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Conifer plantations in grassland and subtropical forest: Does spider diversity respond different to edge effect?

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ABSTRACT

Two adjacent habitats separated by an abrupt transition often cause strong alterations in environmental conditions resulting in what is called the edge effect. The structural similarity between the adjacent habitats determines how abrupt the transition is. We explored the response of spider communities to the edge effect in mature pine plantations and compared for the first time those responses in contrasting biomes (subtropical forest and grassland) in southern South America. We expect that the higher the contrast between the natural habitat and the conifer plantation, the higher will be the magnitude and the lower the extent of the response of species richness and abundance to edge effect. We sampled spiders using pitfall traps located from the edge to the plantation interior, and environmental variables were measured in pine plantations (*Pinus taeda*) adjacent to native grassland and subtropical forest. Results revealed that wandering spiders were sensitive to edge effect in both subtropical forest and grassland, primarily reflected by a decline in the abundance toward plantation interiors. However, the magnitude and the extent of spider abundance response to the edge effect were similar between pine plantations developing in forest and grasslands biomes. Microclimatic conditions and vegetation cover partially explained species abundance from the edge to plantation interior. Our findings suggest that conifer plantations would promote spider richness if a wide range of microhabitats were provided and support the use of spider abundance to assess edge effect in forested landscapes.

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Introduction

The development of human activities such as forestry and agriculture typically creates abrupt edges between natural and human-modified habitats (Fischer and Lindenmayer 2007). The abrupt transition between adjacent habitats results in drastic alterations in biotic and abiotic conditions, known as edge effect (Murcia 1995). In response to the edge effect, communities, populations, species interactions and ecosystem processes often show changes through the transition between habitats (Ries et al. 2004). Although some studies on population or community responses to the edge effect have considered the transition from the interior of one of the habitats to the other (e.g. Peyras et al. 2013; Barnes et al. 2014), most research has focused from the edge toward the natural habitat (Malmivaara-Lämsä et al. 2008; Soga et al. 2013) and responses to the interior of the human modified habitat have been overlooked.

Commercial tree plantations are expanding worldwide over different biomes, and there is much debate about their role in biodiversity conservation compared to other land uses. In forest biomes, tree plantations may contribute to the conservation of native species by providing complementary habitats and increasing forest connectivity at the landscape scale (Brockerhoff et al. 2008). In grassland biomes, however, other land uses such as agriculture may be a better option for fauna conservation (Corbelli et al. 2015). In the Neotropics, forestry was

originally developed in forest biomes, growing later over grasslands. Studies on the consequences of commercial tree plantations on biodiversity are increasingly required for land-use planning and management. Understanding ecological patterns in different biomes, such as biodiversity responses to edges created by forest plantations, is highly relevant to assess the value of this land use for native species conservation.

Human-modified habitats may exhibit a wide range of physiognomic contrasts with the natural or semi-natural habitat that they replace (Harper et al. 2005). Habitats that preserve, at least partially, the original environmental conditions are expected to be more suitable for native species than highly modified habitats. For example, a previous study conducted in plantations and cropfields developing in subtropical forest and grassland biomes showed that native birds of the subtropical forest were better preserved in eucalypt plantations than in cropfields, whereas native grassland birds were better preserved in cropfields than in eucalypt plantations (Filloy et al. 2010). Thus, the suitability of patches of anthropogenic habitats, including their edges, may differ with the biome where human activities are developed (Allen and O'Connor 2000; Corbelli et al. 2015).

Environmental changes caused by edge creation tend to be drastic and often go beyond the original range of variation, and native organisms are usually negatively

affected (Bieringer and Zulka 2003). At the community level, a decline in species richness and abundance is expected as a result of reductions in resource quality, quantity and spatial distribution, and in the intensity of interactions such as predation or competition (Wimp et al. 2011). Previous studies showed that the edge effect is highly influenced by the physiognomic similarity between the adjacent habitats (Aragón et al. 2015). Two adjacent habitats could range from high- to low-contrast depending on the habitat features; the architecture of the edge may strongly influence edge permeability (Ries et al. 2004), even acting as barriers for certain species (i.e. specialist) because of drastic changes in habitat suitability (Peyras et al. 2013). Harper et al. (2005) proposed a quantification of the response to edge effect based in the magnitude of the change in species diversity and the distance from the edge where its influence can be detected. The magnitude of the edge effect is the difference of a given community attribute between the edge and the plantation interior, and the extent is the distance from the edge into the plantation where there is a significant change in a given community attribute. Then, edge effect could range from steep and short (i.e. large magnitude, small distance) when the edge permeability is low; to shallow and long (i.e. small magnitude, large distance) when the edge permeability is high. Thus, we expect that the magnitude of edge effect on community diversity will be greater, and the extent lower in plantations with high-contrast edges (i.e. low permeability) than in plantations with low-contrast edges (i.e. high permeability).

