


# Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss

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## Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 307689/2014-0, 309934/2015-0, 310022/2015-0 and 563271/2010-8; Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul, Grant/Award Number: 11/2185-0; European Commission, Grant/Award Number: FPA 2023-0224/532524-1-FR-2012-1-ERA MUNDUS-EMMC

Handling Editor: Jeremy James

## Abstract

- Habitat loss is one of the greatest threats to biodiversity, exerting negative effects on the ecological viability of natural vegetation remnants. The south Brazilian grasslands belong to one of the largest temperate grassland regions in the world, but have lost 50% of their natural extent in the past 35 years. To date, there is no empirical evidence for the effects of habitat loss on these grasslands' biological diversity, undermining their conservation.
- Using data from a large-scale biodiversity survey, we asked if local plant communities respond to levels of habitat loss representative of the entire region ( $\leq 50\%$ ). Vegetation in grassland remnants was sampled in 24 landscapes at three localities each, using nine plots per locality. To investigate whether species losses were a consequence of stochastic or nonrandom local extinctions and whether plant communities became more homogenized, we evaluated species richness, beta-diversity components (spatial turnover and nestedness), and phylogenetic diversity, in respect to landscape change. In part of the landscapes, arthropods were sampled to investigate if loss of plant diversity had a cascading effect on other trophic levels. We evaluated generic richness of ants, an omnivore group with high levels of plant associations, in respect to a plant community's phylogenetic diversity.
- Local plant communities in landscapes with less grassland cover had fewer species, less spatial turnover, increased nestedness and lower phylogenetic diversity. Our results suggest that the observed species loss can be linked to taxonomic homogenization and is nonrandom, decreasing evolutionary diversity within the community. Furthermore, ant richness declined by 50% in plant communities with the lowest phylogenetic diversity, suggesting that effects of habitat loss propagate to higher trophic levels.
- Policy implications.* We conclude that the biological diversity of south Brazilian grasslands, at the producer and consumer level, is at risk under the current rate of land-use conversion, even at habitat losses below 50%. To avoid substantial biodiversity loss, conservation and more restrictive policies for conversion of native grasslands to different land uses in South Brazil are urgently needed.

## KEYWORDS

ants, biodiversity, grasslands, land-use conversion, nestedness, phylogenetic diversity, resource diversity, spatial turnover, species richness, trophic cascade

## 1 | INTRODUCTION

Habitat loss has been, and still is, the greatest threat to global biodiversity (Balmford et al., 2005; Rands et al., 2010). When analysing threats to biodiversity, it is important to consider the effects of larger spatial scales on the species composition of local ecological communities (Fahrig, 2001; Ricklefs, 2008). As the amount of natural habitat in anthropogenically modified landscapes declines, continuous habitat is usually broken into multiple smaller fragments (Gardner & O'Neill, 1991) and the average distances between habitat fragments increase (With & Crist, 1995). As a result, the importance of ecological drift increases, while recolonization that could counterbalance stochastic local extinctions decreases. Moreover, a greater exposure to human land uses is likely to influence community assembly processes in habitat remnants (Mack & D'Antonio, 1998).

Communities post-habitat loss is in a process of disassembly and assembly, i.e. stochastic and deterministic local species extinction and colonization occur simultaneously (Connell & Slatyer, 1977; Diamond, 1975; Ostfeld & LoGiudice, 2003; Zavaleta et al., 2009). Driven by anthropogenic stressors, the species favoured during assembly typically differ from those lost during disassembly (Zavaleta et al., 2009). Favoured species are disturbance-tolerant, widely distributed and sometimes cosmopolitan, ruderal or exotic species, whereas the species lost are rare, specialist, endemic or narrowly distributed native species (Naaf & Wulf, 2010; Tabarelli, Peres, & Melo, 2012). This human-induced process of replacement of species types typically leads to biotic homogenization (McKinney & Lockwood, 1999; Tabarelli et al., 2012), i.e. reduced beta-diversity (taxonomic homogenization) and/or increased ecological similarity of species (ecological homogenization; Olden & Rooney, 2006). Increased ecological similarity of species may be the result of nonrandom extinctions that are not only restricted to endemic and rare species but to species of particular guilds or evolutionary lineages, in which traits vulnerable to effects of habitat loss are conserved (Heard & Mooers, 2000; Winter et al., 2009).

If evolutionary lineages of primary producers are lost with habitat loss, this will likely affect associated mutualists and antagonists as well (Dinnage, Cadotte, Haddad, Crutsinger, & Tilman, 2012). For instance, many herbivores show phylogenetic structure in their diets—they feed on groups of closely related genera or species (Ødegaard, Diserud, & Østbye, 2005; Weiblen, Webb, Novotny, Basset, & Miller, 2006)—or respond to the diversity of resources, i.e. plant traits (Armbrecht, Perfecto, & Vandermeer, 2004). Thus, plant biotic homogenization may lead to bottom up effects and/or trophic cascades, in which community reorganization is not only restricted to plants but propagates through all trophic levels. Biotic homogenization may thus collapse intricate networks of interactions of various trophic levels, result in

taxonomic, ecological and genetic impoverishment and thereby reduce ecosystem functioning and resilience (Cadotte, Dinnage, & Tilman, 2012; Fraser et al., 2015; Norden, Chazdon, Chao, Jiang, & Vilchez-Alvarado, 2009; Olden, 2006).

