Edge influence on plant litter biomass in forest and savanna in the Brazilian *cerrado*

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Abstract Edge influence, characterized by differences in ecosystem characteristics between the edge and the interior of remnants in fragmented landscapes, affects a variety of organisms and ecosystem processes. An important feature that may be affected by edges is the amount of plant litter, which provides important habitat for a large variety of organisms and influences ecological processes such as fire dynamics. We studied edge influence on plant litter and fine woody debris in the *cerrado* of São Paulo state, south-eastern Brazil. We collected, sorted, dried and weighed plant litter along 180 m-long transects perpendicular to three savanna and eleven forest edges adjacent to different anthropogenic land uses, with four to five transect per edge. There tended to be less biomass of the finer portions of fine woody debris at both savanna and forest edges. Graminoid litter at savanna edges was greater than in the corresponding interior areas, whereas other litter portions were either unaffected by edges or did not show consistent patterns in either savanna or forest. Edge influence was usually restricted to the first 20 m from the edge, was not influenced by edge characteristics and exhibited no clear differences between savanna and forest areas. Several mechanisms may have led to the variable patterns observed including variation in the plant community, plant architecture, and invasive species. The edge-related variation in plant litter may putatively lead to, for example, increased fire frequency and intensity at the savanna edges and altered trophic dynamics at forest edges; the mechanisms and consequences of this edge influence should be addressed in future studies.

Key words: *cerrado*, edge effects, edge influence, fine woody debris, grasses.

INTRODUCTION

Edge influence has a major impact in fragmented landscapes, where a once continuous native ecosystem is replaced by a mosaic of habitat patches of different sizes surrounded by an anthropogenic matrix (Fahrig 2003). Edge influence comprises modifications that occur at the edge of vegetation fragments as a result of the influence of the adjacent matrix and may result in profound modifications to the structure, composition and functioning of an ecosystem close to the edge when compared to the interior (Harper *et al.* 2005). In addition to the commonly observed changes in microclimate at the forest edge (e.g. Didham & Lawton 1999; Pohlman *et al.* 2007), edges may affect vegetation structure and composition (Delgado *et al.* 2007; Magrach *et al.* 2014), soil characteristics (Bettez *et al.* 2013), ecological processes such as decomposition and primary productivity (Didham 1998; Bowering *et al.* 2006), and plant-animal interactions (Valladares *et al.* 2006; Huang *et al.* 2009). These effects are not restricted to forest environments, as they have also been observed in savannas and grasslands in different continents (Cilliers *et al.* 2008; Dodonov *et al.* 2013). Specifically for savannas, edge influence has been observed for vegetation structure and composition (Lima-Ribeiro 2008; Smit & Asner 2012), distributions of native and exotic grass species (Pivello *et al.* 1999a,b), plants with different dispersal syndromes (Jardim & Batalha 2009), and interactions between plants and invertebrates (Christianini & Oliveira 2013). However, some ecosystem properties and processes, including those related to plant litter, have been little studied at edges despite their ecological importance (but see Didham & Lawton 1999; Delgado *et al.* 2013a,b).

Plant litter, that is fallen leaves and fine woody material (Sayer 2006), is important habitat for many invertebrates (Delgado *et al.* 2013a,b) and a critical type of fuel (Hoffmann *et al.* 2012). Litter results

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from the balance of the ecological processes of senescence and decomposition, and may influence regenerating plant communities (Loydi *et al.* 2014). Thus, edge-related variation in plant litter may be influenced by and result in cascading effects (Harper *et al.* 2005) on various ecological patterns and processes. Edge-related patterns in the biomass or depth of plant litter have been observed in different ecosystems, including the Amazonian rainforest (Didham & Lawton 1999), subtropical forests in the Canary Islands (Delgado *et al.* 2013a), European temperate forests (Taboada *et al.* 2004) and North American forests (Matlack 1993; Haskell 2000). Such patterns, however, are not consistent, as some studies report significant edge influence on plant litter at some sites but not at others (Didham & Lawton 1999). Whereas some studies observed a greater quantity of plant litter at the edge (Didham & Lawton 1999), others found more plant litter in the forest interior (Matlack 1993; Haskell 2000; Taboada *et al.* 2004; Delgado *et al.* 2013a).

The large variation in the observed patterns may be due in part to the combination of processes determining the amount of plant litter. In addition to variation in species composition (Didham & Lawton 1999), the amount of plant litter is determined mainly by primary productivity, leaf loss and litter decomposition; therefore changes in litter biomass may be considered part of a secondary stage of edge influence (c.f. secondary response, Harper *et al.* 2005). Increases in primary productivity have been observed at some edges and were related to a greater light incidence (Bowering *et al.* 2006) or water availability (Smit & Asner 2012). Increases in wind speed leading to a greater leaf loss are also a common pattern at forest edges (Laurance & Curran 2008). Accordingly, increased litter production at edges has been observed in the Amazonian rainforest (Vasconcelos & Luizão 2004) and in an atlantic forest fragment in Brazil (Portela & Santos 2007). However, opposite patterns, with decreased litterfall at forest edges, were observed in a different Brazilian atlantic forest area (Vidal *et al.* 2007) and in the Canary Islands (Arévalo *et al.* 2008). Temporal variation in litterfall patterns have also been observed, with litterfall being greater at the edge than in the interior only in the first year after edge creation (Sizer *et al.* 2000). Similar variation in edge influence has been also reported for litter decomposition rates, with decomposition at the edge being either greater (Didham 1998), smaller (Riutta *et al.* 2012) or equal to that in the reference conditions (Rubinstein & Vasconcelos 2005; Moreno *et al.* 2014).

