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Tree Responses to Soil and Edge Effects in a Semideciduous Forest Remnant

Marcela de Castro Nunes Santos Terra¹ ^(D), Grazielle Sales Teodoro², Daniel Salgado Pifano³, Fernando Bonillo Fernandes⁴, Tainá Mamede Cirne Silva¹, Eduardo van den Berg¹

¹Universidade Federal de Lavras - UFLA, Lavras/MG, Brasil ²Universidade Federal do Pará – UFPA, Belém/PA, Brasil ³Universidade Federal do Vale do São Francisco – UNIVASF, Petrolina/PE, Brasil ⁴Universidade do Vale do Sapucai, Pouso Alegre/MG, Brasil

ABSTRACT

The present study seeks to characterize the composition, structure, and functional traits of the tree stratum of a Semideciduous Forest in Pouso Alegre, MG, Brazil (22°12'43"S and 45°59'30"W), by comparing Edge and Interior habitats and their relation to human impacts and soil variables. The tree community (diameter at 1.3 m (DBH) higher than 5 cm) was inventoried using the point-centered quarter method by laying out 12 transects of 450 m each (six transects in the Edge and six in the Interior). Functional traits - wood density and seed mass - were obtained by genus. The impact evaluation and soil sample collection were realized per transect. We found significant differences in terms of the basal area (higher in Interior), diversity (higher in Interior) and community seed mass (higher in Edge). The effects of higher values of soil traits such as Calcium, Magnesium, cation sum (CS) and base saturation (V) on species composition were stronger in the Interior, while human induced impacts and soil Potassium had an overwhelming effect on the Edge.

Keywords: Brazilian biodiversity hotspot, forest ecology, fragmentation, anthropic impact, forest edges.

1. INTRODUCTION

The Brazilian Atlantic Forest, one of the world's most diverse tropical forests with remarkable levels of diversity and endemism, has suffered a five centuries history of habitat loss, fragmentation, logging, burning and hunting (Joly et al., 2014). These disturbances have caused an alarming loss of biodiversity, collapse of key ecosystem services and erosion of cultural heritage. The Atlantic Forest is now a mosaic of forest fragments of different shapes and sizes surrounded by open-habitat matrices such as pastures and agricultural fields (Pereira et al., 2007; Tabarelli et al., 2012; Joly et al., 2014).

Many studies have highlighted the changing patterns of species richness, diversity, community composition and horizontal structure between contiguous forest and fragments, across gradients of forest fragment sizes, and from the forest edge to its interior (e.g. Magnago et al., 2014; Mendes et al., 2016). Most of these studies report that severe abiotic changes such as desiccation, wind disturbance, increase in light and temperature, and decreased air humidity are likely to cause conspicuous biological changes in the recent forest edges formed due to fragmentation (Murcia, 1995; Magnago et al., 2014).

In addition, empirical approaches have demonstrated that edge effects are complex and widespread, occurring over a larger spatial scale than had previously been appreciated (Faria et al., 2009). We still know little about how much and in what way edge effects impact tree community composition and structure in forest fragments given that fragmentation is a transition process that progressively separates the fragments from the original (often unknown) primary condition (Paula et al., 2015). One of the most widespread consequences of fragmentation and its resulting edge effects is the so called "replacement paradigm" - the proliferation of disturbance-adapted native organisms, such as pioneer tree species, over the later successional tree species (e.g. Tabarelli et al., 2012; Magnago et al., 2014; Santo-Silva et al., 2016).

Adding another level of complexity to this ecological context, many ecological studies have focused on the important insights provided by functional plant traits about mechanisms of community assembly (ter Steege et al., 2006; Poorter et al., 2008). Functional plant traits are physical plant attributes caused by genetic expression, which might serve as indicators or estimators of plant responses to environmental factors (Lavorel & Garnier, 2002). Thus, in fragmented forests, traits that determine how species respond to a disturbance or change in the environment, the so called 'functional response traits' (Lavorel & Garnier, 2002), such as seed mass and wood density (ter Steege et al., 2006), may lead to a better understanding of how different kinds of environments, or drivers, can cause changes in biodiversity that, in turn, affect ecosystem functioning.