Given the fast rate of land-use change in many regions of the world, including southern Brazil (Overbeck et al., 2015), there is an urgent need to understand at which amount of habitat loss these processes unfold. There is empirical evidence for considerable local extinctions to occur with severe rates of habitat loss, e.g. when the remaining natural habitat occupies below 10% to 30% of the landscape (Andr n, 1994; Cousins, Lavorel, & Davies, 2003). However, there is little and less coherent information on biodiversity erosion under less dramatic dimensions of habitat loss.

Due to their fertile soils and favourable topographic features, the temperate grassland biome has become the most extensively modified ecosystem by humans (Henwood, 1998). The grasslands of South Brazil, Argentina and Uruguay are jointly one of the largest temperate grasslands regions in the world and the most extensive in South America (Soriano et al., 1991). In South Brazil, these grasslands are named *Campos Sulinos* or simply *Campos* (Lindman, 1906) and form Brazil's Pampa biome until transitioning into the more northern Atlantic Forest biome. While harbouring high levels of biodiversity—estimates reach a total number of 3,000 grassland plant species (Boldrini, 1997)—and endemism, the *Campos* of Rio Grande do Sul have lost 50% of their original distribution in only 35 years due to agri- and silvi-cultural expansion (Cordeiro & Hasenack, 2009). This contrasts with a low protection level: A negligible percentage of 2.58% of *Campos* area is protected (Brand o, Trevisan, & Both, 2008). In fact, Brazil's Pampa biome presents the highest Conservation Risk Index of all Brazilian biomes (Overbeck et al., 2015).

Here, we used data from a large-scale biodiversity survey carried out in the *Campos* of Rio Grande do Sul and investigated different aspects of community organization. We hypothesized that relatively moderate levels of habitat losses—i.e. up to 50%, the current overall level of landscape change in the region—may already lead to locally species-poorer plant communities. We then asked if this species loss is linked to taxonomic homogenization because of altered post-habitat loss community assembly. For this, we disentangled overall beta-diversity into its antithetic species gain (turnover) and species loss (nestedness) components. We expected a decline of species turnover and a simultaneous increase of nestedness in response to habitat loss. Further, we addressed plant community composition from an evolutionary perspective. We expected ecologically more similar local plant communities due to nonrandom species loss, thus a decrease in phylogenetic diversity (Nee & May, 1997), measured at the basal nodes and at the tips of the plant community's phylogeny.

Given the shared evolutionary history of particular plant clades with their mutualists and antagonists, we expected more habitat and/or feeding niches for consumer communities in phylogenetically more diverse plant communities. We used ants as a model system since they comprise high levels of association with plants, benefiting both from plant-derived food resources and also herbivore insects as prey (Mayer, Frederickson, McKey, & Blatrix, 2014). We expected declines in ant richness if plant evolutionary lineages are lost with habitat loss.