Patterns of edge influence on microclimate, vegetation structure and other variables often differ among vegetation types (Delgado *et al.* 2007; Dodonov *et al.* 2013; but see Delgado *et al.* 2013a). Specifically for plant litter, different patterns may be expected for forest and savanna environments, which have markedly different ground layer structure (Hoffmann *et al.* 2012) and are likely to face different mechanisms of edge influence. For example edge influence in savanna environments may be caused by factors such as altered hydrological regime leading to increases in woody plant cover (Smit & Asner 2012) and increased abundance of invasive grasses (Pivello *et al.* 1999a,b; Dodonov *et al.* 2013; Mendonça *et al.* 2015). This may result in varying patterns of edge influence. Whereas increases in woody plant cover may lead to an increase in fine woody debris on the ground, grass invasion is most likely to increase the amount of grass litter to the detriment of other leaf litter categories. We are unaware of studies that have explored edge influence on plant litter in savanna areas. In tropical forests, conversely, edge influence appears to be mostly driven by microclimatic changes (Magnago *et al.* 2015). Varying patterns of edge influence on plant litter may be observed, possibly depending on species composition and time since edge creation.

Edge characteristics are also important, as higher contrast edges, where there is a greater difference in vegetation structure between the two sides of the edges, are expected to have stronger edge influence (Cadenasso *et al.* 2003; Reino *et al.* 2009; Noreika & Kotze 2012). However, low-contrast edges, such as narrow forest roads, may also significantly affect vegetation structure and composition by changing, for example, vegetation height and the abundance of different species (Avon *et al.* 2010; Dodonov *et al.* 2013). Edge influence on plant litter has been shown to differ between maintained and regenerating edges (Didham & Lawton 1999) and between road and trail edges (Arévalo *et al.* 2008). In other studies, however, forest type (Delgado *et al.* 2013a) and edge development (Matlack 1993) did not influence edge-related patterns in plant litter. Edge influence may also vary among categories of plant litter, that is woody and non-woody material or fine woody debris of different sizes. For example increases in graminoid abundance at edges are likely to increase the biomass of graminoid litter while reducing that of other litter categories, whereas an increase in woody cover would have an opposite effect. Similarly, input of plant material from outside the fragment, for example from a tree plantation, may lead to increases in fine branches or leaves but not in coarser material, which is less likely to be transported across the edge. We are, however, unaware of any studies that have explored such differences.

We studied edge influence on different categories of plant litter in fragments of Brazilian *cerrado*, a vegetation type encompassing both forest and savanna physiognomies, surrounded by high and low-contrast

edges with different anthropogenic land uses. Our objectives were: (i) to quantify magnitude and distance of edge influence for different categories of plant litter, (ii) to compare edge influence among different categories of plant litter and of fine woody debris, (iii) to test whether edge and vegetation characteristics explain the variation in edge influence on fine woody debris and (iv) to qualitatively compare the patterns of edge influence observed in savanna and in forest. Due to the variation among previous studies of edge influence on plant litter, we did not make explicit predictions on the patterns that would be observed at forest edges. However, we expected that (i) there would be a marked increase in graminoid litter with concomitant decreases in other litter categories at savanna edges, (ii) edge influence would be restricted to the first 20 to 30 m from the edge, as has been observed for other variables in the *cerrado* (Dodonov *et al.* 2013); (iii) edge influence would be more strongly pronounced on finer portions of woody debris, as they are probably more susceptible to changes in vegetation structure and microclimate at the edges, (iv) edge influence would be stronger at higher contrast edges (Harper *et al.* 2005) and (v) edge influence in forest and savanna fragments would be qualitatively different, with stronger edge influence on woody debris in forest. This study complements the findings of Dodonov *et al.* (2013), who explored similar questions for microclimate and vegetation structure and composition in the Brazilian *cerrado*.

METHODS

Study site

We studied fourteen edges of eight *cerrado* fragments in São Paulo state with forest and savanna vegetation (Fig. 1). The study fragments were located between the coordinates 21°33.18′S, 47°36.83′W and 22°49.79′S, 50°22.57′W, and were all characterized by a subtropical climate with warm rainy summers and mild dry winters. We classified one of our edges as *campo cerrado*, a grassland with scattered shrubs and trees (Fig. 1a); two as typical *cerrado*, a savanna vegetation (Fig. 1b); three as dense *cerrado*, a woodland with a nearly continuous canopy (Fig. 1c); and eight as *cerradão*, a dry forest (Fig. 1d) (Table S1) (Coutinho 1978; Ribeiro and Walter 2008). We refer to the dense *cerrado* and *cerradão* as forest sites and to the typical *cerrado* and *campo cerrado* as savanna sites. The dense *cerrado* and *cerradão* edges were characterized by an average canopy height of approximately 8–11 m, whereas the typical *cerrado* and *campo cerrado* sites had an average canopy height of approximately 2–3.5 m (Table S1). All sites had a ground layer with a high abundance of grasses (Dodonov *et al.* 2013), as well as other herbaceous and woody plants including a lot of shrubs, trees and vines (P. Dodonov, pers. obs., 2010). The differences in the number of forest and savanna edges were because our study site selection was limited by the

land uses adjacent to the *cerrado* fragments, as we wanted to sample the land uses that are most frequent next to *cerrado* vegetation in São Paulo state (Durigan *et al.* 2007). Two edges were adjacent to narrow (approximately 5 m wide) firebreaks with *cerrado* vegetation on the other side, whereas the other edges were adjacent to different anthropogenic land uses (sugar cane and eucalypt plantations, highways, and pastures) (Table S1). All edges were located at least 300 m (but usually more) from other edges to avoid multiple edge effects (Porensky & Young 2013). All edges were either facing downslope (with the forest side upslope) or were on level ground and had been maintained for at least 20 years. Additional information on the study sites is available in Dodonov *et al.* (2013).