Although fragmentation and its biotic and abiotic consequences seems to be the strongest force driving structure and composition of small fragments, many studies have reported synergistic action of the edge effects and local environmental variables in structuring forest fragments. Additionally, besides past-disturbance and edge effects (e.g. Higuchi et al., 2008), several papers have reported the important role played by soil fertility, water saturation and topography (e.g. Baker et al., 2003) on the local structure and composition of forest fragments. Mendes et al. (2016), for example, found significant differences between forest interior and edge in terms of sand and clay contents in an Atlantic Forest fragment with these habitats presenting different species richness/diversity. In addition, the same authors found higher soil pH in the interior and higher Al content in an intermediate habitat and suggested that these variables should be taken into account when investigating fragmented habitats.

Understanding how habitat modification affects forest biodiversity, structure and functional traits at the community level of fragmented tropical forests is one of the main challenges for ecologists and conservation biologists concerned with the Brazilian Atlantic Forest. The present study aimed to characterize the composition, structure, and functional traits of the tree stratum in a semideciduous forest fragment in Southeast Brazil by comparing Edge and Interior environments and their relation with human impacts and soil variables. We sought to answer the following questions: a) what are the main structural differences between forest Edge and Interior environments? We expected the Edge to be denser and to have lower basal area as a consequence of edge effects acting in this habitat and the Interior to have higher remnant species richness and diversity; b) do functional response traits in terms of response to disturbance (wood density and seed mass) follow the differences between forest Edge and Interior? We expected the Edge to have lower wood

density and lower seed mass due to the eventual higher abundance of fast-growing species; c) do soil variables and impacts have different weights on species abundance variability at the Edge and in the forest Interior? We expected different drivers for each habitat: the differences between Edge samples should be more correlated with impacts and the differences between Interior samples should be more correlated with soil variables.

2. METHODS

2.1. Study area

The study area was a 186 ha Atlantic semi-deciduous forest remnant, located in the municipality of Pouso Alegre, Minas Gerais State (22°12'43" to 22°13'09"S and 45°59'30" to 46°00'31"W, altitudinal range of 860-1140 m). The climate was classified as Cwb according to the Köppen climate classification (Alvares et al., 2013) with wet summers and dry winters. The soils were classified as Ferralsols and Acrisols. The area belongs to the Reserva Biológica Municipal de Pouso Alegre (RBPA) and is very close (almost contiguous) to the Parque Municipal de Pouso Alegre, consisting of a total of 700 ha of forested area. The fragment is surrounded by pasture, with a few scattered trees. The remnant shows signs of anthropogenic disturbances such as waste, fences, trails, fire and selective logging.

2.2. Data gathering

The tree community was inventoried using the point-centered quarter method (Cottam & Curtis, 1956), laying out 12 transects of 450 m each (31 points spaced by 15 m) (Figure 1). The transects were laid out in the Interior and Edge of the fragment, six in each habitat. The ones on the Edge were located in the immediate edge at a distance no greater than 50 m from the surrounding matrix. The ones in the Interior were located at a distance greater than 150 m from the surrounding matrix. At each point-centered quarter, the closest four individuals with circumference at breast height at 1.3 m (CBH) higher than 15.7 cm were recorded. Each individual had its CBH measured (converted into diameter at breast height - DBH) and its height estimated. Species identification was performed in loco and/or by comparison with the Herbarium ESAL (Universidade Federal de Lavras) collection.

Functional traits were obtained by genus. For seed mass (g) data from the Royal Botanic Gardens Kew Seed Information Database (Royal Botanic Gardens Kew, 2015) were used, converted in logarithmic classes according to ter Steege et al. (2006). For the two genera not included in this database, data from Francisco et al. (2007) (*Pera*) and Araújo & Cardoso (2006) (*Amaioua* – assuming the value of Rubiaceae as a reasonable average) were used, respectively. Wood density (g.cm⁻³ – oven-dried weight divided by green volume; for further methodological details



Figure 1. Localization of the forest studied (22°12'43" to 22°13'09"S and 45°59'30" to 46°00'31"W), in the municipality of Pouso Alegre, Minas Gerais, and the distribution of the 12 transects (white lines) in the area (1, 2, 3, 7, 8 and 9 are Edge Transects and 4, 5, 6, 10, 11 and 12 are Interior Transects).

see Chave et al. (2009)) were taken from Zanne et al. (2009), which provided data for all genera recorded in the area.