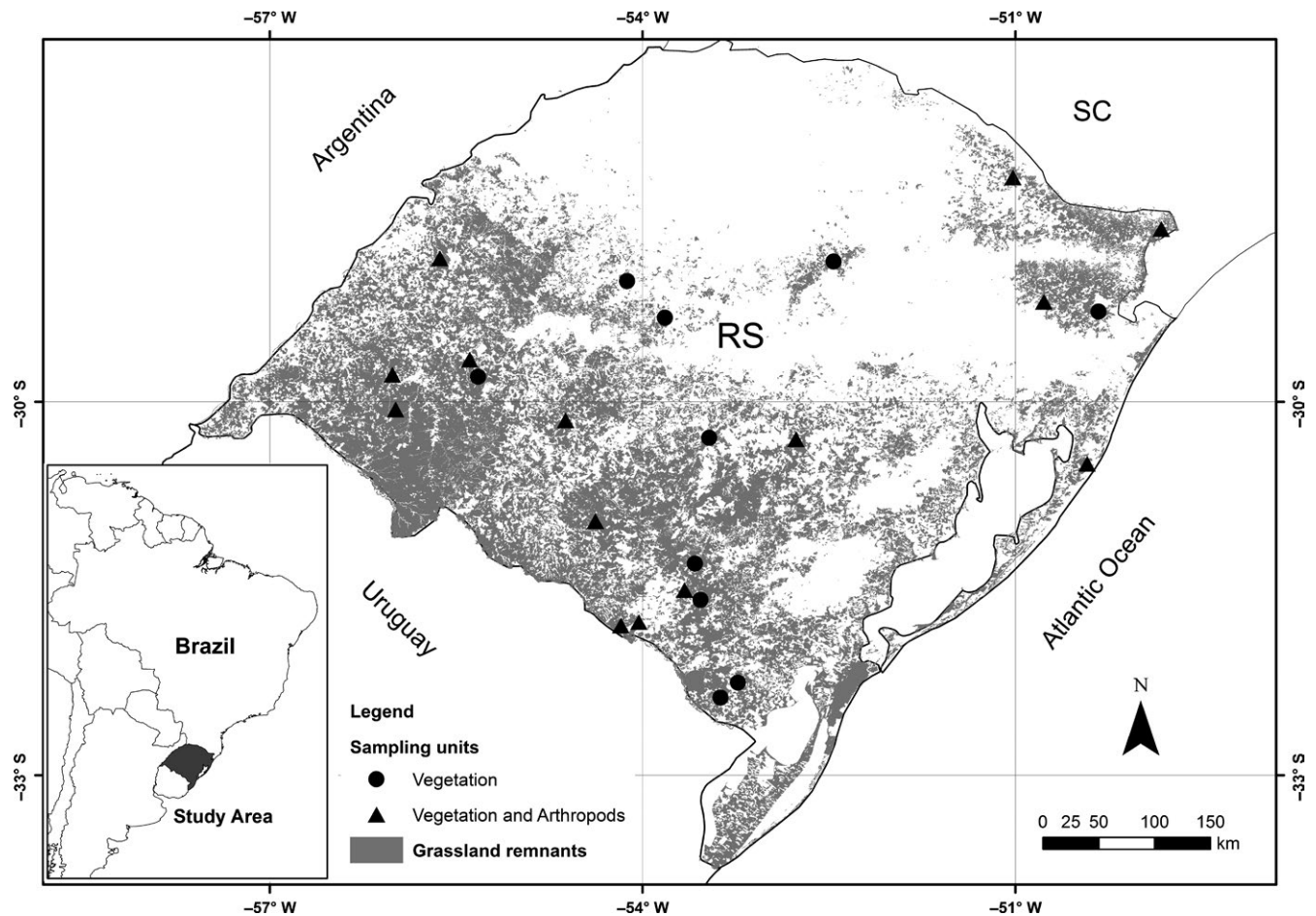
## 2 | MATERIALS AND METHODS

### 2.1 | Study region

Climate in the *Campos Sulinos* region in Rio Grande do Sul is humid subtropical with warm summers and no pronounced dry seasons (mostly Koeppen's Cfa, at higher altitudes Cfb; Alvares et al., 2013). An existing sampling network of the *Campos* from Brazil's National System of Research on Biodiversity (Sistema Nacional de Pesquisa em Biodiversidade, SISBIOTA) was used to study the effect of landscape habitat amount on local biodiversity. SISBIOTA sites cover the natural distribution of the *Campos* (based on RADAMBRASIL,

IBGE, 1986). Here, we focused on sites located in Rio Grande do Sul with more than 50% *Campos* habitat. Landsat 5 satellite images (from 2009; no more recent data available) for the entire territory of Rio Grande do Sul were georeferenced to identify and evaluate, through visual interpretation, the spatial distribution of land use/cover types (Weber, Hoffmann, Oliveira, & Hasenack, 2016). In total, 24 SISBIOTA sites met the criteria of having more than 50% *Campos* remnant area in a landscape (delimited to 2 × 2 km) and represented the selected landscape sampling regions (Figure 1).

Within each landscape sampling region, clusters of three local sampling units (70 × 70 m each, with a mean minimum interdistance of 538 m and a mean maximum interdistance of 1,125 m) were established inside the boundary of *Campos* remnants. The distribution of local sampling units within each landscape sampling region followed judgement by botanists and operational criteria (presence of natural grassland, accessibility and permission). The average condition of these three local sampling units was assumed to represent a local community in the respective landscape. Since other natural land cover showed small areas within landscape sampling regions and there was a strong negative correlation between *Campos* area and agricultural area ( $r = -.798$ ), we used *Campos* area as a predictor variable inversely expressing habitat loss.



**FIGURE 1** Location of the 24 landscape sampling units (more than 50% remaining *Campos* area) in Rio Grande do Sul (RS), South Brazil

## 2.2 | Data collection

### 2.2.1 | Vegetation data

Data collection took place from 2011 to 2013 during spring and early summer in all 24 landscape units. Vegetation data, confined to angiosperms, were sampled within each one of the three local sampling units, recorded in nine plots of 1 × 1 m, systematically allocated in a grid of 3 × 3 with 17 m spacing. Species were identified in the field, and unidentified species were collected for subsequent identification with the help of bibliography, consultation of the ICN Herbarium (Porto Alegre, Brazil), or of specialists.

### 2.2.2 | Arthropods

Sampling of arthropods was carried out in a subset of 14 of the 24 landscape sampling regions, always in all three local sampling units. Sampling occurred between 09:30 a.m. and 4:30 p.m. under sunny and dry weather conditions during spring and summer of 2011 and 2012. Each local sampling unit was sampled by sweeping the grassland vegetation with a net (50 cm large; 0.1 m<sup>2</sup>) along four transections, totalling about 120 pendulum sweeps. Arthropods were stored in containers with alcohol 70% and brought to the laboratory, where all ants (Formicidae) were sorted and identified to genera.

## 2.3 | Quantitative analysis

### 2.3.1 | Species richness

All quantitative analyses were performed in R version 3.3.2 (R Core Team, 2014). To estimate plant species richness for each of the three local sampling units, we calculated Chao 2 (Chao, 1987; Colwell & Coddington, 1994) for occurrence data from multiple samples ( $n = 9$ ) using `specpool` in package `vegan` (Oksanen et al., 2015). Values were averaged for each landscape sampling region. Chao 2 was regressed on landscape *Campos* area (%).

### 2.3.2 | Beta-diversity

Multiple-site dissimilarity and its partitioning into turnover and nestedness components were calculated for each of the three local sampling units ( $n = 9$ ) using the package `betapart` (Baselga & Orme, 2012) and averaged for the respective landscape sampling region. The dissimilarity measures used were multiple-site versions of the Sørensen dissimilarity index ( $\beta_{SOR}$ ), and their turnover (Simpson index of dissimilarity,  $\beta_{SIM}$ ) and nestedness (nestedness resultant index of dissimilarity,  $\beta_{SNE}$ ) components (Baselga, 2010). These measures were regressed on landscape *Campos* area (%).

