the instrument. To differentiate between temporal variation and edge influence, at each edge we walked three transects from edge to interior and two transects from interior to edge. Microclimate measurements started between 10:15 and 11:30 a.m., and sampling the five transects took between 90 and 180 minutes. We registered the time of each measurement and detrended the values with the equation $d = o - e + \bar{o}$, where d is the detrended value, o is the observed value, $\bar{o}$ is the average of all values measured along the five transects at the given site, and e is the value predicted by ordinary least sum of squares regression between the measured values and time in the software Past 2.03 (Hammer et al. 2001).

We used a 15 m expandable measurement pole to measure maximum tree height up to the highest leaf or branch within one meter of each sampling point. When the trees were taller than the length of the pole (eight sampling points in three sites), we estimated the remaining height; the greatest height estimated in this way was 16.5 m. To measure canopy closure, which was used as a proxy for light availability, we took hemispheric photographs with a Nikon FC-E8 fisheye converter attached to a Nikon Coolpix 5000 digital camera, placed on a tripod 1.3 m above ground and leveled. Canopy openness (%) was then measured in the software Gap Light Analyzer (Frazer et al. 1999) and transformed into canopy closure by subtracting from 100%.

We collected aerial parts of all graminoids (Poaceae, Cyperaceae and Commelinaceae) in one 0.5 x 0.5 m plot placed haphazardly up to 0.5 m from each sampling point. The graminoids were then separated into native species and the three most common exotic species: *Urochloa decubmens* (Stapf) R. D. Webster, *Melinis minutiflora* P. Beauv. and *Panicum maximum* Jacq. Afterwards, all graminoids were kiln-dried at 70^{o}C for 72 h and weighed.

Data analysis

Analysis of EI

We compared fragments with different edge contrasts by analyzing variation in the significance (SEI), magnitude (MEI), and distance (DEI) of EI (Harper et al. 2005). We define SEI as the presence/absence of statistically significant EI, MEI as the difference between edge and interior for a given variable, and DEI as the distance into the forest for which this difference is statistically significant (Harper et al. 2005). We calculated these parameters separately for each edge (study site with five transects) for the following variables: air temperature, moisture, maximum tree height, canopy closure and graminoid biomass (all graminoids, exotic graminoids, native graminoids, *U. decumbens* and *M. minutiflora*). We used the data collected at 120, 150 and 180 m as interior reference values in the analyses because EI on microclimate or vegetation is not likely to extend beyond 100 m in shorter forests (Harper et al. 2005). At the site F2, we used 80 and 100 m as the reference.

At each site, MEI was calculated as $(\overline{e}-\overline{i})/(\overline{e}+\overline{i})$, where $\overline{e}$ is the mean of the five values at a given distance from the edge and $\overline{i}$ is the mean of the interior reference values at the given site (Harper et al. 2005). This measure restricts MEI for all variables to between -1 and +1. For temperature, which has no true zero value (absolute zero is not ecologically meaningful), we calculated MEI as the difference, in ^{o}C, between edge and interior divided by the range of temperatures observed in this study (i.e. max. - min. observed temperatures = 16.8^{o}C). This permitted a comparison among the edges but did not affect the results of the DEI estimates; however, the MEI values for temperature are not directly comparable to the other variables.

We estimated DEI for each variable at each site by means of a randomization procedure, Randomization Test for assessing Edge Influence (RTEI, Harper and

Macdonald 2011), with a routine in R 2.12 (R Development Core Team 2012; code in Online Resource S1). Using this analysis we: 1) calculated MEI using the values at a given distance from the edge, e.g. 0 m, and the reference values; 2) created a pooled dataset with the edge values and the reference values; 3) randomly assigned five of these as edge values and the remaining as reference values; 4) recalculated MEI for the randomized values and repeated steps 2-4. The MEI values obtained from 10 000 iterations were then used to calculate the significance of the observed MEI. The analyses were conducted separately for each distance from the edge for each variable. Thus, for each site-variable combination, this test provided the significance of the difference (measured as MEI) between each distance from edge and the reference values.

We accounted for multiple testing during the interpretation of the RTEI results by looking for consistent patterns. A significant difference far from the edge that was not preceded by other significant values was ignored unless it was in the first 10 m from the edge. Thus, SEI was considered significant if at least one of the distances between 0 and 10 m was significant, and DEI was estimated as the farthest distance from the edge that was preceded by no more than one non-significant consequent value.