Spiders are among the most diverse group of predators on terrestrial ecosystems (Wise 1993), and exhibit several characteristics that make them highly suitable as biological indicators of ecosystem quality (Prieto-Benítez and Méndez 2011). They usually show rapid responses to disturbances, are sensitive to changes in environmental conditions (e.g. temperature and humidity) and in the quantity or quality of resources, and are relatively easy to sample (Pearce and Venier 2006). Moreover, recent research emphasized the key role of spiders in top-down regulation of communities, in addition to the view of predators as biological control agents (Nyffeler and Birkhofer 2017).

Previous studies showed that some arthropods, including spiders, responded negatively to edge effect in forested landscapes (e.g. Larrivé et al. 2008; Kowal and Cartar 2012; Soga et al. 2013). However, it remains to answer whether that response depends on the biome where tree plantations are developed. The goal of this study was to examine the response of ground-dwelling spider assemblages to the edge effect toward the interior of mature pine plantations, and compare the magnitude and extent of such response between plantations developing adjacent to natural habitats in subtropical forest and grassland biomes. Biomes were selected to provide contrasting vegetation types and regional species pools, and because vegetation structure in mature pine plantations is more similar to the subtropical forest than to the grassland. Given that spiders usually respond to environmental changes at the microsite scale (Petcharad et al. 2016), we also investigated the environmental factors associated to spider species distribution within the transition from the edge to plantation interior.

Materials and methods

Study area

The study was conducted in pine plantations developing in a forest and a grassland biome. Study sites in the forest and grassland biome were located in the southern Atlantic Forest (25°36'S, 54°24'W) and in the Campos and Malezales ecoregion (29°42'S, 57°05'W), respectively, in Argentina. The southern Atlantic Forest is characterized by a mosaic of native forest remnants in protected areas, commercial tree plantations in private lands and patches used for subsistence farming. Primary land use is for commercial exotic tree plantations of pine (*Pinus taeda*), eucalypt (*Eucalyptus* spp.) and the native *Araucaria angustifolia* (Zurita and Bellocq 2010). The canopy is dominated by Myrtaceae, Lauraceae and Leguminosae trees, and the understory is composed mainly by ferns and bamboos (Oliveira-Filho and Fontes 2000). The climate is subtropical, mean annual rainfall and temperature is 2000 mm and 21° C, respectively, with a cold season extending between June and August. Rainfall is evenly distributed throughout the year (Servicio Meteorológico Nacional 2006). The Campos and Malezales ecoregion is characterized by grasses such as *Paspalum*, *Schizachyrium*, *Andropogon*, and *Axonopus*; and forbs such as *Gomphrena*, *Mitracarpus*, and *Euphorbia* (Matteucci 2012). The area has been used for extensive cattle raising for the last three centuries, thus grasslands became a mixture of native and exotic grass species growing spontaneously (i.e. seminatural grasslands). Currently, financial incentive to the forestry industry promotes a change in land use into tree plantation (MAGyP and SAyDS 2015). The climate is subtropical without dry season; mean annual temperature varies between 19 and 20°C, and a mean annual precipitation is approximately 1200 mm evenly distributed throughout the year (Matteucci 2012).

Study design

To study the influence of habitat contrast on the edge effect in community attributes, we analyzed spider species richness and abundance in plantations adjacent to two contrasting native habitats: subtropical forest and semi-natural grassland. In each ecoregion, we selected three 09-year-old *Pinus taeda* plantations (replicates), separated by at least 1.5 km, mostly surrounded by either natural forests or seminatural grasslands (Figure 1). At each pine plantation, we established sampling stations along a transect at 0, 5, 15, 30, 50, 100, 150, 200, and 300 m from the first line of trees into the plantation interior. Previous studies have found that the effect of edges on invertebrates disappear within the first 100 m into the forest (Bieringer and Zulka 2003; Ries et al. 2004; Petcharad et al. 2016); to avoid the influence of other edges and ensure that the sampling station at 300m from the edge represented a clear interior environment, each transect was at least 600-m apart from other edges.