### 2.3.3 | Phylogenetic diversity

A hypothesized phylogenetic tree for the plant species occurring in the sampled area was constructed using the Phylomatic tree version

R20031202 software (Webb & Donoghue, 2005) with the Angiosperm Phylogeny Group classification III (APG III, 2009). Branch lengths to the phylogenetic tree were assigned using the branch length adjustment function `BLADJ` of the `Phylocom` version 4.2 software package (Webb, Ackerly, & Kembel, 2008), creating a pseudochronogram with branch lengths based on clade ages reported by Wikström, Savolainen, and Chase (2001). The phylogenetic structure was calculated using the Standardized Effect Sizes for Mean Pairwise Distance (SES MPD) and Mean Nearest Taxon Distance (SES MNTD). These indices quantify how strongly the phylogenetic relatedness of a set of co-occurring species deviates from a null expectation. SES MPD measures the overall distance of taxonomic clades present in a community and is strongly influenced by branch lengths at the deepest nodes of the phylogeny and as such is sensitive to replacement of taxa that differ in broad taxonomic placement. SES MNTD provides a measure of the average distances between each species and its nearest phylogenetic neighbour in the community. SES MNTD is sensitive to replacement of closely related taxa and is much less sensitive to changes at the basal nodes of the phylogeny. If phylogenetic distance is correlated to ecological similarity, i.e. closely related species exhibit similar traits (trait convergence; Webb, 2000), SES MNTD is a proxy of how ecologically similar two co-occurring species are and SES MPD is a proxy of the ecological similarity of an entire community. SES MPD and SES MNTD were calculated with the package `picante` (functions `ses.mpd` and `ses.mntd`) by comparing the observed phylogenetic relatedness to a null model that randomly draws species while keeping sample species richness constant (null model richness in `picante`; Kembel et al., 2010). The phylogenetic structure was calculated for each of the three local sampling units and averaged for the respective landscape sampling region. SES MPD and SES MNTD were regressed on landscape *Campos* area (%).

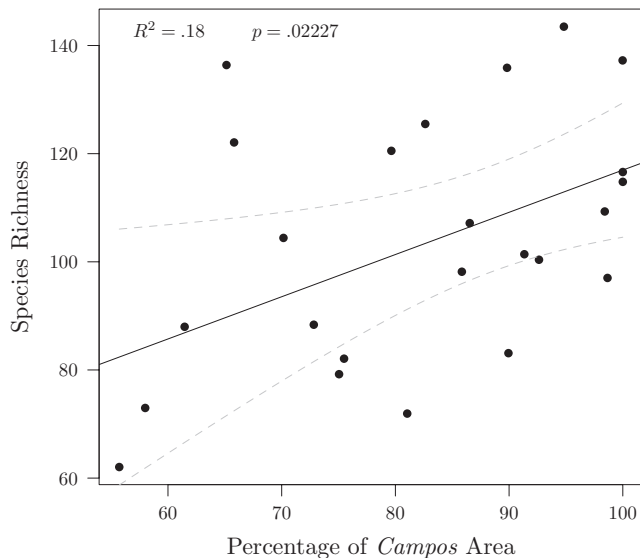
### 2.3.4 | Trophic cascades

Ant data from transects were pooled for each of the three local sampling units and averaged for the landscape sampling region. We used ant generic richness instead of species richness to put a higher magnitude on potential biological diversity loss, since genera regionally comprise many species. Ant generic richness was regressed on phylogenetic diversity (SES MPD and SES MNTD) of the respective plant community reflecting both the importance of nonsubstitutable specific evolutionary lineages (Mayer et al., 2014) and resource diversity (Armbrecht et al., 2004).

### 2.3.5 | Regressions

We applied robust inferential methods, which perform well with relatively small sample sizes, where data often slightly depart from normality assumptions. Robust methods mitigate the effect of single influential data points and heteroscedasticity, i.e. whereas ordinary least square regression breaks down quickly when error distributions are heavy-tailed, robust regression does not. Robust regression was performed as implemented by `lmrob` of the package `robustbase`





**FIGURE 2** Relationship between local plant species richness and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries

(Rousseeuw et al., 2015). The Robust Wald Test was used for an analysis of variance (ANOVA), comparing the model with estimates for intercept and landscape *Campos* amount to the model with the intercept estimate only. Effect size  $r$  was calculated for each regression. Confidence intervals of  $r$  were obtained via Fisher's  $z$ -transformation and classified following Cohen's effect size benchmarks (Cohen, 1977).

Spatial autocorrelation of plant species richness and ant generic richness was assessed through Mantel tests (Legendre & Legendre, 1998), using `mantel.rtest` in package `ade4` (Dray & Dufour, 2007; see Appendix S1).

### 3 | RESULTS

In total, 652 angiosperm species and 14 ant genera were found in the 24 and 14 landscape sampling regions (mean values: 104.1 and 3.2), respectively. Neither plant species richness nor ant generic richness showed spatial autocorrelation ( $p > .05$ ).

#### 3.1 | Species richness

We found that local plant species richness was significantly related to landscape *Campos* area (%). Landscapes with little *Campos* cover had locally less species than those landscapes with a high proportion of *Campos* ( $df = 22$ , adjusted  $R^2 = .18$ ,  $p = .022$ ; Figure 2 and Table 1).