Correlations between edge influence and characteristics of the edge

Because of differences in the patterns of EI between savanna and forest edges, we used only the latter ones to verify whether SEI, MEI and DEI were related to edge exposure, edge height, matrix height, and edge contrast. When SEI was not significant, we used MEI at 0 m and gave a value of 0 for DEI. Otherwise we used the most extreme MEI, which could be located at any distance within the DEI estimate. We used logistic regressions for SEI and linear correlations for MEI and DEI, and assessed their significance by permutation tests with 5000 randomizations.

Edge exposure, or the size of the opening adjacent to the edge (Olofsson and Blennow 2005), was defined as the distance to the nearest vegetation as tall or taller than the cerrado vegetation (e.g., eucalypt plantation, another cerrado area), up to a maximum value of 50 m to avoid the influence of very large values. For edge height, we used the average maximum vegetation height at the sampling points between 0 and 20 m on the forest side of the edge. For matrix height, we used the maximum height between 0 and 40 m on the non-forested side of the edge, considering the following estimates for the different elements of the matrix: 0 m for firebreaks, roads and highways, 0.3 – 2 m for grass (Table 1), 1 m for abandoned pasture, 10 m for bamboo patches, and 13 m (edge S3) or 20 m (edges F10 and F11) for eucalypt plantations.

Measurement of edge contrast

We used a weighted measure of edge contrast that considers the contrast between the forest and different land uses close to the edge (Figure 2a), based on two assumptions: 1) land uses closer to the edge have greater impact on EI and 2) land uses far from the edge also affect EI, though their effect is smaller. This is represented by a weighting function which monotonically decreases to satisfy assumption 1 and reaches an asymptote to satisfy assumption 2. We used two weighting functions, the right-hand side of a normal curve and the negative exponential curve, scaled so that their value at 0 m is equal to 1, generated by the functions *dnorm* and *dexp* in R 2.12. Both may be described by a single parameter, σ (Figure 2c), which is equal to the standard deviation of the normal curve or to (1/rate) of the negative exponential curve. This parameter represents the distance at which the weighting function is roughly equal to 2/3 and 1/3 of its maximum value for the normal and exponential curves, respectively. Edge contrast was then calculated as follows (code in Online Resource S2):

1) a function *f(x)* was created to define edge contrast at each distance, such as $f(x) = C_1$ for $0<x<d_1$, C_2 for $d_1<x<d_2$, etc, where x is the distance into the matrix (Figure 2b);

2) it was multiplied by the weighting function *w(x)* (Figure 2c) to obtain the weighted contrast function *g(x)* (Figure 2d);

4) *g(x)* was integrated from 0 to the distance d_{max} and divided by the same integral of *w(x)* to obtain the weighted edge contrast (WEC) value. The distance d_{max} is the furthest distance into the land use which is considered as having an ecologically meaningful effect on EI. We used Monte-Carlo integration, which approximates the area beneath a curve by generating a large number of random numbers (10^5 in our case), calculating the average value of *g(x)* for these values, and multiplying by d_{max} (James 1980).

For the normal and exponential weighting functions, we calculated WEC for three values of σ (5, 15 and 30 m) and three of d_{max} (10, 20 and 40 m) (Table 2). Small values of these parameters put greater emphasis on the land uses closest to the edge, and the use of different values may aid in determing what land uses are most critical in determing EI. We also used a relative measure of edge contrast (WECrel), calculated as edge contrast divided by edge height.

We calculated the average correlation between the 39 explanatory variables and used Bonferroni correction with an adjustment for correlation to adjust the 0.05 significance level (Uitenbroek 1997) for the tests performed for each response variable.

We did not further adjust the tests for the number of response variables in order not to increase the possibility of type 2 error.

Results

There was much variation in both MEI and DEI among and within variables (Figure 3, Online Resource S3). MEI varied the most for grass biomass, whereas DEI was most variable for microclimate but showed intermediate variation for vegetation height and canopy closure in forest and for grass biomass in savannas (Figure 3). Edge influence on microclimate was significant both for forest and savanna areas, but significant EI on vegetation structure was found mostly in forest areas. Although there were few noticeable differences in EI on microclimate between forest and savanna sites, differences in EI on vegetation structure between the two ecosystem types were more apparent including greater DEI for grass biomass in savannas and for vegetation height in forest.