Spider sampling and identification

At each sampling station, two pitfall traps (subsamples) were placed 10-m apart from each other to avoid interference between traps. We used two traps to minimize the

probability of losing samples, and when both subsamples persisted the analyses were conducted on one sample randomly selected. Each trap consisted of two plastic cups of 1000 cm³ stacked together, with 8.5 cm diameter and 10.5 cm deep buried flush with the ground. Traps were half filled with a mix of propylene glycol and water (30:70) to preserve arthropods. A plastic roof was placed 10 cm above the trap to prevent flooding and evaporation (Duelli et al. 1999). Pitfall traps operated during the whole summer (from January to March 2013), and were visited every three weeks for arthropod collection and liquid renewal. Adult spiders were identified to species or morphospecies using taxonomic keys (see supplementary material S1) and assistance of arachnologists.

Environmental variables

To estimate microclimatic conditions relevant to invertebrate macrofauna, temperature sensors were placed at the ground level at each sampling station. Sensors were left in the field during three 7-day periods, covering the complete sampling period. Because of the limited number of sensors, they rotated among replicates and sampling periods; thus, we obtained an overall estimation of mean temperature (T_{mean}) for each distance from the edge by averaging the values for the three sampling stations located at the same distance from the edge.

At each sampling station, vegetation was classified by life form and coverage was estimated in a 5 m × 5 m quadrant using an adaptation of the Braun-Blanquet quantification (Braun-Banquet 1964). Thus, a percentage cover was assigned for grasses (GRAS), forbs (FORB), shrubs (SHRU), ferns (FERN), bare soil (BARE), and leaf litter (LITT). To estimate the percentage canopy cover (CANO) at each sampling distance, one photograph was taken up from 1.5 m above the ground (Peyras et al. 2013).

Data analyses

We first described spider responses to edge effect for each biome. Because both species richness and abundance (response variables) were variables obtained from counts, we ran generalized linear models (GLMs) with mixed effects suitable for Poisson distribution (Zuur et al. 2009). We entered distance from the edge as a quantitative predictor and each pine plantation as a random factor to account for the correlation structure of data obtained from the same plantation. We fitted different models describing a proportional response (straight linear), and a peak or valley response to describe the loss or gain of species at intermediate distances from the edge (second and third degree polynomial) using the logarithmic link function. For each biome, the most parsimonious model was selected based on the smallest value of the Akaike information criterion (AIC). When two or more models showed similar AIC values (this is $\Delta\text{AIC} < 2$), the simplest model (i.e. with less parameters) was retained. GLMs and the model selection procedure were performed using R software (R Core Team 2015).

To examine the extent of edge effect (EE) and magnitude of edge effect (ME) response, we ran mixed effect GLM including distance, biome and their interaction as categorical predictors and plantation as a random factor. The

Pearson's residuals against predicted value plots were checked for a random pattern (e.g. to avoid potential effects of spatial autocorrelation). Then we ran Tukey multiple comparisons and obtained the minimum significant difference (MSD). Thus, the EE was obtained by identifying the distance at which mean richness or abundance significantly changed with respect to 0 m (adapted from Harper et al. 2005). The ME was estimated as the difference in mean richness or abundance between the sampling stations at the extreme distances of the edge (0 m and EE). Using the MSD from Tukey estimations we calculated the 95% confidence intervals for the ME. GLMs and Tukey multiple comparisons were performed using R software (R Core Team 2015).

Finally, a single redundancy analysis (RDA) including data for both biomes was performed using R software (R Core Team 2015) to describe station ordination based on species responses to local environmental conditions. We characterized sampling stations taxonomically and environmentally and identified the environmental variables primarily associated with the distribution of individual spider species toward plantation interiors. The species matrix included abundance data, and the environmental matrix included habitat type (Forest and Grassland), microclimatic and land-cover variables as well as distance from the edge (reflecting the potential influence of a non-measured environmental variable covarying with distance).

Results

We collected a total of 195 individual spiders from 44 species or morphospecies (Table S1 in Supplementary Material). Of the 126 individuals collected in pine plantations developing in the grassland biome, 42% were adults from 15 families and 33 species or morphospecies. The most abundant families were Theridiidae (26%) and Lycosidae (26%), considering only adults. In plantations located in the subtropical forest, we collected 69 individuals representing five families and 12 species/morphospecies. Adult individuals were 32% of the total spiders caught; dominant families were Lycosidae (39%) and Ctenidae (30%).