#### 3.2 | Beta-diversity

Landscape *Campos* area (%) significantly explained variation of the multiple-site dissimilarity indices  $\beta_{SIM}$  and  $\beta_{SNE}$ . Whereas Sørensen dissimilarity  $\beta_{SOR}$  remained constant ( $df = 22$ , adjusted  $R^2 = .06$ ,  $p = .141$ ),

$\beta_{SIM}$  increased ( $df = 22$ , adjusted  $R^2 = .12$ ,  $p = .043$ ) and  $\beta_{SNE}$  decreased ( $df = 22$ , adjusted  $R^2 = .26$ ,  $p = .002$ ) with landscape *Campos* area (%) (Figure 3 and Table 1).

#### 3.3 | Phylogenetic diversity

Landscape *Campos* area (%) was significantly related to the overall distance of taxonomic clades present in a local community, measured by SES MPD ( $df = 22$ , adjusted  $R^2 = .18$ ,  $p = .049$ ), as were the average distances between each species and its nearest phylogenetic neighbour in the community, measured by SES MNTD ( $df = 22$ , adjusted  $R^2 = .5$ ,  $p \leq .001$ ; Figure 4 and Table 1). Local plant communities were increasingly phylogenetically clustered in landscapes with less *Campos* area (%).

#### 3.4 | Trophic cascade

SES MPD, being more sensitive to the overall distance of taxonomic clades present in a community and to replacement of taxa that differ in broad taxonomic placement, did not significantly explain variation in ant generic richness ( $df = 12$ , adjusted  $R^2 = 0$ ,  $p \leq .259$ ). On the other hand, SES MNTD, a measure sensitive to replacement of closely related taxa and much less sensitive to changes at the basal nodes of the phylogeny, significantly predicted ant generic richness ( $df = 12$ , adjusted  $R^2 = 0.31$ ,  $p \leq .012$ ; Figure 5 and Table 2).

## 4 | DISCUSSION

Using data from Brazil's southern grasslands that in recent years have been subjected to extensive land-use changes, we show that landscape habitat amount explains variation in species richness, beta-diversity components and phylogenetic diversity of local plant communities. Our results suggest that local plant communities respond to landscape habitat loss even at levels that can still be considered relatively moderate ( $\leq 50\%$ ), i.e. before reaching severe reduction (less than 30% habitat availability; Andr n, 1994; Cousins et al., 2003). We found species-poorer (Figure 2 and Table 1), more homogenized (Figure 3 and Table 1) and phylogenetically less diverse (Figure 4 and Table 1) local plant communities in landscapes with less *Campos* habitat. Ants, an animal group with high levels of plant interactions, responded to changes in plant community phylogenetic structure (Figure 5 and Table 2). This suggests that effects of habitat loss may propagate to higher trophic levels.

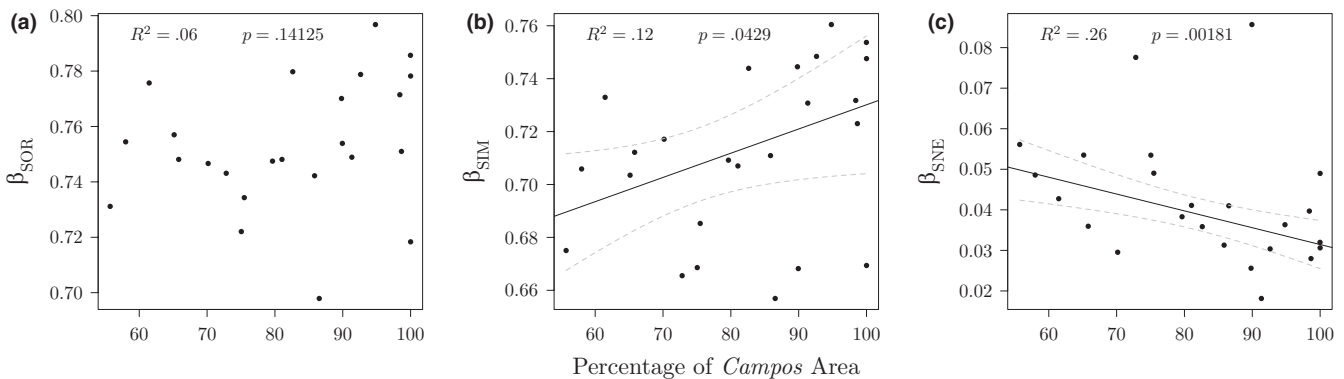
While overall, our study gives clear indication of the negative consequences of habitat loss for both producer and consumer communities, two factors potentially could obscure the results. First, we were not able to compare pre- and post-land-use change data. However, it has been shown before that space-for-time substitution, i.e. use of only post-disturbance data (as in our case), usually underestimates biodiversity losses (Fran a et al., 2016). Second, there is a time difference of 2 to 4 years between our biodiversity sampling (2011–2013) and the land-use data (2009). It thus is possible that

**TABLE 1** Regression parameter estimates with standard errors (in parenthesis), test statistics and effect sizes with 95% confidence intervals for the relationship between landscape *Campos* area (%) and species richness (Chao 2), beta-diversity ( $\beta_{\text{SOR}}$ ) and beta-diversity components (turnover  $\beta_{\text{SIM}}$  and nestedness  $\beta_{\text{SNE}}$ ), and phylogenetic diversity (SES MPD and SES MNTD) of local plant communities