Impact evaluation was performed at two randomly selected points in each transect. From these values, one single value was extracted for each transect. The impact evaluation at each point was based on the methodology proposed by Pereira et al. (2007), consisting of one matrix where a semi-quantitative evaluation of several impacts (scores varying from 0 to 4, depending on the impact intensity) is multiplied by the impact weights, resulting in a synthetic value per transect. The impact weight followed the subjective adoption proposed by Pereira et al. (2007), assuming: 1=fence; 2=waste, trail or farmer activities; 3=external road or pasture proximity; 4=internal road constructions; 5=evidence of fire or selective logging; and 6=evidence of clear cutting.

Three superficial soil sub-samples (0-20 cm), equidistantly distributed along the transects were collected, and then mixed, producing a single sample for each transect. The fertility of the soil samples was analyzed according to EMBRAPA (1999).

2.3. Data analysis

In order to describe the overall structure, the absolute and relative density, dominance and frequency and the importance value (IV) of all tree species recorded were calculated, as well as the Shannon-Wiener Index (H') and the Pielou Evenness (J') (Brower & Zar, 1984) for the whole tree community.

In order to answer the first question (a), the Edge and Interior environments were first compared by calculating Sørensen similarity coefficient. Additionally, the Shannon-Wiener Diversity Index rarefaction curves (Gotelli & Colwell, 2001) were plotted with standard error (SE) interval calculated based on 100 randomizations for both environments.

Statistical tests comparing Interior and forest Edge were performed after normality checking via Kolmogorov-Smirnov (KS-test) (Sokal & Rohlf, 1981). The data that did not fit were compared by non-parametric Mann-Whitney U-Test. The number and range of diameter classes were set by Sturges algorithm (Gerardi & Silva, 1981) and compared between the two environments by homogeneity chi-squared test. The comparison for average wood density between the two environments (question b) was conducted via Mann-Whitney U-Test (no normal data). The distribution of individuals within seed mass classes was compared between the environments via homogeneity chi-squared test.

In order to analyze the relationship between the environmental variables and the vegetation structure (question c) a canonical correspondence analysis (CCA) (Ter Braak, 1987) was run in PC-Ord 5. The abundance matrix was constructed with the number of individuals from species with 10 or more individuals per transect, given that low abundance species present a small contribution to ordination and increase the amount of calculus and noise in the analysis (Causton, 1988). The main matrix values were transformed by the expression $\log_{10} (x+1)$ to avoid distribution distortions from a few high values. Pearson correlation and significance of the species-environment correlation given by the CCA.

The environmental matrix included, at the beginning, all chemical variables and textural variables of soil and the impact values (7 variables were removed due to redundancy). The final CCA was run with the 10 most representative variables: impacts, cation sum (CS), effective cation exchange capacity (t), base saturation (V), as well as concentration values of Phosphorus (P), Potassium (K⁺), Calcium (Ca²⁺), Magnesium (Mg²⁺), Potential Acidity (H+AI) and Remaining Phosphorus (P-rem).

3. RESULTS AND DISCUSSION

3.1. Overall structure

We sampled 1484 individual trees belonging to 148 species, 102 genera and 51 botanical families. Fabaceae showed the greatest richness (19 species), followed by Myrtaceae (18). Other notable families were Lauraceae (11 species), Melastomataceae (8) and Rubiaceae (7). The richest genera were *Miconia* (6), *Myrcia* (6), *Calyptranthes* (5), *Annona* (4) and *Machaerium* (4). The species with the largest number of individuals were *Tapirira obtusa* (85), *Chrysochlamys saldanhae* (75), *Psychotria suterella* (67), *Eremanthus erytropappus* (56) and *Cabralea canjerana* (36). The species with higher IV are the same as those with a higher number of individuals: *T. obtusa, C. canjerana, C. saudanhae, E. erythopappus* and *P. suterella* (Table 1). The overall Shannon index was 4.392 nats.ind⁻¹ and Pielou Equability was 0.879.

The Shannon-Wiener Index value was higher than that found for semi-deciduous forests of the Southeast Region, which range from 3.37 to 4.29 nats.ind⁻¹ (Oliveira-Filho, 1989). However, the Pielou Equability value fell within the interval observed for these forests (0.69 to 0.98). Some studies have reported surprisingly high levels of residual species diversity in small Atlantic forest fragments (Higuchi et al., 2008; Magnago et al., 2014; Mendes et al., 2016; Santo-Silva et al., 2016), suggesting a temporary increase in diversity after disturbance - as the Intermediate Disturbance Hypothesis states (Connell, 1978) - and/or that the deleterious effects of fragmentation may be a very slow process (Helm et al., 2006). The high diversity found in this fragment supports this residual species diversity in small fragments in Atlantic forest and highlights the importance of small fragments, such as the present one, for conservation.