Sampling

We established five 180-m-long transects, going into the forest or savanna, from each study edge, except at edges F1 and F9, where we sampled only four transects. The distances between adjacent transects were determined randomly and varied between 20 and 40 m. The first plot of each transect was located either on an embankment, which represented the edge creation line, or, in the absence of such an embankment, at a line represented by an abrupt change in the vegetation. Between November 2009 and November 2010, we collected all plant litter on the ground within 0.5 × 0.5-m quadrats along each transect at the following distances from the edge: 0, 2, 5, 10, 15, 20, 30, 40, 50, 60, 80, 100, 120, 150 and 180 m, except for edge F3, where we limited the sampling to the first 100 m because the vegetation further from the edge had a different disturbance history. In the study areas there was a clear difference between the litter layer and the underlying soil. Although sampling took place over an extended time period, we usually took at most 3 days to sample each edge and at most two hours to sample a given transect.

We separated the litter into fine branches (diameter ≤1.5 cm), thick branches (diameter >1.5 cm), bark and other litter. In the dense *cerrado* and *cerradão* areas we were unable to process the other litter, including leaf litter, because of time constraints. In the typical *cerrado* and *campo cerrado* areas we discarded only the parts of the litter that were too fragmented to be further classified, and separated the remaining other litter into graminoid litter and dicot leaf litter. Therefore, we had information on the biomass of twigs and bark (collectively referred to as fine woody debris – FWD) at all sites, but for graminoid and dicot leaf litter (collectively referred to as leaf litter) only at he three savanna sites, resulting in a total of three and five categories at the forest and savanna sites respectively. After sorting the litter categories, we placed them in paper bags and oven-dried them for 72 h at approximately 70°C. We then used a digital scale (precision of 0.1 g) to weigh the paper bags containing the litter samples and the empty litter bags, and obtained the dry weight of the litter samples by subtracting the two values. At the same spots in which we collected plant litter we also measured several other variables related to vegetation and microclimate: canopy closure, measured from hemispheric photographs with the Gap Light Analyser software (Frazer *et al.* 1999); maximum
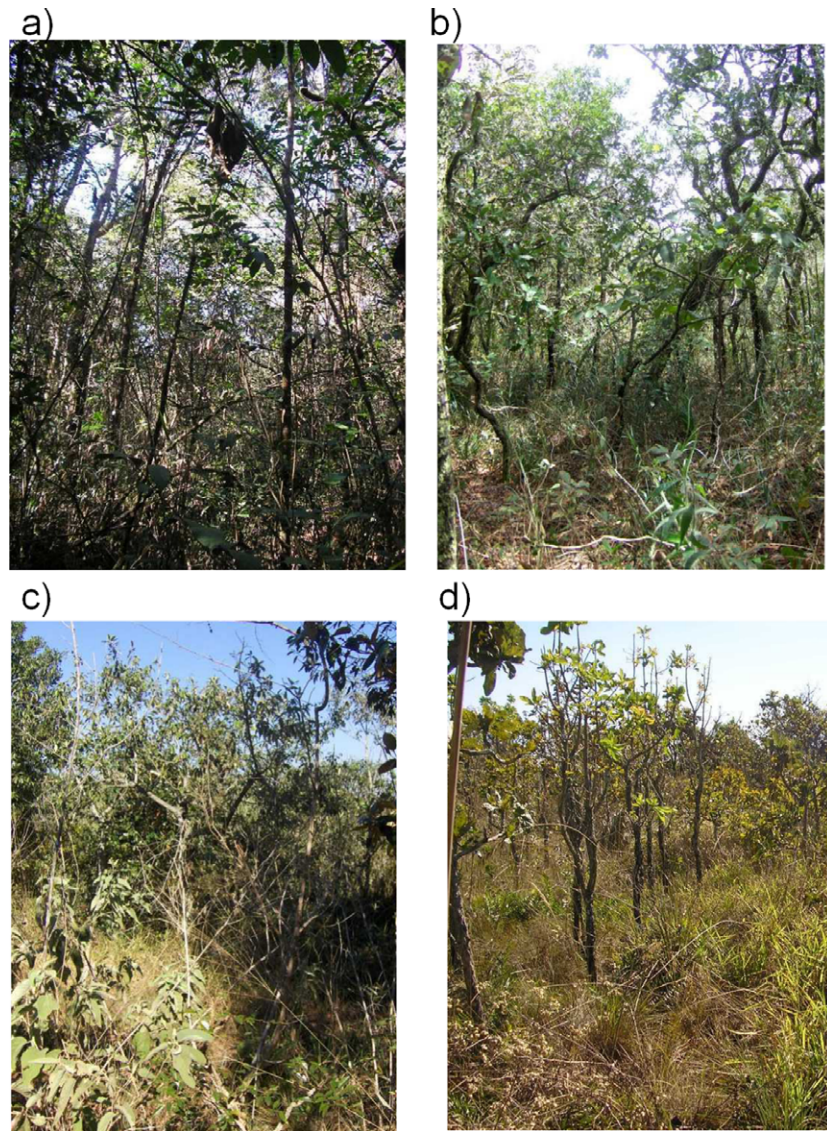
Fig. 1.   Examples of the forest (a, b) and savanna (c, d) vegetation at the study edges: (a) *cerradão* at edge F2, (b) dense *cerrado* at edge F11, (c) typical *cerrado* at edge S1, (d) *campo cerrado* at edge S3.