Edge influence on microclimate was significant at eight forest edges and one savanna edge. Mean temperature was significantly higher in the first 5-60 m at one savanna edge and three forest edges and lower in the first 10-80 m of two forest edges (Table 3). Moisture was lower in the first 2-50 m at one savanna edge and six forest edges and higher in the first 40 m at one forest edge.

Edge influence on maximum vegetation height was observed at six forest edges and one savanna edge (Figure 3). Lower vegetation was observed in the first 2-10 m at two forest edges and one savanna edge. At one forest edge maximum vegetation height was greater than in the interior (DEI of 20 m), and at three other forest edges we observed a non-monotonic pattern, with maximum tree height increasing in the first 5 to 10 m and then decreasing, returning to the reference values 15 - 20 m from the edge (Figure 4). Magnitude of EI varied from 0.19 to 0.21 at edges with positive and non-monotonic EI and -0.37 to -0.10 at edges with negative EI (Online Resource S3).

Significant EI on canopy closure was observed at nine forest and one savanna edges, with MEI between -0.16 and 0.09. We observed negative EI at eight forest edges, (DEI = 15 m at one edge and up to 2 m at the other edges) and at one savanna edge (DEI = 0 m), and positive EI at one forest edge (DEI = 100 m). Significant EI on graminoids was observed at five forest and three savanna edges. We observed increased total graminoid biomass in the first 0 to 5 m at three forest edges and lower biomass in the first 5 m at one forest edge (Table 2), but no significant EI on total graminoid biomass at the other edges. At the forest edges, exotic species were found only at the immediate edge except for three plots between 2 and 10 m at two edges, with significant EI at only two edges. At the savanna sites, exotic grasses were found throughout and were significantly more abundant in the first 5 to 20 m from the edge. The biomass of the exotic species *U. decumbens* was above reference values up to 15 m from edge at the savanna sites, and it was also found at 0 m at three forest edges (Figure 5). *M. minutiflora* was found at two savanna edges without significant EI, and at 0 m at two forest edges. *P. maximum* was found only at two forest-highway edges. Native graminoids were found throughout all sites, with positive EI at one forest edge (DEI = 0 m) and negative EI at one forest and two savanna edges (DEI of 5 to 10 m).

Edge contrast explained little of the variability in measures of EI. The average correlation between the explanatory variables was 0.80, resulting in a Bonferroni-adjusted significance level of 0.0237. Of the 829 tests performed, only 22 were significant at the 0.05 level and only 5 at the adjusted significance level (Table 4, Online Resource S3). The correlations significant at the 0.05 level indicate a possible effect of edge contrast on EI patterns observed for grass biomass (total and native) and air moisture; four of the latter relationships were also significant at the adjusted significance level. In addition, greater matrix height resulted in a greater MEI on canopy closure,. The results obtained for both weighting functions were similar. Smaller values of σ and d_{max} seemed to give more significant results for moisture and total grass biomass, whereas larger values gave more significant results for the biomass of native grasses.

Discussion

Patterns of EI in forest and savanna

There were some similarities in the patterns of EI between forest and savanna areas. For example, the DEI of 15 to 60 m observed for microclimate is similar to that observed in other studies (Davies-Colley et al. 2000, Wright et al. 2010) and supports the notion that both forest and savanna fragments may have their microclimate affected by edges. Increased light availability may explain the altered microclimate at our forest edges. However, DEI for canopy closure, a proxy for light incidence, was much smaller than for temperature, possibly due to edge sealing (Strayer et al. 2003). Not all changes in canopy closure were accompanied by EI on microclimate, and the greater canopy closure at one edge did not lead to lower temperatures. Therefore, light availability may not be the only factor affecting microclimate at forest and savanna edges. For example, the movement of warmer, drier air from the matrix towards the vegetation fragment may also play an important role. The unexpected decreases in temperature at two of our edges may have resulted from the movement of cooler air from increased wind at edges (Laurance and Curran 2008, Wright et al. 2010).