3.2. Structural and functional comparison between habitats

The comparison between habitats (Edge vs Interior) resulted in a Sørensen floristic similarity of 66.37%. The rarefaction curves of the two habitats for the Shannon-Wiener Index had no overlaps in their standard error (Figure 2). Although the Edge displayed less diversity, Edge and Interior were very



Figure 2. Shannon-Wiener Index (H') rarefaction curves and standard error bars for the whole tree community, Edge and Interior in a semideciduous forest in the municipality of Pouso Alegre, Minas Gerais.

Family	Species	Ν	BA	RD	RDo	RF	IV
Anacardiaceae	Tapirira obtusa (Benth.) J.D.Mitch.	85	1.14	5.728	3.426	5.728	14.881
Meliaceae	Cabralea canjerana (Vell.) Mart.	36	3.15	2.426	9.444	2.426	14.295
Clusiaceae	Chrysochlamys saldanhae (Engl.) Oliveira-Filho	75	0.86	5.054	2.577	5.054	12.685
Asteraceae	Eremanthus erythropappus (DC.) MacLeish	56	0.86	3.774	2.576	3.774	10.123
Rubiaceae	Psychotria suterella Müll.Arg	67	0.20	4.515	0.586	4.515	9.615
Lauraceae	Persea rufotomentosa Nees & Mart. ex Nees	30	1.60	2.022	4.793	2.022	8.837
Primulaceae	Myrsine umbellata Mart.	35	0.60	2.358	1.811	2.358	6.528
Melastomataceae	Miconia cinnamomifolia (DC.) Naudin	28	0.89	1.887	2.668	1.887	6.442
Thymelaeaceae	Daphnopsis fasciculata (Meisn.) Nevling	34	0.61	2.291	1.835	2.291	6.418
Clethraceae	Clethra scabra Pers.		0.59	2.224	1.767	2.224	6.215
Celastraceae	Maytenus salicifolia Reissek		0.74	1.954	2.214	1.954	6.122
Euphorbiaceae	Croton floribundus Spreng.		0.73	1.752	2.180	1.752	5.684
Lamiaceae	Vitex sellowiana Cham.		0.97	1.146	2.894	1.146	5.185
Apocynaceae	Aspidosperma australe Müll.Arg.	20	0.73	1.348	2.200	1.348	4.895
Rubiaceae	Amaioua guianensis Aubl.	30	0.27	2.022	0.822	2.022	4.865
Euphorbiaceae	Alchornea triplinervia (Spreng.) Müll.Arg.	20	0.66	1.348	1.982	1.348	4.678
Fabaceae	Machaerium villosum Vogel		1.01	1.280	3.027	0.337	4.644
Arecaceae	Euterpe edulis Mart.		0.42	1.685	1.253	1.685	4.622
Apocynaceae	Aspidosperma parvifolium A.DC.		0.86	0.943	2.585	0.943	4.472
Lauraceae	eae Ocotea diospyrifolia (Meisn.) Mez		0.44	1.550	1.326	1.550	4.426

 Table 1. Structure parameters for tree species* sampled in a semideciduous forest in the municipality of Pouso

 Alegre, Minas Gerais.

N=number of individuals; BA=basal area; RD=relative density; RDo=relative dominance; RF=relative frequency; and IV=importance value index; *Data for 20 species with the highest IV from the total of 151 species in the sampled area.

similar in terms of composition. The similarity in floristic composition between Edge and Interior environments showed by the Sørensen coefficient may have been increased by the presence of a trail about eight meters wide along the fragment parallel to Transect 5 (Interior). This trail certainly caused changes in structure and composition of the community next to it, allowing the establishment of pioneer species commonly correlated with disturbed or edge environments, found at the Edge of RBPA such as Croton floribundus, Clethra scabra and Tapirira obtusa (Oliveira-Filho et al., 2004), making it more similar to the Edge, following the replacement paradigm (Tabarelli et al., 2012). However, the lower diversity found on the Edge, associated with its similarity to the Interior, indicates that its composition is rather a parcel of the pool of species found in the Interior than a specific and specialized group of species.

Structurally, only the basal area differed between Edge and Interior (Table 2). This means that the Edge has roughly the same density as the Interior but with thinner trees. More individuals were found in the first diameter classes for both environments, resulting in similar J-reverse shape curves for the diameter classes according to chi-squared test (p=1) (Figure 3), something typical of tropical forests (Ige et al., 2013). Although there were no statistical differences between Edge and Interior for diameter distribution, the lower number of Edge individuals in the larger diameter classes (from class 2 onwards) is probably one of the consequences of the disturbances that occur at the Edge (Faria et al., 2009).