vegetation height, measured with an expandable 15-m ruler; air temperature and moisture; and the biomass of invasive and native graminoids. Edge influence on these variables has been explored by Dodonov *et al.* (2013).

Data analysis

We estimated magnitude, significance and distance of edge influence by comparing values at each distance from the edge with reference conditions. We considered samples collected at 120, 150 and 180 m from the edge as representative of interior conditions and used them as reference values, except for edge F3, where we used samples collected at 80 and 100 m as reference. We first calculated the magnitude of edge influence as $(E - I)/(E + I)$, where E is the mean value at a given distance from the edge and I the mean of interior values (Harper *et al.* 2005). We used a

randomization procedure (randomization test for assessing edge influence – Harper & Macdonald 2011) to assess whether this magnitude was significantly different from zero at each distance from the edge. This analysis proceeds as follows:

1. calculate the magnitude of edge influence using the values at a distance from the edge and the reference values;
2. create a data set containing both the edge values and the reference values;
3. randomly assign five of these values as edge and the remaining as reference;
4. recalculate magnitude of edge influence for the randomized data set and repeat steps 2–4."

The magnitude of edge influence values from 9999 randomizations plus the observed value were then used to calculate the significance of the difference between edge and interior values for each distance. We considered distances

with a *P*-value of 0.05 or lower as significantly different from reference conditions.

We considered edge influence to be significant (i.e. significance of edge influence = 1) when at least one distance within the first 15 m from the edge was significantly different from reference conditions, and estimated distance of edge influence as the set of distances that were significantly different from reference conditions interrupted by no more than one non-significant distance. At the edges with significant edge influence we estimated the magnitude of edge influence as the maximum absolute value that was significantly different from reference conditions. At the other edges we recalculated the magnitude of edge influence by comparing the mean values at the first 15 m from the edge to the reference conditions.

We tested whether the magnitude of edge influence differed among the FWD categories (fine branches, thick branches, bark, and total amount of FWD) by means of Friedman's test followed by pairwise Wilcoxon tests. We did not assess differences in the significance or distance of edge influence because of the low number of edges with significant edge influence for some categories, and we did not include leaf litter because we had data for only three edges.

We also tested whether vegetation and edge characteristics explain the variation in the significance and magnitude of edge influence by means of a model selection with generalized linear models with a binomial distribution for significance and a normal distribution for magnitude of edge influence. We used three explanatory variables: canopy closure, edge contrast, and edge exposure. For canopy closure, we used the mean values measured between 0 and 20 m from the edge. For edge contrast, we used the weighted edge contrast measure (Dodonov *et al.* 2013), which considers the difference in height between the fragment (measured as the average height between 0 and 20 m from the edge) and the surrounding land uses at different distances into the matrix, giving more emphasis to land uses closer to the edge. This measure is calculated by (i) calculating the contrast with the land use at all distances

from the edge (in our case between 0 and 40 m), (ii) multiplying these contrasts by a weighting function (we used a half-normal with a mean of 0 and a standard deviation of 5 m) and (iii) calculating the area below the resulting curve (Dodonov *et al.* 2013). Edge exposure is the distance to the nearest land use as tall or taller than the fragment's vegetation, up to a maximum of 50 m.

For each FWD category, we compared six models: three models with one explanatory variable each, two models combining canopy closure with each of the other explanatory variables, and a null model. We compared them with Akaike's information criterion corrected for small sample size (AICc). We considered a model to be significantly better than the other when its AIC was at least two units lower than the next best model; when two or more models had similar AIC values (ΔAICc < 2), we chose the models with fewer variables. We restricted these analyses to the forest edges to avoid the confounding effects of differences in vegetation structure, as our number of savanna edges was too small for a two-way analysis. We did not analyse the distance of edge influence because of the low number of edges with significant edge influence, and we did not perform this analysis on the significance of edge influence for thick twigs because it was significant at a single edge.

We performed the randomization tests and the model selection in R 2.15.3 (R Core Team 2013) and the Friedman and Wilcoxon tests in Past 2.17c (Hammer *et al.* 2001). The codes used for the randomization tests and calculation of weighted edge contrast are available in Dodonov *et al.* (2013) and at https://github.com/pdodonov/EdgeInfluence.

