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Research Letters

Processes related to habitat selection, diversity and niche similarity in assemblages of non-volant small mammals at grassland–forest ecotones

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ABSTRACT

Habitat suitability for mammal species in grassland/forest ecotones may be affected by changes in abiotic conditions (e.g. light incidence), grazing and burning disturbances, and woody encroachment. We evaluate models addressing the role of such factors on structuring non-volant small mammal assemblages considering (1) only disturbed and (2) all ecotones (disturbed and undisturbed). A complete model (i.e., abiotic gradients, disturbances and woody encroachment) was the most plausible for abundance considering all ecotones, and for niche similarity considering both all and only disturbed ecotones. Niche similarity increased with distance from hydric resources, and abundance with increasing vegetation height. Further, disturbed habitats harbored simplified species assemblages. Habitat selection was detected in all ecotones due to the occurrence of habitat-specialist species on undisturbed sites. We did not find an exclusive influence of woody encroachment on mammal diversity. Patterns described here are relevant for management of productive lands and for biodiversity conservation.

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Introduction

Habitat suitability is a pre-requisite for species occurrence. Selection of specific habitats – triggered by different niche requirements of species – generate non-random patterns of small mammal distribution across gradients (Kingston and Morris, 2000), which might influence the structure and

ecological roles performed by mammal assemblages. Non-random patterns of species distribution along ecological gradients (as grassland–forest ecotones) may be an effect of changes on vegetation structure along edges, which alter edge permeability to abiotic factors (e.g. light, temperature), flux nutrients and individuals, and also alters resource distribution, availability and acquisition by species (Ries et al., 2004).

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Edge effects alter assemblage's diversity and lead non-volant small mammals to select specific microhabitats (Kingston and Morris, 2000; Wilson et al., 2010). Besides edge effects, moisture gradients seem related to the presence of refuges areas, which makes habitat colonization by small mammal populations more probable (Milstead et al., 2007). Changes in abiotic conditions along ecotones suggest a strong selection of preferable habitats by small mammals (Wilson et al., 2010). However, diversity patterns across grassland-forest habitats may be generated by processes that alter vegetation heterogeneity – e.g. grazing, woody encroachment – rather than abiotic gradients (Pedo et al., 2010; Sponchiado et al., 2012).

Ecological disturbances such as woody encroachment, burning and/or cattle grazing/trampling deeply alter the structure of grassland and forest habitats, and likely shape the spatial and temporal dynamics of ecotones in southern Brazil (Müller et al., 2012). Woody encroachment over grasslands is a natural process caused by higher precipitation and humidity during the Late Pleistocene-Holocene (4000 years-today) compared to Middle Pleistocene ($\approx 10,000$ years) (Behling et al., 2004). Warm climate favors forest expansion and has created, in some regions of southern Brazil, vegetation mosaics of grasslands interspersed with forests (Behling et al., 2004). Woody encroachment is mainly observed where disturbances such as fire and grazing have been suppressed (Müller et al., 2012). Forest expansion is considered a global threat to biodiversity of grassy biomes (Bond and Parr, 2010; Veldman et al., 2015) due to species turnover mediated by increases in the frequency of shrubs and trees on grasslands, allowing colonization of forest flora/fauna. In southern Brazil, management to prevent woody encroachment usually includes burning, grazing and mowing (Pillar and Velez, 2010). These disturbances affect the heterogeneity and suitability of forest and grassland habitats, and offer differential conditions for small mammal colonization, reproduction and food acquisition (Dunstan and Fox, 1996; Fox et al., 2003).

Woody encroachment and light disturbance also promote local heterogeneity by adding vegetation strata and increasing habitat complexity (Fox et al., 2003). Concerns about the management of grassland and forest habitats with disturbances – generally applied throughout landscapes – have arisen recently for southern Brazilian grasslands – *Campos Sulinos* (Luza et al., 2014) and for other regions worldwide (Andersen et al., 2012), because sites where disturbance are absent or at low levels (i.e., high vegetation, deep litter layer, presence of tree/shrub strata) are preferred by small mammals (Pedo et al., 2010; Sponchiado et al., 2012). Rodents and marsupials are the richest mammal orders in *Campos Sulinos* – together with Carnivora (Luza et al., 2015b). Ecological roles performed by small mammals include seed removal and dispersal, predation of seedlings, seeds, fruits and arthropods (Iob and Vieira, 2008), biological resistance against invasive plants (Muschetto et al., 2015), nutrient cycling, bioturbation, and as vectors of human diseases (Medan et al., 2011). Improper management may cause species losses and environmental disequilibria, which may alter both assemblage diversity and functional roles performed by mammals. Thus, grassland-forest ecotones are useful to contrast hypothesis on the effect of abiotic gradients from

hypothesis that depict different sources and levels of disturbances that alter habitats and the structure of small mammal assemblages.

The study aimed to identify processes that affect the diversity of non-volant small mammal assemblages from grassland-forest ecotones under different management regimes. We used species composition, richness, total abundance and niche similarity between co-occurring species as assemblage descriptors, and then built models that embraced: (1) abiotic gradients, (2) grazing/burning, and (3) woody encroachment. For species richness and for specialist species (differentiating between forest and grassland habitats) we expected a strong effect of abiotic gradients (mainly canopy openness). We expected a negative effect of grazing/burning for abundance, but a positive effect to generalist species and to niche similarity. We expected a positive effect of woody encroachment for forest mammals. We also built models disregarding ecotones where grazing/burning were absent for a long time (22 years), and expected a positive effect of grazing/burning on assemblage structure, due to higher frequency of mammals adapted to disturbances.

Materials and methods

Study area and sampling of non-volant small mammals

The study area comprised nine sites at *Campos Sulinos* (Fig. 1A), distributed along several grasslands and forest physiognomies in southern Brazil. We essentially considered ecotones under different intensities of burning and/or grazing disturbances, and where forest expansion occurs by the presence of nurse plants and forest patches within grasslands (Duarte et al., 2006).

Captures took place from October through November 2011, January through April and September and December 2012, and February 2013. To evaluate a wide range of habitat characteristics, we regionally distributed our surveys (mean distance between sites = 326.48 ± 153.28 km; longest distance = 553 km). In each of the nine sites, we established two 140×140 m grids (Fig. 1B) at least 1 km distant from each other (total 18 grids) and sampled each site during ten days (five days for each grid); eight transects 20 m apart (four at forest and four at grassland) disposed along the interface between grassland and forest composed the grid (Fig. 1C). We employed as a basic sampling unit a transect composed of eight capture points – a point contained one Sherman ($25 \times 8 \times 9$ cm) and one Tomahawk trap ($45 \times 17.5 \times 15$ cm). We reset traps in the morning and afternoon, totaling an effort of 1280 traps/grid. We measured, marked with small cuts on the ear, and released animals at the same capture point; identification of specimens at species level was performed using DNA sequencing (details in Luza et al., 2015a).

Habitat structure

We evaluated variables in each capture point, and then averaged at the transect scale. Abiotic gradients were characterized by distance from the nearest hydric resource (streams,

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