Seed mass was significantly higher at the Edge, contrary to what was expected (Table 2). This is probably due to the abundance of the genera *Persea*, which increased the community average seed mass at the Edge. This species has been found in fragmented areas and even in Cerrado patches where species seem to show higher seed mass as an investment in high root-to-shoot ratio of biomass allocation at the seedling stage (Sassaki & Felippe, 1999). Additionally, the impacts and gaps mentioned above probably contributed to reducing the average seed mass of the Interior, due to the presence of nearby fast-growing species with low seed mass such as *Cecropia* next to the trail and gaps.

A similar effect could be seen in wood density. There was no statistical difference between the habitats regarding wood density (Table 2), contrary to what we expected. This is probably due to the high abundance of species found in Cerrado-like vegetation at the Edge, mainly *Eremanthus erythropappus*. These species tend to have higher wood density that might be related to drought-induced embolism resistance (Chave et al.,



Figure 3. Diametric distribution histogram for trees (absolute frequency) in Edge and Interior environments in a semideciduous forest in the municipality of Pouso Alegre, Minas Gerais. The percentages above the bars represent the relative frequency of trees in each diameter at breast height at 1.3 m (DBH) class. (Classes: 1: >12.73 cm; 2: >20.45 cm; 3: >28.18 cm; 4: >35.91 cm; 5: >43.64 cm; 6: >51.36 cm; 7: >59.09 cm; 8: > 66.82 cm).

Table 2. Average values for Basal area, Density, Wood density and Seed mass for Edge and Interior in a semideciduous
forest in the municipality of Pouso Alegre, Minas Gerais, p-values from the U-test for Basal Area, Density and Wood
Density and the homogeneity chi-squared Test for Seed Mass.

Forest habitats	Basal area (m².ha⁻¹)	Density (ind.ha ⁻¹)	Wood density (g.cm ⁻³)	Seed mass (mode class [g])		
Edge	13.37	1182.76	0.614	4 [0.586]		
Interior	21.70	1151.24	0.589	4 [0.388]		
	p=1.54e-13*	p=0.0669	p=0.4469	p = 1.708e-07*		

*statistically significant p-value at 95% confidence level.

2009), increasing the average values of the Edge, making it more similar to the Interior.

3.3. Relation to environmental variables

Soil and impact data by transect used in the CCA are available in Table 3.

The eigenvalues found in the CCA for the three first axes were very low (0.244 and 0.172 and 0.128; < 0.5 *sensu* Ter Braak (1995), indicating that the

differences between the transects along the axes were more strongly related to changes in species abundance than species composition, with cumulative percentage of variance explained in the first three axes equal to 26.5, 45.3 and 59.2%. The CCA showed a high correlation between species and environmental variables both for Pearson (0.990, 0.998, 0.999, for the first three axes) and Kendall (0.879, 0.939, 1.000) correlations and Monte Carlo test for abundance while the variables test was significant (p<0.05) (Figure 4).

Table 3. Average soil and impact values for transects at Edge (E) and Interior (I) environments in a semideciduous forest in the municipality of Pouso Alegre, Minas Gerais.

Habitat	Transect	Р	К	Ca	Mg	H+Al	CS	t	V	P-rem	Impacts
Edge	T1-E	1.7	70	0.15	0.2	19.1	0.5	3.5	2.8	5.1	18.8
	Т2-Е	2.3	64	0.2	0.1	26.7	0.5	5.4	1.7	5.6	7.5
	Т3-Е	1.7	87	0.2	0.2	33.4	0.6	5.8	1.8	11.8	27.5
	Т7-Е	2	83	0.2	0.2	17.1	0.6	3.4	3.4	31.1	27.5
	Т8-Е	1.7	36	0.1	0.1	19.1	0.3	3.4	1.5	3.7	8.8
	Т9-Е	2.8	86	0.4	0.5	33.4	1.1	5.1	3.2	17.8	28.8
	Mean	2	71	0.2	0.2	24.8	0.6	4.4	2.4	12.5	19.8
Interior	T4-I	3.1	55	0.7	0.2	21.4	1	4.1	4.6	9.4	12.5
	T5-I	1.7	61	0.2	0.3	11	0.7	2.9	5.7	25.2	10
	T6-I	1.4	41	3.5	1	4	4.6	4.8	53.5	31.1	0
	T10-I	1.4	45	0.1	0.1	23.9	0.3	4.7	1.3	14.7	1.3
	T11-I	2.8	56	0.1	0.1	26.7	0.3	4.7	1.3	4.5	0
	T12-I	3.7	28	0.1	0.1	19.1	0.3	3.2	1.4	0.8	5
	Mean	2.4	47.7	0.8	0.3	17.7	1.2	4.1	11.3	14.3	4.8