RESULTS

Edge influence was significant at two or more edges for all response variables except for thick twigs and total leaf litter, which were significantly different from references conditions at only one edge each (Fig. 2,
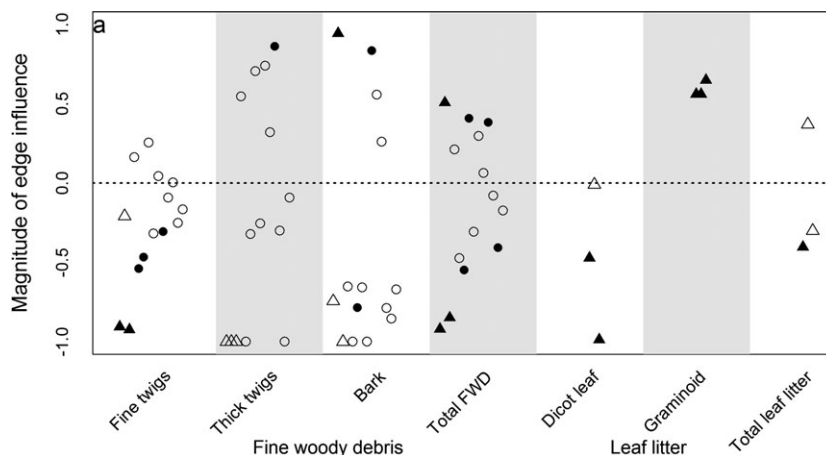

Fig. 2. Variation in magnitude of edge influence (MEI; varying from −1 to +1) for different categories of fine woody debris (FWD) and leaf litter. Each point is a study edge, with triangles representing savanna edges and circles representing forest edges. Filled symbols represent edges for which a significant edge influence was detected. Magnitude of edge influence for bark was significantly greater (*P* = 0.001, Wilcoxon test) than that for fine twigs and for total FWD.

Table 1). All three savanna edges and seven of the eleven forest edges had significant edge influence for at least one FWD category. At the edges with significant edge influence, the biomass was smaller for fine twigs and dicot leaf litter and greater for graminoid litter at the edge compared with reference conditions, whereas bark and total FWD variables showed variable patterns regardless of vegetation type. At these edges, magnitude of edge influence was most variable for bark and least variable for fine twigs and for graminoid litter.

Distance of edge influence usually ranged between 0 and 20 m, although values of 40 and 50 m were also observed (Table 1, Figs 3,4). There was great variation in distance of edge influence for all FWD categories except thick twigs and total leaf litter, from 0 to 40 or 50 m for fine twigs, bark, total FWD, and dicot leaf litter, which was only sampled at three edges. Edge influence on graminoid litter was more consistent and only extended from 0 to 5 m.

The magnitude of edge influence for thick twigs was greater than for fine twigs or for total FWD (Friedman test, $P = 0.02$; pairwise Wilcoxon tests, $P = 0.01$; Fig. 2). When assessing the effects of edge characteristics on magnitude of edge influence and the number of edges with significant edge influence, the null model was always the best model ($\Delta AICc = 0$), except for significance of edge influence on total FWD, for which the best model included canopy cover but the null model was also plausible ($\Delta AICc = 1.4$, Table 2). There were no

clear differences between edges adjacent to different land uses (Table 1).

DISCUSSION

Even though we observed large differences in the magnitude of edge influence on plant litter among our *cerrado* edges, the distance of edge influence had reasonably consistent values of around 20 m, which agrees with estimates for other vegetation characteristics, including canopy closure, vegetation height and the abundance of native and invasive graminoids, at the same study sites (Dodonov *et al.* 2013). It therefore appears that, agreeing with our expectations, most edge-related ecological changes in *cerrado* vegetation occur within 20 m of the edge. To our knowledge, these are among the first estimates of distance of edge influence for the litter or other variables in the *cerrado* and for plant litter in general (but see Matlack 1993; Didham 1998; Delgado *et al.* 2013a, b; Dodonov *et al.* 2013). We also detected differences in the patterns observed for different parts of the plant litter, which, to our knowledge, had not been explored in previous studies.

The large variation in the observed patterns has been previously found in other studies relating plant litter to edges (Didham & Lawton 1999; Portela & Santos 2007; Delgado *et al.* 2013a,b). However, we also noticed that different portions of plant litter were affected by edges in different ways, which suggests

Table 1. Set of distances (m) that were significant from reference conditions for the biomass of fine woody debris (FWD) and leaf litter at the savanna and forest study sites

Edge	Main adjacent land use	Fine twigs	Thick twigs	Bark	Total FWD	Graminoid litter	Dicot leaf litter	Total leaf litter
Savanna								
S1	Pasture	*0*	ns	ns	*0*	5	*0*	*0*
S2	Urban	20	ns	10, 15, 40	*5, 10, 20, 80*	*0*	ns	ns
S3	Eucalyptus	5, 40	ns	ns	5, 40	2, 5, 40	*0-5, 15, 20, 40*	ns
Forest								
F1	Firebreak	ns	ns	ns	ns	N/A	N/A	N/A
F2	Firebreak	5	ns	30	ns	N/A	N/A	N/A
F3	Highway	10, 20, 40-50	ns	10	10, 20, 50	N/A	N/A	N/A
F4	Pasture	20	ns	ns	10, 20	N/A	N/A	N/A
F5	Pasture	ns	ns	ns	ns	N/A	N/A	N/A
F6	Highway	ns	ns	2	ns	N/A	N/A	N/A
F7	Highway	*0, 100*	100	ns	ns	N/A	N/A	N/A
F8	Sugarcane	ns	5	80	5, 80	N/A	N/A	N/A
F9	Sugarcane	ns	ns	20	ns	N/A	N/A	N/A
F10	Eucalyptus	60	ns	50	*0*	N/A	N/A	N/A
F11	Eucalyptus	ns	ns	ns	ns	N/A	N/A	N/A