Vegetation structure and composition was also affected by edges, although the patterns observed for forest and savanna areas were more different. Whereas EI on vegetation height was more conspicuous in forest areas, savanna fragments had more apparent patterns of EI on grass biomass. Our forest edges showed a reasonably consistent pattern of increased maximum vegetation height near the edge, contrary to what has been observed in other studies (Didham and Lawton 1999; Delgado et al.2007; Lima-Ribeiro 2008). Trees at our study edges may have been favored by reduced competition for light (Bowering et al. 2006) and especially water, resulting in increased growth. The non-monotonic pattern observed at several edges may have resulted from the additional action of stressful agents, e.g. windthrow (Laurance and Curran 2008), leading to reduced height at the immediate edge (0 m). A similar non-monotonic pattern has been observed elsewhere for tree basal area (Wright et al. 2010), indicating that EI may be more complex than the commonly assumed two-zone pattern of a gradual and monotonic change from the edge towards the more homogeneous interior forest (see also Alignier and Deconchat 2011).

Changes in the biomass of native and exotic species were also common. As has been observed elsewhere (Gehlhausen et al. 2000; Avon et al. 2010), exotic grasses were restricted to the immediate edges of our forest areas, probably due to increased light only at the immediate edge. In our savanna areas, however, exotic grasses were found throughout the transects and were most abundant in the first 20 m from the edge, with a concomitant decrease in native graminoids. As we had only three savanna edges, these results must be interpreted with care. Still, they suggest that edge-mediated invasions, common in savannas and grasslands (Morgan 1998; Pivello et al. 1999; Cilliers et al. 2008), may be a primary process that is a direct result of edge creation (Harper et al. 2005). The removal of native vegetation during edge creation may open up space and facilitate the arrival and establishment of exotic grasses, which then spread gradually into the fragment regardless of changes in microclimate or vegetation structure. The invasion of exotic grasses at edges affects native herbaceous and woody species (Pivello et al. 1999; Hoffmann and Haridasan 2008).

Relationship with edge contrast

Our measure of edge contrast explained little of the variability in EI at the forest edges, as only moisture and grass biomass presented some relationship with edge contrast. It is possible that other measures of contrast, such as canopy cover or species composition, would give different results. However, canopy cover is not always appropriate since a short dense canopy would still allow a lot of light and wind to penetrate the forest at the edge, and composition such as the abundance of exotic species would be relevant only for specific variables. In addition, the difference in species composition would be not be a good measure when assessing edges adjacent to highly modified land uses such as agriculture or highways. The difference in vegetation height can be easily measured for a wide range of land uses with very different characteristics and can also be modified to include temporal variation in land uses. The variation in edge contrast at different distances through time could be multiplied by a two-dimensional weighting function with spatial and temporal dimensions and integrated to provide a weighted measure of edge contrast.

The small number of significant results may be related to a somehow restricted range of edge contrast in this study. For example, almost all edges were adjacent to a firebreak, which probably played a large role in determining EI patterns. The variability in factors such as edge orientation and age also plays an important role, as well as regional heterogeneity in vegetation structure and composition. Vegetation structure in the *cerrado* is structurally complex at multiple scales (Gonçalves and Batalha 2011). Therefore, a larger sample size and a wider range of values of edge contrast may be needed to detect clearer effects on EI. The pattern of more intense EI on moisture at lower-contrast edges was unexpected, probably reflecting the more negative MEI on moisture at the firebreak (low-contrast) edges than at the high-contrast plantation edges. As linear openings often result in EI on microclimate and vegetation (Bowering et al. 2006; Avon et al. 2010), the existence of EI at firebreak edges was not unexpected; it is possible that increases in temperature at some higher-contrast edges were buffered by wind from the adjacent land use (Wright et al. 2010).

Apart from microclimatic variables, only SEI and MEI for total and native grasses were related to edge contrast. Both relationships appear to indicate that higher-contrast edges exert a stronger edge influence on native grasses and, as shown by the σ and d_{max} parameters used in the weighting functions, that this effect is governed by all the different land uses close to the edge, and not only the immediate edge. Given the large number of tests performed, the significant results must be considered carefully, as they may have arisen by chance alone; still, there are indications that edge contrast may explain some variation in EI, which has some practical implications. For example, edge-mediated invasions by exotic grasses seem to be favored by high-contrast edges such as highways, and this may be addressed in conservation and management projects.