	Dependent variable					
	Chao 2	$\beta_{\text{SOR}}$	$\beta_{\text{SIM}}$	$\beta_{\text{SNE}}$	SES MPD	SES MNTD
	(1)	(2)	(3)	(4)	(5)	(6)
<i>Campos</i> (%)	0.781* (0.317)	0.001 (0.0003)	0.001* (0.0004)	-0.0004** (0.0001)	0.058* (0.028)	0.037*** (0.008)
Intercept	38.888 (28.471)	0.713*** (0.025)	0.639*** (0.033)	0.073*** (0.010)	-7.234** (2.447)	-3.652*** (0.637)
Observations	24	24	24	24	24	24
$R^2$	.216	.097	.160	.291	.217	.520
Adjusted $R^2$	.180	.056	.122	.259	.182	.498
Res. SE (df = 22)	20.583	0.022	0.028	0.010	1.635	0.474
Wald	6.047*	2.329	4.618*	12.573***	4.345*	20.043***
Effect size $r$	0.46	0.31	0.42	0.60	0.41	0.69
95% CI of $r$	0.39, 0.90	0.21, 0.79	0.40, 0.87	0.45, 0.96	0.40, 0.87	0.37, 0.98

\* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$

SES MPD, Standardized Effect Sizes for Mean Pairwise Distance; SES MNTD, Standardized Effect Sizes for Mean Nearest Taxon Distance.

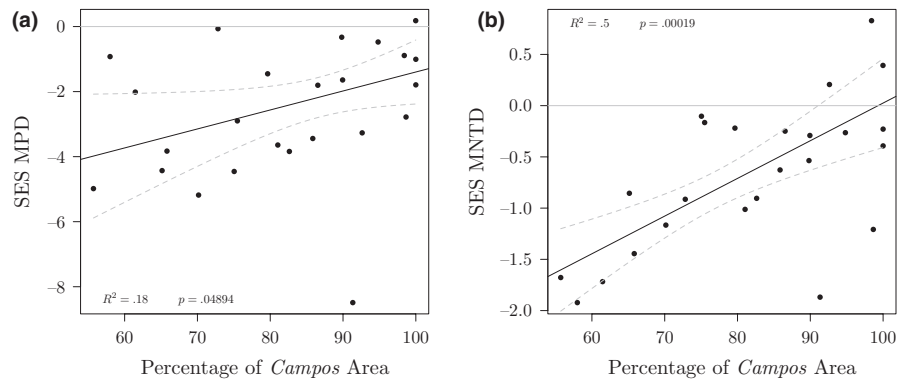


**FIGURE 3** Relationship between local floristic heterogeneity ((a)  $\beta_{\text{SOR}}$ , (b)  $\beta_{\text{SIM}}$  (turnover), (c)  $\beta_{\text{SNE}}$  (nestedness) multiple-site dissimilarities) and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries

more recent land-cover change (post-2009) somehow influenced the results. However, it is well known that there usually is a time-lag between habitat loss and effects on remnant communities ("extinction debt", Kuussaari et al., 2009). Nonetheless, results and implications of our study are clear. Even relatively intact *Campos* landscapes need already to be in the focus of decision and policy making for conservation. In line with Betts et al. (2017), who showed that globally forest loss in intact landscapes can degrade biodiversity disproportionately, our findings imply that substantial biodiversity declines do occur even though habitat availability did not yet fall to very low levels (less than 30%). This appears to be especially the case, when initial intrusions, such as biological invasions, coincide with the effects of habitat loss and impose an extinction filter whereby the most sensitive species (typically specialist, narrowly distributed, endemic species) are lost rapidly; leading not only to local but global biodiversity decline.

#### 4.1 | Species richness

Species-poorer local plant communities in landscapes with less *Campos* amount may be the result of at least four processes: (1) stochastic local extinctions due to smaller population sizes (Orrock & Watling, 2010), (2) lower recolonization rates due to decreased habitat connectivity (Haddad et al., 2015), (3) taxonomic homogenization, as generalist species that are widely distributed in the changed landscape replace more specialist grassland species (Tabarelli et al., 2012) and (4) nonrandom local extinctions, i.e. particular evolutionary lineages are more vulnerable to effects of habitat loss (Nee & May, 1997; Winter et al., 2009) leading to ecological homogenization. All here suggested processes are likely to contribute in an orchestrated fashion to the observed pattern. To regard underlying processes in more detail, we investigated beta-diversity and phylogenetic diversity metrics. Beta-diversity may detail on whether observed species loss is



**FIGURE 4** Relationship between local phylogenetic relatedness ((a) SES MPD: standard effect size for mean pairwise distance, (b) SES MNTD: standard effect size for mean nearest taxon distance) and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries

stochastic (increased beta-diversity; Segre et al., 2014) or rather due to “winner-loser” replacement (decreased beta-diversity). Measures of phylogenetic diversity may support whether species loss is stochastic or nonrandom (Nee & May, 1997; Purvis, Agapow, Gittleman, & Mace, 2000), thereby furthermore allowing inference about ecological homogenization (Cavender-Bares, Kozak, Fine, & Kembel, 2009).