N/A, this variable was not measured at this edge; ns, no significant edge influence was observed at this edge. Results for FWD are divided into fine and thick twigs (< and >1.5 cm in diameter respectively), bark, and total FWD; results for leaf litter are divided into dicot leaf litter, grasses and total leaf litter. Distances considered to represent edge influence are underlined. Distances with values lower than in the interior (negative edge influence) are in italics.
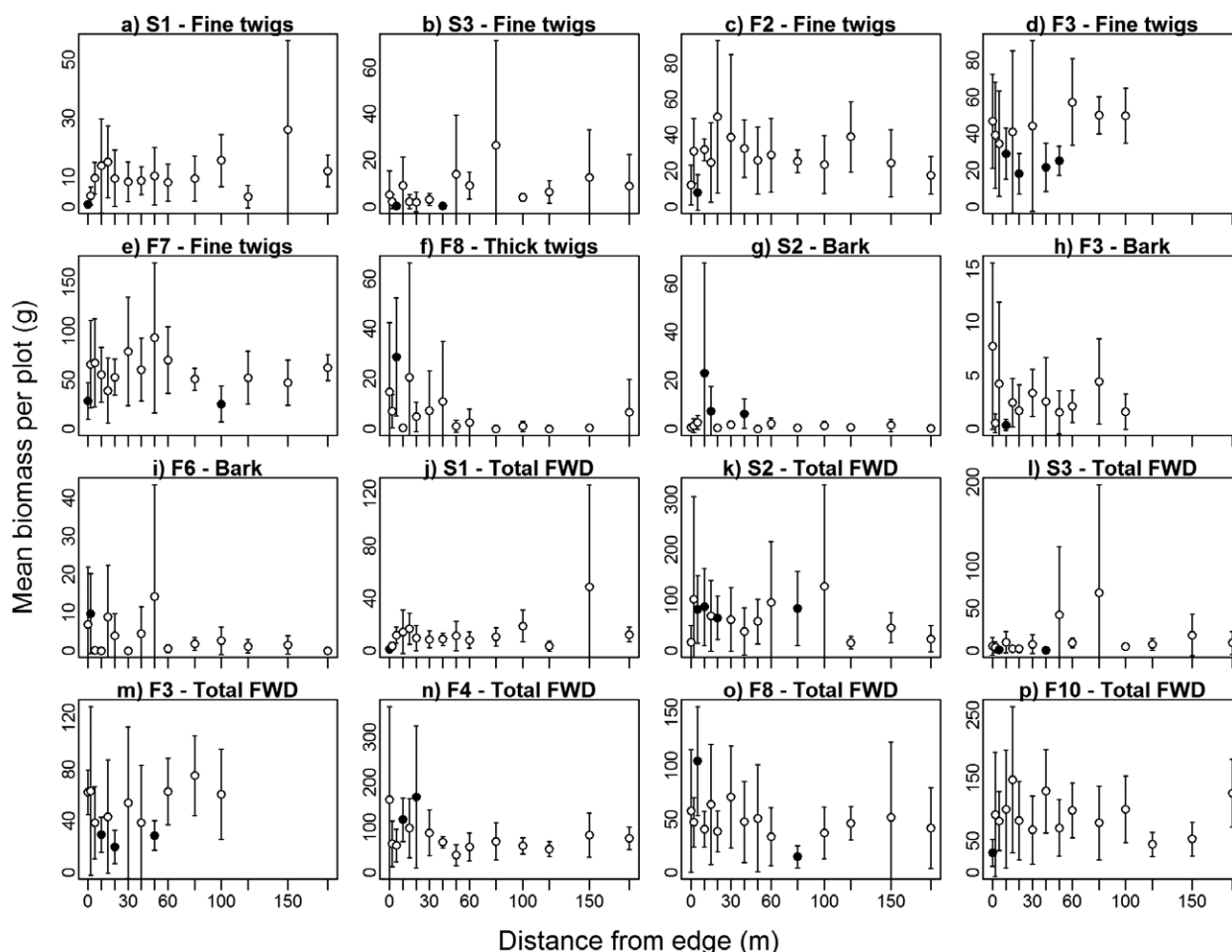
Fig. 3. Variation in fine woody debris (FWD) biomass with distance from edge for the edges with significant edge influence. Filled symbols were significantly different from reference values (80–100 m at edge F3 and 120–180 m at the other edges).

that an assessment of total plant litter biomass may hide underlying patterns. For example as expected, edge influence was more pronounced on fine twigs than on thick twigs or bark. Edge influence on fine twigs tended to be negative, whereas thick twigs were little affected by edges. Edge influence at savanna sites also agreed with our expectations, as the biomass of graminoid litter increased at the edges, whereas that of dicot leaf litter decreased. The greater magnitude of edge influence observed for thick twigs than for fine twigs provides further support for different effects of edges on different components of litter.