Conclusions and implications

In this study, we showed that both forest and savanna areas may be subject to edge influence on microclimate and vegetation. For management purposes, we recommend to consider at least 60 m for microclimate and at least 20 m for vegetation structure in the *cerrado* and similar vegetation types when an estimation of DEI is needed. It is also important to keep in mind the possibilities of cascading EI (Ries et al. 2004); for example, microclimatic changes may alter the distribution of insects and consequently plant-insect interactions (Meyer and Sisk 2001), whereas grass biomass is related to fire dynamics (Hoffmann et al. 2012). The use of different parameters in the weighted contrast measure may provide clues as to the range of contrasts that have to be considered. Our results show that both the immediate and the overall contrasts can influence EI. Studies on how these contrasts may be managed to minimize EI on different variables could be important for the conservation of fragmented ecosystems. Insightful results may be obtained by using other variables in addition to vegetation height to measure edge contrast and by increasing the number of sites with similar vegetation structure, i.e. forest or savanna.

Acknowledgments

We thank R. Xavier, E. Recco, C. Zanelli, A. Viscardi, F. Oliveira and others for extensive help with the fieldwork; A. Viscardi for aid in analyzing canopy closure; M. Batalha, A. Peret, M. Bichuette, M. Melo, V. Pivello, A. Braga, I. Paneczko, F. Tiberio, as well as the editor and two anonymous reviewers for valuable comments on previous versions of this manuscript; C. Zanelli for the drawing in Figure 2; the Forestry Institute of São Paulo State, the Municipal Botanical Garden of Bauru and to the owner of Farm América for permissions and logistic support; and FAPESP – São Paulo State Research Foundation for financial support provided to PD (MSc grant 2008/07772-0).

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Table 1. Characteristics of the study sites including location, vegetation type, land use near the edge and edge characteristics. Sites are listed in order of increasing contrast within the savanna and forest categories.

Site	Latitude, longitude	Vegetation in the fragment	Land use(s) in the first 40 m[a]	Edge age [a] (yr)	Orientation (°)	Altitude (m asl)
Savanna						
S1	22° 49.79' S, 49° 11.88' W	cerrado *sensu stricto* native pasture before 1984	1 m-tall grass-dominated firebreak (10 m), pasture	26	15	630
S2	21° 58.62' S, 47° 52.79' W	*cerrado sensu stricto* *Eucalyptus* before ~1978	road (10 m), buildings; before 2007: firebreak (8 m), eucalyptus	~32	20	870
S3	22° 12.76' S, 47° 55.59' W	*campo cerrado* native pasture before 1984	firebreak (14 m), eucalyptus	>20	55	770
Forest						
F1	21° 35.61' S, 47° 46.42' W	dense cerrado	firebreak (5 m), dense cerrado	~20	355	580
F2	22° 36.18' S, 50° 22.55 W	*cerradão*	firebreak (7 m), cerradão	30	310	570
F3	22° 36.63' S 50° 22.57' W	*cerradão* *Eucalyptus* before 1996	firebreak (5 m), 1 m tall Brachiaria grass (5-23 m), bamboo (23-35 m), highway	> 50	310	570

F4	22° 20.20’ S, 49° 00.38’ W	*cerradão*	firebreak (3 m), pasture	~30	35	560
F5	21° 55.87’ S, 47° 49.22’ W	*cerradão*	firebreak (6 m), pasture	>100	40	740
F6	21° 55.57’ S, 47° 49.38’ W	*cerradão*	firebreak (5 m), 2 m tall Guinea grass (5-21 m), highway (21-31 m), cerradão	> 70	110	740
F7	21° 38.38’ S, 47° 36.83’ W	*cerradão*	2 m tall Guinea grass (5 m), 0.3 m tall grass (5-23 m), highway	~80	260	680
F8	21ò 33.32’ S, 47° 44.80’ W	*cerradão*	firebreak (6 m), sugarcane	>30	330	615
F9	21° 33.18’ S, 47° 49.20’ W	*cerradão*	firebreak (7 m), sugarcane	>30	90	640
F10	21° 37.68’ S, 47° 38.75’ W	dense *cerrado*	firebreak (10 m), eucalyptus	> 21	125	670
F11	21° 38.11’ S, 47° 39.04’ W	dense *cerrado*	firebreak (10 m), eucalyptus	> 21	125	650

[a] Information on past land uses and edge age was obtained from landowners, managers and employees of the study areas (A. C. G. Melo, L. C. A. Neto, P. H. P. Ruffino, A. Fiorucci, A. Malagutti, M. I. S. Lima, R. M. Silva).