Along the 300-m transects in plantations developing in the grassland biome, spider richness was best described by a second degree polynomial function ($y = 3.020 - 1.200x + 0.033x^2$), declining from the edge to a minimum at 150 m, and then increasing toward the plantation interior (Figure 2(a)). A different response was observed in plantations from the subtropical forest, where spider richness linearly declined from the edge to the interior ($y = -0.126 + 0.0027x$, Figure 2(b)). Total abundance responses to the distance from the edge were best described by the same models as for species richness: polynomial ($y = 2.110 - 0.249x + 0.036x^2$) and straight linear ($y = 1.200 - 0.0032x$) functions in grassland and subtropical forest, respectively (Figure 2(c,d); models selected with their AICs see Table S2 in Supplementary Material).

Results from GLMs with distance as a categorical factor showed that distance-biome interaction was detected neither for spider richness ($p = 0.08$) nor for spider abundance ($p = 0.25$). However, species richness changed with distance ($p = 0.01$); Tukey comparisons showed a significant decrease in mean species richness, only at 15m and 150m from the edge to the plantation interior ($p < 0.05$ for both

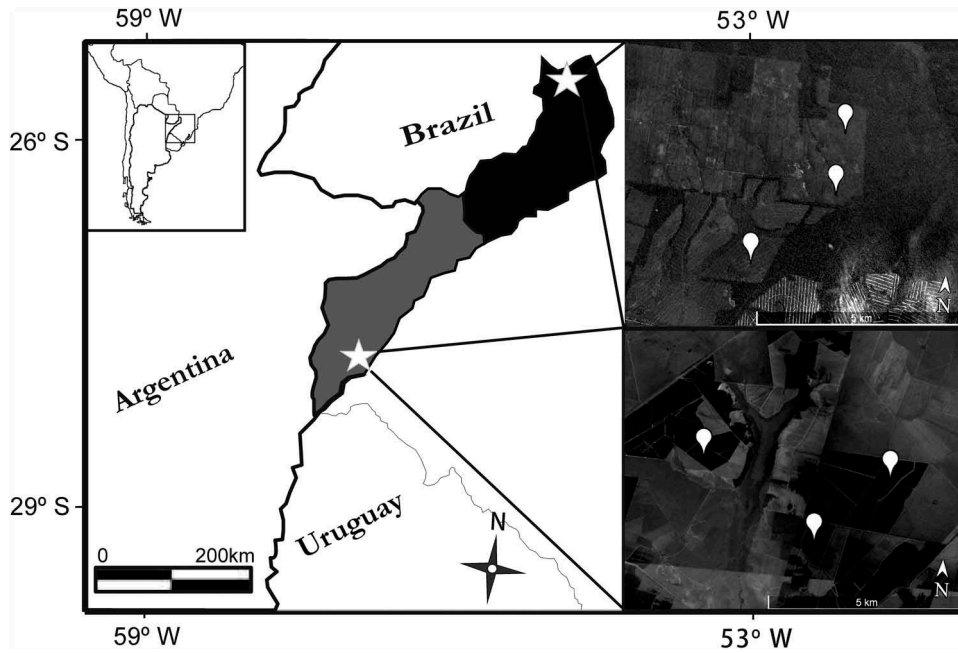


Figure 1. Location of study pine plantations (white stars) in the Atlantic forest (black area) and Campos and Malezales grassland (gray area) of Argentina. It is detailed the location of the three replicates (white balloons).