## 4.2 | Beta-diversity

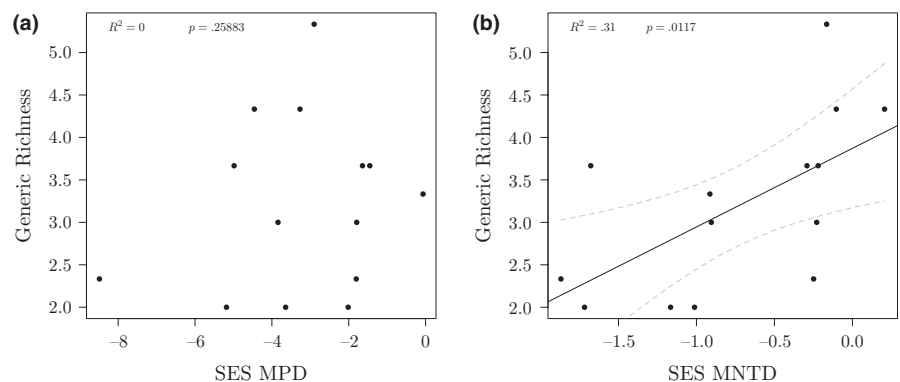
If overall beta-diversity, which remained unaltered by landscape habitat amount, were not disentangled into its species turnover and nestedness components, we would have erroneously concluded that local floristic variation remained similar across landscapes with differing habitat amount. However, the correlation between *Campos* amount and overall beta-diversity components, species turnover and nestedness, were both significant with medium effect sizes. Species turnover decreased with decreasing landscape habitat amount, whereas nestedness increased (Figure 3 and Table 1), suggesting taxonomically more homogenized local plant communities in landscapes with less *Campos*. The pattern of decreased turnover and increased nestedness is generally attributed to the persistence and proliferation of disturbance-tolerant, abundant and/or widespread species, and the extinction of narrowly distributed species with small populations (Solar et al., 2015; Villegas Vallejos, Padiá, & Vitule, 2016). However, a greater exposure to anthropogenic land uses may also increase the propagule pressure of exotic species and thus the potential of biological invasions (Mack & D’Antonio, 1998). Exotic species establishment

and spread may then additionally account for taxonomic homogenization. A recent study using data from the same sampling network in Rio Grande do Sul showed that the four most problematic alien species invading natural grasslands respond positively to decreasing *Campos* cover in the surrounding landscape (Guido, Vélez-Martín, Overbeck, & Pillar, 2016). This makes a case that observed taxonomic homogenization may in part be due to a few highly resilient exotic species replacing multiple rare, specialist species—in our study 24 species were identified as exotic (classification according to Rolim, de Ferreira, Schneider, and Overbeck, 2015). Upon establishment, exotic species may disperse, proliferate and replace other species in remnant habitat, thereby establishing a gradient of occurrence probability being highest closer to habitat edge (With, 2002) increasing nestedness and decreasing turnover.

That taxonomic homogenization of grassland communities at the focal spatial scale, i.e. within a locality, may occur as a result of exotic species proliferation is also supported by studies examining exotic-dominated prairie grasslands, which—when compared to native grasslands—reveal lower beta-diversity locally (Martin & Wilsey, 2015).

## 4.3 | Phylogenetic diversity

We found that landscape *Campos* amount significantly explained variation in local phylogenetic diversity. We investigated phylogenetic structural changes at basal branches (SES MPD) and tips (SES MNTD) of the focal phylogeny. Both SES MPD and SES MNTD declined with landscape *Campos* amount (Figure 4 and Table 1). This suggests that



**FIGURE 5** Relationship between local Formicidae genera richness and phylogenetic diversity ((a) SES MPD: standard effect size for mean pairwise distance and (b) SES MNTD: standard effect size for mean nearest taxon distance) of local plant communities. Hatched lines represent the 95% confidence boundaries

**TABLE 2** Regression parameter estimates with standard errors (in parenthesis), test statistics and effect sizes with 95% confidence intervals for the relationship between plant phylogenetic diversity (SES MPD, SES MNTD) and ant generic richness

	Dependent variable	
	Generic richness	
	(1)	(2)
SES MPD	0.087 (0.073)	
SES MNTD		0.926* (0.312)
Intercept	3.465*** (0.348)	3.871*** (0.321)
Observations	14	14
R <sup>2</sup>	.030	.365
Adjusted R <sup>2</sup>	0	.312
Res. SE (df = 12)	1.201	0.843
Wald	1.405	8.821**
Effect size r	0.32	0.65
	0.07, 0.86	0.53, 0.98

\* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ .

SES MPD, Standardized Effect Sizes for Mean Pairwise Distance; SES MNTD, Standardized Effect Sizes for Mean Nearest Taxon Distance.

local extinctions occur nonrandomly in landscapes with less habitat amount; particular evolutionary lineages erode, leading to phylogenetic clustering. There is growing evidence that phylogenetic diversity and niche differentiation is positively related to primary productivity in plant communities (Cadotte, Cardinale, & Oakley, 2008). A loss of evolutionary history may thus affect facets of ecosystem functioning. Moreover, as greater evolutionary diversity buffers ecosystems against environmental variation, a loss of evolutionary information may ultimately result in decreased ecosystem resilience (Cadotte et al., 2012).

Albeit currently being compiled, we did not yet have access to sufficient amounts of trait data for the majority of sampled plant species. Therefore, we did not investigate the phylogenetic signal of key functional traits. However, phylogenetic conservatism of ecologically important traits is common in plants (Futuyma & Agrawal, 2009; Wiens et al., 2010). Under the assumption of trait conservatism, we can hypothesize that certain traits are selected for by the effects of landscape habitat loss, for instance a specific agricultural disturbance regime, land-use history and management may select for species with high seed production and specific leaf area (Dinnage et al., 2012). Further research should investigate whether there are particular functional traits, e.g. low wind dispersal potential, low seed production per ramet, low growth rate, etc., that make plants more vulnerable to the effects of habitat loss. This link to functional diversity may potentially allow for the prediction of trajectories in other systems undergoing habitat loss and fragmentation.