P=Phosphorus [mg/dm³]; K⁺= Potassium [mg/dm³]; Ca²⁺=Calcium [mg/dm³]; Mg²⁺=Magnesium [mg/dm³], H+Al=Potential Acidity [cmol/dm³]; CS=Cation sum [cmol_c/dm³]; t=Effective cation exchange capacity [cmol_c/dm³]; V=Base saturation [%]; P-rem=Remaining Phosphorus [mg/L]; Impacts=Synthetic weighted value of impacts.



Figure 4. Canonical correspondence analysis (CCA) for the sampled area in a semideciduous forest in the municipality of Pouso Alegre, Minas Gerais: ordination diagram for the transects based on the distribution of individuals from 48 species with 10 sampled individuals or more and its correlation to soil traits and impacts. The identification of the transect (T) is composed by its number and a letter: 'E' for Forest Edge and 'I' for Forest Interior. The marker size is related to its position on the third axes. K⁺=Potassium [mg/dm³]; Ca²⁺=Calcium [mg/dm³]; Mg²⁺=Magnesium [mg/dm³]; H+Al=Potential Acidity [cmolc/dm³]; CS=Cation sum [cmolc/dm³]; V=Base saturation [%].

In the study area, species abundance was correlated with soil variables and impacts. The ordination weakly distinguished three transect groups in the first two axes: the first one consists of Edge transects 1, 7, 3 and 2, with values highly correlated with K+ and Impacts; the second one consists of Interior transects 4 and 6, with higher Calcium and Magnesium values, which contributed to the higher CS and V values; and the third one consists of 10, 11 and 12, the less impacted Interior transects. These relationships are closely linked to the distribution of species such as Eremanthus erythropappus and Ixora brevifolia, which dominated the first group. These species are favored by light at the edge, impacts and higher K⁺ levels. The north and south Edges in RBPA are on hilltops where the soil is generally deeper and more acidic than at the middle slope and lower heights (Resende et al., 2007). Therefore, Edge soils are sandier and consequently have better drainage, which leads to higher H+Al concentration and lower Ca²⁺ and Mg²⁺. This explains the high weighted correlations between Ca, Mg, CS and V, increasing towards the Interior. Additionally, Edge transects are more susceptible to impacts coming from the matrix (impacts at the Edge were nearly four times higher than in the Interior). Furthermore, the high weighted correlations for impacts and K+ (0.839), both decreasing towards the Interior suggest that at the Edge, where it is more susceptible to fire, there is an increase in K storage due to its incorporation by the occasional burning of organic matter (Faria et al., 2011). The permanence of K in the soil however, is compromised by the sandy texture at the edge, which facilitates the leaching of this nutrient (Werle et al., 2008).

4. CONCLUSIONS

The high diversity and low dominance found in the forest remnant highlight the importance of this site for conservation and highlight the need of further research about vegetation ecology of the often under evaluated fragmented areas.

As expected, we observed differences between Edge and Interior in relation to basal area and diversity (both attributes with higher values in the Interior). However, community seed mass was not as expected (higher value at the Edge). The correlation between species distribution, soil variables, and impacts was significant. The effects of higher values of soil traits such as Ca²⁺, Mg²⁺, CS and V on species composition were stronger in the Interior, while human induced impacts and soil Potassium had an overwhelming effect on the Edge.

We consider the protection of small forest fragments imperative, given the lack of large forest remnants and the current conservation status of the Brazilian Atlantic Forest. Therefore, we strongly recommend conservation efforts to focus on mitigating edge effects in small forest fragments.

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CORRESPONDENCE TO

Marcela de Castro Nunes Santos Terra

Departamento de Ciências Florestais, Universidade Federal de Lavras – UFLA, Av. Doutor Sylvio Menicucci, 1001, Kennedy, CEP 37200-000, Lavras, MG, Brasil e-mail: marcelacns@gmail.com

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