The lower amount of fine twigs at edges may appear counter-intuitive, as increased wind incidence, which is common at tropical forest edges (Laurance & Curran 2008), would result in the opposite pattern. We propose two mechanisms to explain the observed pattern. First, species composition may be different between edge and interior of *cerrado* fragments (Jardim & Batalha 2009), and decreased FWD

production would be expected if the species at the edge had a reduced tendency to lose small branches. Second, intra-specific variation in plant growth and architecture has been previously related to edges (Lima-Ribeiro 2008; Habermann & Bressan 2011) and to other disturbances (Dodonov *et al.* 2011, 2014) in the *cerrado*. It is thus possible that species growing at *cerrado* edges have a different architecture, with a smaller propensity for twig breakage, than those growing in the interior. An overall decrease in primary productivity at the edges would also explain the observed pattern, but this is not likely in our study site as the woody vegetation is often taller and denser at *cerrado* edges compared to interior areas (Lima-Ribeiro 2008; Dodonov *et al.* 2013; Mendonça *et al.* 2015).

Agreeing with our expectations, other FWD categories were either not influenced by edges, as for thick twigs, or had no consistent patterns. This probably reflects the large spatial and temporal variation in these variables and their dependency on other
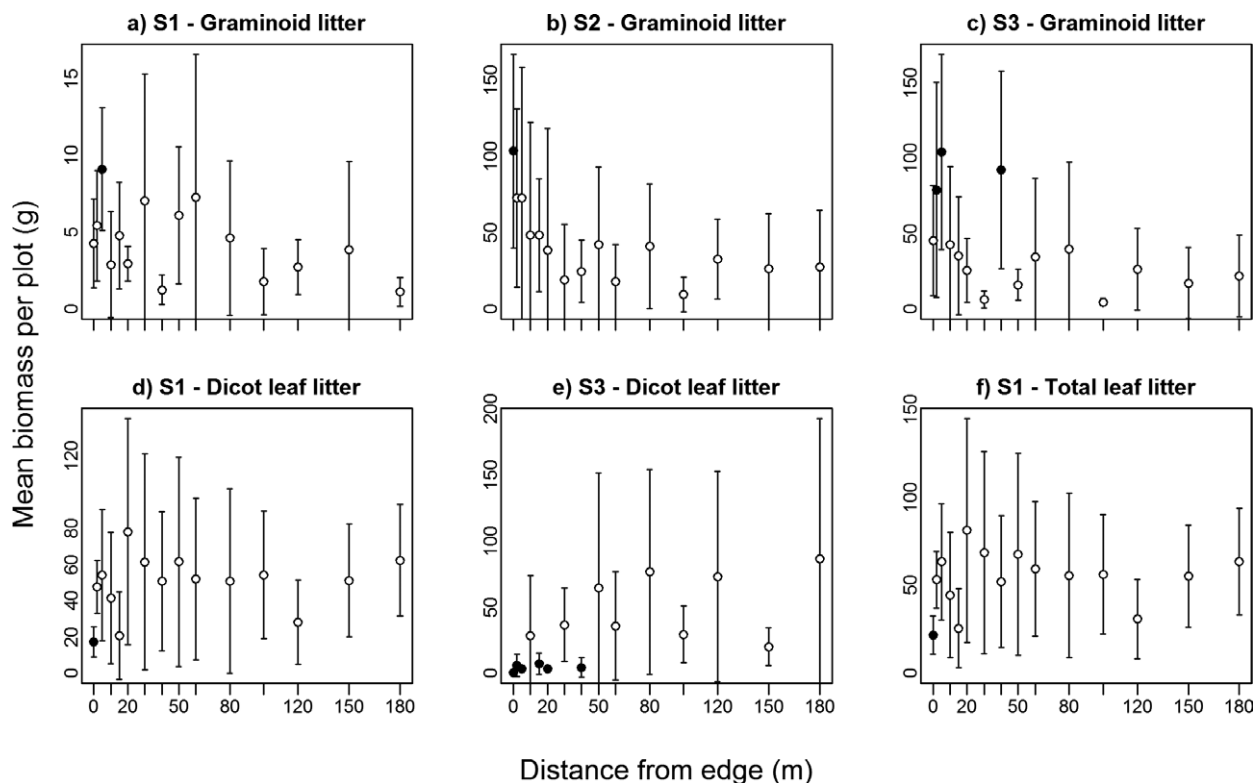
Fig. 4. Variation in leaf litter biomass with distance from edge for the savanna edges with significant edge influence. Filled symbols were significantly different from reference values (120–180 m).

Table 2. Model selection relating edge influence on different categories of fine woody debris (FWD) with different edge characteristics, performed for our 11 forest edges

Edge influence parameter	Response variable	Explanatory variables in the model					
		Null	Closure	Contrast	Exposure	Closure, contrast	Closure, exposure
Significance	Fine twigs	0	2.8	0.8	2.9	4.7	6.6
	Bark	0	3	2.7	3	6.6	6.9
	Total FWD	1.4	0	3.5	4.3	2.7	3
Magnitude	Fine twigs	0	3.9	3.6	3.3	8.8	8.5
	Thick twigs	0	2.8	3.7	1.4	7.8	5.8
	Bark	0	1.9	2.9	2.5	6.2	6
	Total FWD	0	3.5	3.6	1.5	8.5	6.6

Each model is represented by its ΔAICc, or the difference in Akaike's information criterion between a given model and the best model for this response variable. Results are divided into fine and thick twigs (< and >1.5 cm in diameter respectively), bark, and total FWD. Edge influence was characterized by its significance (a binary variable representing whether edge influence was significant at a given edge) and magnitude (calculated as $(E - I)/(E + I)$, where E is the average biomass at the edge and I is the average biomass in reference conditions). Significance of edge influence on thick twigs was not assessed because it was significant at a single edge.