#### 4.4 | Trophic cascade

As phylogenetic diversity of the local plant community declines, we found that ant generic richness follows. While not related to SES

MPD, ant generic richness responded to SES MNTD (Figure 5 and Table 2). Formicidae's taxonomic rank is that of a family, subsuming genera and species. Its taxonomic associations to plants are likely restricted to a range of closely related genera or species, i.e. ants rather respond to changes at the tips (SES MNTD) than to changes at the basal nodes (SES MPD) of the plant phylogeny. Although the model estimates the loss of only up to two ant genera in phylogenetically less diverse plant communities, this represents a diversity loss of 50% and may further have magnified effects on ant species richness.

Since (1) the strong relationship of SES MNTD to landscape *Campos* amount suggests that plant species in communities subjected to landscapes habitat loss pertain to fewer genera, and since (2) ants responded to this loss of lineage diversity, we infer that niche dimensions of ants are locally lost in landscapes with less *Campos* amount. For instance, sampled genera such as *Pseudomyrex*, *Myrmelachista* and *Cephalotes* that have specialized nesting requirements (Brandão, Silva, & Delabie, 2012) may respond to the loss of specific evolutionary lineages, whereas sampled genera with broader niches, such as *Camponotus* or *Pheidole*, may respond to phylogenetic diversity as proxy for resource diversity (e.g. Armbrrecht et al., 2004). We argue that the loss of more distantly related plant species (SES MPD decreases with landscape *Campos* area, too) is likely to affect the host range of a variety of herbivores.

Regarding the positive relationship between plant phylogenetic diversity and plant productivity, further research should address whether a decrease in plant productivity, which may reduce resource abundance for herbivores and consequently their diversity (Dinnage et al., 2012), has an effect on predators and parasitoids too.

While we here elaborate on only a single taxa of higher trophic hierarchy, future research should also investigate if broader taxonomic levels, e.g. birds, amphibians or mammals, respond to habitat loss in the *Campos Sulinos* too, and at what focal spatial scale and by which mechanisms (e.g. niche vs. resource abundance hypothesis; Dinnage et al., 2012). For instance, grassland specialist birds may be more reliant on *Campos* cover at larger spatial scales and this would have important implications for conservation, e.g. for the definition of maximum values for land conversion in a given region.

## 5 | CONCLUSIONS

We conclude that species loss, taxonomic homogenization and the loss of phylogenetic diversity of plant communities of Brazil's southern grasslands may occur under moderate habitat loss scenarios, and that changes in plant community structure may propagate to higher trophic levels. Our results suggest that species loss can be linked to taxonomic homogenization, in which species are replaced and go extinct nonrandomly, leading to ecologically more similar plant communities. Since losses of phylogenetic information are linked to declines of ecosystem functions, e.g. plant productivity, and since greater evolutionary diversity buffers ecosystems against environmental variation, we ultimately expect that ecosystem resilience, not only in



respect to adaptability to environmental change but also to biodiversity restoration post-agricultural abandonment, may decrease.

We provide empirical evidence that the biological diversity of south Brazilian grasslands, both at the producer and consumer level, is at risk under the current rate of land-use conversion and that with the loss of evolutionary information ecosystem resilience may be affected too. To avoid substantial losses of these grasslands' high biological diversity and to prevent a state from which biodiversity cannot be restored anymore, more efficient conservation, e.g. a higher protected area coverage, and more restrictive policies for conversion of native grasslands to different land uses in South Brazil are urgent.

## ACKNOWLEDGEMENTS

We thank all members of the SISBIOTA field team for data collection, and all landowners for permission to work on their lands. The SISBIOTA project was funded by CNPq/Fapergs (grants 563271/2010-8 and 11/2185-0, respectively, to V.P.). I.S. acknowledges financial support by the European Commission through the program Erasmus Mundus Master Course - International Master in Applied Ecology (FPA 202 3-0224/532524-1-FR-2012-1-ERA MUNDUS-EMMC). G.O., I.B. and V.P. have received CNPq productivity grants (respectively, grant 310022/2015-0, 309934/2015-0 and 307689/2014-0), and B.A., E.V. and L.R.P. post-doctorate grants from CNPq, MCTIC and CAPES. The Campos Sulinos research network is funded by CNPq/MCTIC through the PPBio program. Sandra Müller, João André Jarenkow, Anaclara Guido and two anonymous reviewers provided helpful comments on a previous version of the manuscript.

## AUTHORS' CONTRIBUTIONS

V.P., G.O., I.B., E.V. and M.M. conceived conception, design and acquisition of data. B.A., G.O., I.B. and L.R.P. led data collection. I.S. analysed and interpreted the data. I.S. and G.O. led the writing of the manuscript. All authors discussed the results, contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

All relevant data used in this manuscript are publicly available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.v0n1p> (Staudé et al., 2017).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Staude IR, Vélez-Martin E, Andrade BO, et al. Local biodiversity erosion in south Brazilian grasslands under moderate levels of landscape habitat loss. *J Appl Ecol*. 2018;55:1241–1251. <https://doi.org/10.1111/1365-2664.13067>