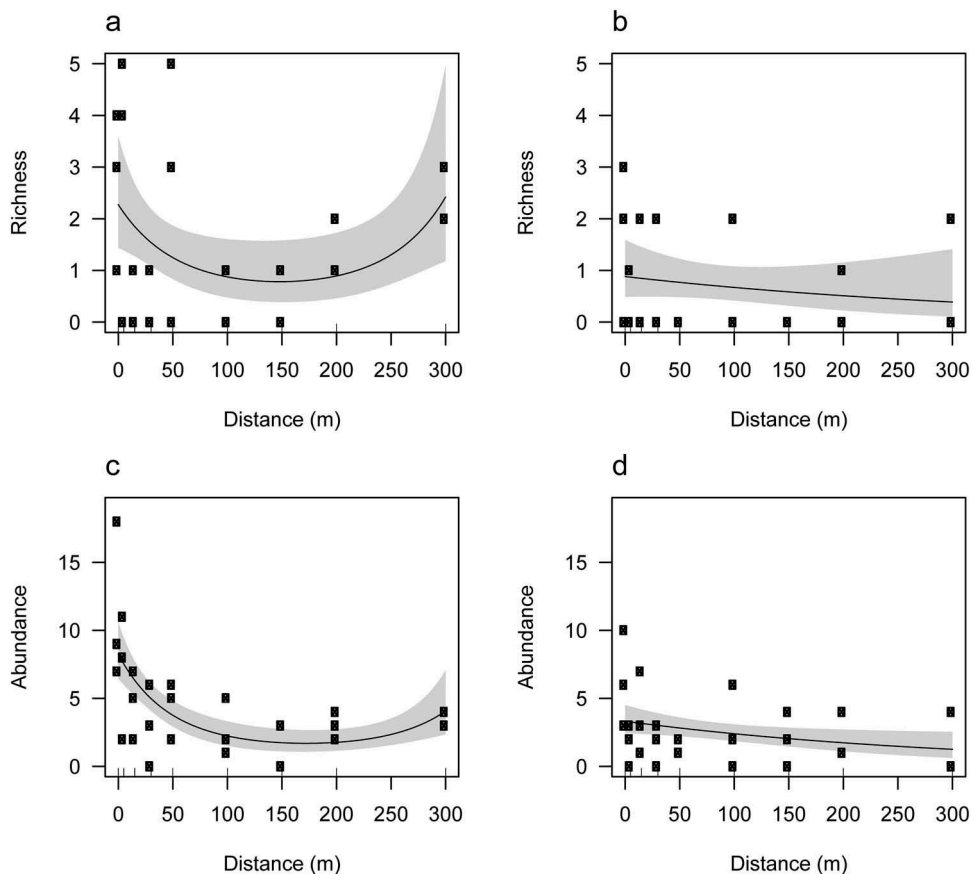


Figure 2. Trends (solid lines), obtained from GLMs, in spider richness and abundance from the edge (0 m) to the interior of pine plantations (up to 300 m) developing in two contrasting biomes, grassland (a and c) and subtropical forest (b and d). Gray areas indicate 95% confidence bands.

comparisons). For spiders total abundance, there was also a significant response to distance ($p < 0.001$). Tukey comparisons revealed that spider abundance decreased for all distances from 5 m to 300 m with respect the 0 m ($p < 0.05$ for all comparisons). Thus, the obtained extent of the response (EE) was 5 m from the edge for both biomes. The

magnitude of the abundance decay due to the edge effect (ME) was 4.53 ± 2.85 (estimate \pm standard error) individuals, between sampling stations located at 0 m and 5 m.

The RDA for spider assemblage responses to environmental variables across plantations explained 61% of the variation in the species abundance, with first and second