vegetation characteristics. The amount of bark would depend mostly on the species present, as there is a lot of variation in bark thickness among *cerrado* plants (Hoffman *et al.* 2003). Similarly, the loss of thick twigs may be related to gap formation, which is highly heterogeneous in both space and time. As

expected, graminoid biomass was consistently greater at savanna edges. Dodonov *et al.* (2013) observed increased biomass of the African grass *Urochloa decumbens* close to the edge at the three savanna sites studied here (distance of edge influence of 0–15 m) and a concomitant decrease in the biomass of native

graminoids (distance of edge influence of 5–10 m) at two of the three sites, but no edge influence on another other dominant African grass, *Melinis minutiflora*. As the total biomass of native graminoids at these sites was smaller than that of *U. decumbens* (Dodonov *et al.* 2013), an increase in the abundance of this species at the edge is probably the main cause of the increase in graminoid litter. Considering that invasion by this species is common at *cerrado* edges (Pivello *et al.* 1999a,b; Mendonça *et al.* 2015) and that African grasses tend to have greater above-ground biomass than Neotropical grasses (Williams & Baruch 2000), an increase in graminoid litter is likely to be common at *cerrado* edges in general. African grasses may also negatively affect native woody species (Hoffman & Haridasan 2008), and their increased abundance at edges may thus explain the lower amount of dicot leaf litter and possibly contribute to edge influence on FWD.

Contrary to our expectations, we did not observe conspicuous differences in edge influence on FWD between forest and savanna vegetation. Thus, the biomass of fine twigs was lower at the edge than in the interior and variable patterns were observed for bark and total FWD regardless of vegetation type. This may be related to the floristic similarity among the vegetation types comprising the *cerrado* vegetation. Although there are considerable differences in vegetation structure among the different phytophysiognomies (Batalha *et al.* 2001), floristic differences are often much smaller, with the same species occurring in both forest and savanna vegetation (Batalha & Mantovani 2001; Pinheiro & Durigan 2012). As the same species occur in both savanna and forest vegetation, they are likely to be adapted to the microclimatic conditions characteristic of open vegetation and of forest edges, and thus likely to be less affected by edge influence than forest specialist species. This, however, does not discard the possibility that the mechanisms of edge influence may vary between forest and savanna vegetation; different mechanisms, for example microclimatic stress and grass invasion, may putatively lead to the same patterns.

Edge characteristics do not appear to explain the variation in either magnitude of edge influence or significance of edge influence. Therefore, it appears that both high- and low-contrast edges may significantly alter plant litter biomass and other ecological characteristics. This was unexpected, as edge contrast and land use often affect the patterns and intensity of edge influence (Wright *et al.* 2012; Aragon *et al.* 2015). However, similar results of no effects of edge contrast on edge influence have been previously found for air temperature, canopy cover and vegetation height in the *cerrado* (Dodonov *et al.* 2013). The large time span over which sampling was performed

may have also added to the variation among edges, hampering the detection of a relation with edge contrast, as there is seasonal variation in litterfall in the *cerrado* (Valenti *et al.* 2008). However, this seasonal variation is likely to be the same between edge and interior areas, as we know of no evidence of an increase in the abundance of deciduous species at *cerrado* edges. The apparent lack of effect of edge contrast may also be due to the limited variation in the land uses immediately adjacent to the edges. All of our edges were adjacent either to firebreaks with no vegetation or to grass-dominated areas, which separated the *cerrado* fragment from the other land uses. It is thus possible that the immediate edge exerts at least as much influence as the nearby dominant land use in the matrix, precluding the detection of differences in edge influence between edge types. For example, eucalypt edges could putatively contribute FWD and leaf litter to the *cerrado*, increasing litter biomass at the edge. However, the existence of a firebreak between the plantation and the *cerrado* may preclude this from happening as most of the fallen litter would remain in the firebreak and not reach the *cerrado*. Similarly, firebreaks may increase the similarity in microclimatic conditions among edges, leading to smaller land use effects than would be observed if there were no separation between the *cerrado* and the dominant land use (Wright *et al.* 2012).

In conclusion, notwithstanding the large variation in edge influence on plant litter in the *cerrado*, smaller portions of FWD tend to have lower biomass near edges whereas dead graminoid biomass tends to be greater. Considering that graminoid biomass is much more representative in savanna areas and the biomass of FWD is more abundant in forests, edge-related variation in plant litter may have different ecological consequences in these environments. Thus, the increased amount of graminoid leaf litter at savanna edges is likely to increase fire frequency at these edges due to increased fuel availability (Hoffmann *et al.* 2012), but the same would not necessarily be observed in forests, especially considering that exotic graminoids are often restricted to the immediate edge of dense *cerrado* and *cerradão* areas (Dodonov *et al.* 2013). The smaller amount of fine twigs and, in some cases, other FWD categories at the edges may also have ecological consequences for litter invertebrates, as a decrease in the amount of litter may lead to decreased invertebrate abundance (Delgado *et al.* 2013b), with possible cascading effects into higher trophic levels by, for example decreasing food availability for insectivorous ground vertebrates. Future studies could explore the mechanisms of edge influence on plant litter in the *cerrado* and other savanna and forest ecosystems, as well as their consequences for different organisms and ecological processes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Edge designation, location, geographical coordinates and edge characteristics of the 14 edges sampled in this study.