Table 2. Edge and matrix characteristics of the study areas including different measures of edge contrast. Edge height is the average height between 0 and 20 m from the edge on the forest side. Exposure is the distance to the nearest cerrado or tall plantation up to 50 m or classified as >50 m. Matrix height is the maximum matrix height in the first 40 m from the edge. Estimates of edge contrast were obtained with weighting functions of different shape (normal = right side of the normal function, or negative exponential), and with different values of σ, and truncation distances ($d = d_{max}$, in m), showing how the effect of different parameters.

Site	Edge height (m)	Exposure (m)	Matrix height (m)	Edge contrast							
				Shape = normal				Shape = exponential			
				$\sigma = 5$		$\sigma = 30$		$\sigma = 5$		$\sigma = 30$	
				$d = 10$	$d = 40$	$d = 10$	$d = 40$	$d = 10$	$d = 40$	$d = 10$	$d = 40$
S1	3.5	>50	1	3.0	3.0	3.0	2.7	3.0	2.9	3.0	2.7
S2	2.2	>50	-2[a]	4.2	4.2	4.2	4.2	4.2	4.2	4.2	4.2
S3	2.0	7	13	1.8	1.9	1.6	6.9	1.8	2.4	1.7	6.3
F1	9.2	5	9.2	6.6	6.3	4.7	1.5	6.7	5.8	5.0	1.9
F2	7.5	7	7.5	6.6	6.3	5.3	1.7	6.6	5.7	5.5	2.1
F3	8.9	23	10.0	8.6	8.6	8.4	6.5	8.6	8.5	8.4	6.8
F4	9.0	>50	1.0	8.4	8.4	8.3	8.1	8.5	8.4	8.3	8.1

F5	9.1	>50	0.5	9.0	9.0	8.9	8.7	9.0	9.0	8.9	8.7
F6	10.3	31	10.3	9.7	9.7	9.3	7.8	9.7	9.6	9.4	8.0
F7	9.7	>50	2.0	8.2	8.2	8.5	9.2	8.1	8.3	8.4	9.1
F8	10.6	>50	2.0	10.2	10.1	9.8	9.0	10.2	10.0	9.8	9.1
F9	10.7	>50	2.0	10.5	10.4	10.1	9.2	10.4	10.2	10.2	9.3
F10	9.4	10	20.0	9.4	9.4	9.4	10.2	9.4	9.5	9.4	10.1
F11	8.7	10	20.0	8.7	8.8	8.7	10.5	8.7	9.1	8.7	10.3

[a]This fragment was located at an elevation of 2 m above the surrounding area.

Table 3. Edge and interior mean values (± SD) and distance of edge influence (DEI) on temperature and moisture at the 3 savanna (S) and 11 forest (F) edges. All patterns were monotonic.

Site	Temperature			Moisture		
	Edge (^{o}C)	Interior (^{o}C)	DEI (m)	Edge (%)	Interior (%)	DEI (m)
S1	40.1 ± 2.2	36.4 ± 0.9	60	33.7 ± 3.4	41.8 ± 3.0	50
S2	N/A	N/A	N/A	14.2 ± 3.6	53.8 ± 2.0	ns
S3	34.2 ± 1.7	33.1 ± 2.3	ns	30.6 ± 3.7	29.6 ± 1.6	ns
F1	31.1 ± 0.9	30.1 ± 0.7	ns	47.4 ± 4.3	55.4 ± 3.9	15
F2	38.4 ± 2.4	34.0 ± 1.4	15	51.5 ± 3.3	63.3 ± 4.2	15
F3	29.7 ± 0.8	31.4 ± 1.5	10	57.6 ± 2.9	58.9 ± 3.6	ns
F4	33.7 ± 2.1	31.1 ± 0.6	60	44.6 ± 1.9	53.2 ± 4.2	30
F5	31.2 ± 1.1	29.5 ± 0.6	40	61.3 ± 4.4	71.7 ± 3.9	30
F6	31.7 ± 0.8	31.7 ± 0.5	ns	63.1 ± 2.7	69.8 ± 6.1	2
F7	36.0 ± 2.2	35.2 ± 0.8	ns	43.2 ± 5.3	45.8 ± 2.4	ns
F8	30.2 ± 0.7	32.2 ± 0.7	80	52.0 ± 2.9	45.8 ± 4.4	40

F9	30.2 ± 0.7	29.9 ± 0.8	ns	52.0 ± 3.4	51.0 ± 3.3	ns
F10	35.3 ± 2.4	33.5 ± 1.2	ns	49.8 ± 7.0	61.3 ± 4.2	10
F11	34.9 ± 1.8	36.3 ± 1.4	ns	56.9 ± 4.0	44.9 ± 2.8	ns

N/A: not available, because of measurement errors at this site.

ns: no significant EI observed at this site.