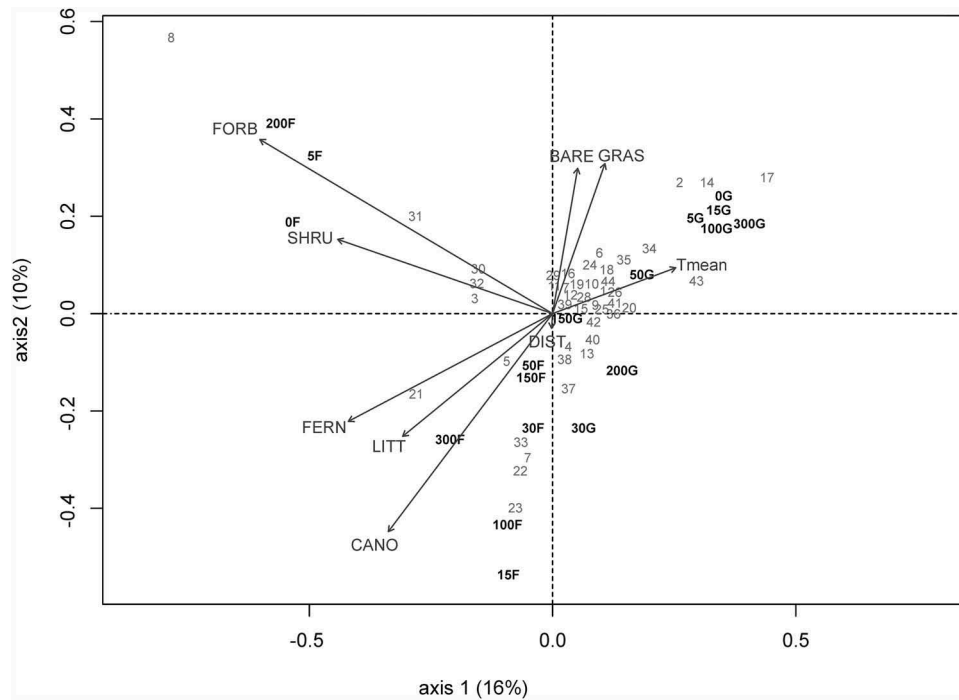


Figure 3. Sampling stations ordination based in spider species responses to environmental variables obtained from RDA analysis for all sampled pine plantations. Sites symbols indicate the distance from the edge (0–300 m) followed by site location in forest or grassland biome (F or G, respectively). Environmental variables abbreviations clarified in Material and Methods. Single numbers represent spider species (details provided in Table S1 in Supplementary Material).

axis accounting for 16% and 10%, respectively. The ordination of sampling stations along Axis 1 clearly separated sampling stations from each biome, locating forest stations at the left and grassland stations at the right of the axis (Figure 3). Plantations developing in the subtropical forest biome were characterized by the highest vegetation cover (i.e. forbs, shrubs, and fern) while plantations in grassland showed the highest mean temperature and grass cover. Within each biome, sampling stations ordered along Axes 1 and 2 (Figure 3) regardless of the distance to the edge. When plotting Axis 1 vs. Axis 2, the abundance of five species/morphospecies from subtropical forest biome (Ctenidae indet. sp.2, Salticidae indet. sp.1, Salticidae indet. sp.2, and Salticidae indet. sp.3) were mostly caught at short distances (0–5 m) and at 200 m from the natural habitat; those sampling stations were characterized by high coverage of shrubs and forbs. Stations with high fern, canopy and leaf litter cover showed high abundance of Ctenidae indet. sp.1, Lycosidae indet. sp.5 and Salticidae indet. sp.4. In the grassland biome, species abundance was positively associated with grass cover and mean temperature (i.e. *Sphecozone cf. novaetetoniae*, *Caponina alegre*, and *Lycosa erythrognatha*) at sampling stations located at 0, 5, 15, 100, and 300m from the edge; other stations at intermediate distances were characterized by *Castianeira* sp., *Dipoena* sp., and *Theridion* sp.

Discussion

The observed patterns of spider richness and abundance from the edge to the interior of the pine plantations differed between grassland and forest biomes. The decay in spider species richness and abundance toward plantation interior seemed to be stronger in the grassland-plantation than in the forest-plantation transition from the edge up to the 150

m into the plantations, where a recovery toward the plantation core was observed in the grassland biome. However, contrary to our predictions, extent and magnitude estimations of spider abundance response to the edge effect, was the same in both biomes (i.e. independently of the level of contrast between the two habitats). Microhabitat environmental conditions accounted for spider individual species distribution irrespective of the distance from the edge, as previously found by Petcharad et al. (2016).

The decay in both richness and abundance was followed by a slight increase at plantation interior in the grassland biome. Spider dispersal ability over long distances with the wind using silk threads (mechanism known as “ballooning”, Bishop and Riechert 1990) may allow movements from the grassland habitat into the pine plantation interior. Thus, once dispersed, they may establish themselves in pine plantations interior if favorable microhabitat conditions were found (Beltramo et al. 2006). Spiders found at pine plantations interior in the grassland biome belonged to the Linyphiidae, Theridiidae, Lycosidae, and Salticidae families, which have been documented to tend to balloon at early instars because that mechanism shows size restrictions (Dean and Sterling 1985). Moreover, species showing ballooning dispersal would be able to move long distances and reach plantations settled in open habitats such as grasslands, as higher wind speed and less structural interference is expected than in habitats such as subtropical forest (Vespa et al. 2014).

The EE and ME of the spider abundance response to the edge effect in conifer plantations did not show differences between grassland and forest biomes. Our results showed that the edge effect on the spider community in conifer plantations had the same strength regardless of the biome where plantations developed. Although tree plantation established in forest biomes result in the development of

vertical structure beneficial to wildlife species (Duran and Kattan 2005), silvicultural management might impact spiders negatively through, for example, the scarce understories due to site preparation (Marcos et al. 2007), the uniformity of plantation forest structure (Aubin et al. 2008), and changes in ecological processes of decomposition and leaf litter (Barlow et al. 2007). On the other hand, our results might be influenced by methodological limitations because we used pitfall traps, and then catches depend on species activity (Downie et al. 1996) and on the vegetation structure surrounding the pitfall trap influencing capture rates of invertebrates (Oxbrough et al. 2005). Therefore, the response of those less mobile individuals, such as web-building spiders, may be overlooked by our trapping system.

The narrow edge extent (i.e. 5 m) recorded in plantations from both biomes was consistent with previous studies on spider assemblages in different types of edge transitions caused by human land use (Bedford and Usher 1994; Gallé and Fehér 2006). For example, Bedford and Usher (1994) reported that the extent of spider and carabid responses to the edge effect between farmlands and managed forests extended no more than 5 m into plantations. Thus, in contrast to natural ecotones which are generally characterized by a gradual environmental change, anthropogenic land-use transitions usually experience abrupt structure alterations, such as the first line of trees in pine plantations. Thus, narrow EE could be explained by the fact that spiders, as small-bodied organisms, may perceive and interact with the habitat at spatial scales much smaller than many vertebrates (De Mas et al. 2009) and would respond at short distances if structural changes occurred at short distances as well. Furthermore, it is possible that our trap spacing failed to detect a gradient between 0 and 5 m from the edge.

We found that spider abundance but not species richness responded to edge effect in both biomes. Previous studies also showed responses in spider abundance but not in richness along anthropogenic land-use transitions (Martin and Major 2001; Prieto-Benítez and Méndez 2011). The study conducted by Martin and Major (2001) in Australia, showed that abundance but not species richness of the Lycosidae family decreased through a woodland–pasture paddock boundary. In our study, Lycosidae was one of the dominant families in both biomes, and individuals from that group were present at different distances showing abundance decay from the edge to the interior of the plantations. However, because lycosids are ground-dwelling spiders, they have lower dependence on vegetation structure than web-building spiders (Bell et al. 2001); more exhaustive surveys using other trapping techniques may reveal additional patterns not only in spider abundance but also in species richness. In addition, the lack of a strong richness response to the edge effect may be explained by the early mechanical disturbances and pesticide applications, that generally occur in the first years of the plantation cycle (Roberts 2002), negatively associated with spider diversity (Prieto-Benítez and Méndez 2011). Species able to disperse into mature pine plantation would have time to establish themselves and reproduce as the plantation is relatively stable ecosystem until harvesting.

The environmental variables we measured were associated with the distribution of individual spider species

from the edge to the interior of pine plantations. In the grassland biome, the abundance of some species (i.e. *Sphecozone* cf. *novaetentoniae* and *Caponina alegre*) was associated with grass cover and this could be caused by the indirect effect of it. For example, herbaceous vegetation may provide support for webs, increase food resources and serve as refuge from predators (Yamazaki et al. 2017). In forest biomes, species that showed high abundance at short distances (i.e. 0 m and 5m) were different from those found from 15 m to the interior (with exception of 200 m); such difference along edge plantations might be associated with changes in environmental conditions that occur from 5 m to the interior, consistent with the estimated edge extent of 5 m. Since microhabitat requirements vary between species, it would be expected that the provision of a range of different microhabitats (i.e. favoring the establishment of grass or understory vegetation) might result in a high number of spider species and total density of individuals in conifer plantation interior (Sunderland and Samu 2000). Thus, it would be also expected that conifer plantations in our study sites would harbor high spider species richness if a wide range of microhabitats were promoted.

In summary, we found that the response of spider abundance to the edge between native habitat and exotic conifer plantations had similar strength in two contrasting biomes (subtropical forest and grassland). In addition, as species abundance responded to plantation variables, further research is required to evaluate land management strategies (i.e. performing understory vegetation manipulation) on spider communities and investigate how to enhance spider populations at edges of conifer plantations, settled in different climatic contexts. To our knowledge, no previous studies have analyzed the EE and the ME in spider assemblages in contrasting biomes. Further research is needed to specifically investigate the influence of alternative factors, not included in this study, on spider responses to edge effect. Finally, our results support the use of spider abundance as a proxy of the spider assemblage response to the edge effect in forested landscapes.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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