Table 4. Relationships for significance (SEI) and magnitude (MEI) of edge influence with edge and matrix characteristics. All characteristics were considered including weighting functions with different shapes and different values of the $\boldsymbol{\sigma}$ and d_{max} parameters. Only the relationships significant at the unadjusted 0.05 level are shown; *p* values significant at the adjusted significance of 0.0237 are in bold. Only 22 of 829 tests were significant.

Response	Edge or matrix characteristic	Shape	σ	d_{max}	*p* value	Effect of edge contrast
MEI for canopy closure	Matrix height	N/A	N/A	N/A	**0.0182**	+ve
MEI for native grasses	Weighted edge contrast	Normal	30	40	0.0454	-ve
		Exponential	30	40	0.0496	-ve
	Relative weighted edge contrast	Normal	30	40	0.0366	-ve
		Exponential	30	40	0.0394	-ve
SEI for total grasses	Weighted edge contrast	Normal	5	10	0.0316	+ve
				20	0.042	+ve
				40	0.0388	+ve
		Exponential	5	10	0.0256	+ve

				20	0.0438	+ve
			15	10	0.047	+ve
			30	10	0.0464	+ve
MEI for moisture	Weighted edge contrast	Normal	5	10	**0.0186**	+ve
				20	**0.022**	+ve
				40	**0.0222**	+ve
			15	10	0.0458	+ve
			30	10	0.0422	+ve
		Exponential	5	10	**0.0176**	+ve
				20	0.0318	+ve
				40	0.0344	+ve
			15	10	0.0346	+ve
			30	10	0.044	+ve

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Figure 1. Maps showing the locations of São Paulo state (a), fragments used in this study (b) and the study sites: F1, F8 and F9 in the Jataí Ecological Station (c), F7, F10 and F11 in Vassununga State Park (d), F5 and F6 at the Brazilian Agricultural Research Corporation (e), S2 at the Federal University of São Carlos (f), S3 at the Itirapina Ecological Station (g), F4 at the Bauru Municipal Botanical Garden (h), S1 at the Santa Bárbara Ecological Station (i) and F2 and F3 at the Assis Ecological Station (j). Refer to Table 1 for coordinates and other information.

Figure 2. Example of edge contrast calculation with an edge schematic (a), the contrast at each distance from the edge (b); the weighting function for three SD values (c) and the weighted edge contrast resulting from each of the weighting functions (d). The example is of the dense cerrado – highway edge (F3) bordered by a firebreak, a grass area, a bamboo strip and a highway. In (c) and (d), the lines are for three different values of σ: 5 (solid line), 15 (long dashes), 30 (short dashes). The resulting contrast value (WEC) is equal to the area below the curve in (d) divided by the area below the weighting function in (c).

Figure 3. Variation in magnitude (a) and distance (b) of edge influence among the study sites for microclimate, canopy structure and grass biomass. Results for the two exotic grass species are not presented because they were common only in the three savanna edges. Circles represent forest edges and triangles represent savanna edges; filled

symbols indicate significant EI. Within each variable, edges are organized in order of increasing contrast (left to right), with savanna edges after forest edges. Note that MEI for temperature was calculated simply as the difference, in ^{o}C, between edge and interior and divided by the temperature range observed (see methods). The dotted line represents MEI equal to 0.

Figure 4. Patterns of maximum vegetation height (mean ± SD) with distance from edge for: (a) F1, (b) F2, (c) F5, (d) F6, (e) F7, (f) F8, (g) F11. Patterns represent significant negative (b,e), positive (d) and non-monotonic (a,c,g) edge influence, as well as a non-significant pattern which resembles the non-monotonic one (f). Black circles: values significantly different from interior reference values EI ($p < 0.05$), gray circles: marginally significant ($0.05 < p < 0.10$), white circles: non-significant ($p > 0.10$).

Figure 5. Biomass of all graminoids (a), of the exotic species *Urochloa decumbens* (b) and *Melinis minutiflora* (c), and of native graminoids (d) along the transects at the three savanna sites: S1 (circles), S2 (triangles), and S3 (squares). Filled symbols represent distances that were significantly different from interior reference values ($p < 0.05$).