

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

**LOCAL BIODIVERSITY EROSION IN SOUTH BRAZILIAN GRASSLANDS EVEN
WITH SLIGHT LANDSCAPE HABITAT LOSS**

Ingmar René Staude

Orientador: Prof. Dr. Gerhard Ernst Overbeck

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Orientador: Prof. Dr. Gerhard Ernst Overbeck

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Local biodiversity erosion in South Brazilian grasslands with even slight landscape habitat loss

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Introdução Geral

As formações campestres em senso mais amplo estão entre os maiores ecossistemas do mundo e cobrem 40,5% da superfície terrestre (Suttie et al. 2005). Devido aos seus solos férteis e características topográficas favoráveis, o bioma de campos temperados tornou-se o ecossistema mais extensivamente modificado pelo homem, 45,8% foi convertido para outros usos do solo, apenas 4,6% é protegido (Hoekstra et al. 2005). Os campos do Sul do Brasil, da Argentina e do Uruguai, denominados conjuntamente como Pastizales del Río de la Plata, são uma das maiores regiões de campos temperados do mundo e os mais extensos da América do Sul. Este tipo de ecossistema é encontrado no Rio Grande do Sul, o estado mais austral do Brasil, onde é denominado *Campos Sulinos* ou simplesmente *Campos* (Overbeck et al. 2007).

Tal como acontece com a Mata Atlântica adjacente, os *Campos* representam um desafio para a conservação da biodiversidade (ibid.). Eles apresentam altos níveis de biodiversidade – estimativas chegam a um total de 2600 espécies de plantas campestres, apenas para o Estado do Rio Grande do Sul (Boldrini 1997) – e endemismo, mas lacunas de conhecimento científico, limitações de recursos financeiros e falta de políticas proíbem a recuperação ou mesmo a desaceleração da conversão de *Campos*. Os *Campos* costumavam cobrir 55% do território do Rio Grande do Sul no passado (IBGE 1977). No período de 1970 a 1996, a área de *Campos* foi reduzida de 14 milhões de ha para 11 milhões de ha, estima-se que 4 milhões de ha foram convertidos de 1996 a 2005, ou seja, devido à expansão agrícola e silvicultural restam somente 50% da área original de *Campos* no Rio Grande do Sul (Cordeiro & Hasenack 2009). Isso contrasta com um nível de proteção baixo: uma porcentagem insignificante de 2,58% da área de *Campos* é protegida nas áreas conservadas em Unidades de Conservação no Rio Grande do Sul (Brandão et al. 2008). De fato, o bioma do Pampa brasileiro, ou seja, os *Campos* na metade sul do Rio Grande do Sul, apresenta o maior Índice de Risco de Conservação de todos os biomas brasileiros (Overbeck et al. 2015).

Uma consequência principal e primária da perda de habitat é o subconjunto da comunidade biológica ali presente. A heterogeneidade ambiental e, portanto, habitat e nichos, em que algumas espécies dependem exclusivamente, são eliminados no processo de conversão de uso do solo. Isso se reflete numa relação ubíqua de área de espécies. Em segundo lugar, com a perda de habitat, o habitat contínuo tipicamente divide-se em múltiplas manchas menores e mais isoladas. De acordo com a teoria da biogeografia de ilhas e de dinâmica da metapopulação, as espécies persistirão

nas manchas do habitat se forem suficientemente grandes para suportar uma população viável e/ou se a configuração de paisagem permitir recolonização. Após a perda de habitat, o efeito da deriva geralmente aumenta enquanto a recolonização que poderia contrabalançar as extinções estocásticas locais diminui. Além disso, uma maior exposição a espécies do habitat matricial é suscetível de influenciar os processos de assembléia da comunidade (Mack & D'Antonio 1998).

O estabelecimento e a proliferação das espécies de matriz, tipicamente espécies generalistas nativas, espécies ruderais e as vezes espécies exóticas, cosmopolitas, pode excluir competitivamente várias outras espécies, tipicamente espécies raras e especializadas, levando à diminuição da diversidade beta e, conseqüentemente, à homogeneização taxonômica. Além disso, se a perda de espécies após a modificação do habitat é devida a uma vulnerabilidade particular aos processos acima mencionados e, portanto, não-aleatória, i.e., alguns atributos funcionais são selecionados sobre outros sob um regime específico de uso do solo, comunidades tornam-se mais homogeneizadas ecologicamente. Como os atributos funcionais são tipicamente conservados nas linhagens evolucionárias das plantas, a diversidade filogenética pode ser usada para detalhar a similaridade ecológica de uma comunidade (Webb 2000). Como há evidências crescentes de que a diversidade filogenética está positivamente relacionada com as funções do ecossistema, e.g., uma maior diversidade evolutiva amortece os ecossistemas contra a variação ambiental, uma perda de informação evolutiva pode, em última instância, resultar na diminuição da resiliência do ecossistema (Cadotte et al. 2012).

Ademais, se as linhagens evolutivas dos produtores primários forem perdidas após a perda de habitat, isso provavelmente afetará também os mutualistas e antagonistas associados. Muitos herbívoros mostram estrutura filogenética em suas dietas - eles se alimentam de grupos de gêneros ou espécies estreitamente relacionados (Ødegaard et al. 2005; Weiblen et al. 2006). Em consequência, a perda não-aleatória de espécies vegetais e, com isso, o declínio da diversidade filogenética devido à perda de habitat pode, por exemplo, diminuir a diversidade de Formicidae que compreende um alto grau de associações com plantas e tem requisitos de habitat e dieta filogeneticamente estruturados. Assim, a homogeneização ecológica no nível da comunidade vegetal pode desencadear as cascatas tróficas nas quais a reorganização da comunidade não se restringe apenas às plantas, mas perpetua-se em todos os níveis tróficos.

Até o momento, há poucas provas empíricas se as consequências da perda de habitat na diversidade biológica dos *Campos Sulinos* são semelhantes às observadas em outros biomas e se as predições teóricas da erosão da biodiversidade são verdadeiras. Esta informação é urgentemente necessária para futuros esforços de conservação

Objetivo geral Aqui, utilizo dados de levantamentos da biodiversidade dos *Campos Sulinos* no Rio Grande do Sul e pergunto como 1) a riqueza de espécies, 2) a diversidade beta 3) a diversidade filogenética de comunidades de plantas locais respondem à perda moderada de *Campos* ($\leq 50\%$), e 4) se níveis tróficos mais altos respondem à estrutura filogenética das mesmas comunidades de plantas, usando Formicidae como sistema modelo.

Estrutura da tese A dissertação é estruturada de acordo com as especificações do manuscrito e diretrizes ao autor da revista "Conservation Biology"¹.

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1 Local biodiversity erosion in South Brazilian grasslands with
2 even slight landscape habitat loss

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15 **Resumo**

16 The *Campos Sulinos*, Brazil's southern grasslands, have experienced considerable
17 land-use change in recent years. 50% of their natural extent in Rio Grande do
18 Sul, Brazil's southernmost state, has been lost in only 35 years due to agricultural
19 expansion. Despite of that, a mere 2.58% are currently represented in conservation
20 units. Up to date, there is little empirical evidence for the effects of habitat loss on
21 the *Campos*' biological diversity. Here we used data from a large-scale biodiversity
22 survey carried out in Rio Grande do Sul and asked how species richness, beta-diversity
23 and phylogenetic diversity of local plant communities respond to even slight losses of
24 *Campos* in a landscape ($\leq 50\%$). Vegetation was sampled in 24 anthropogenically
25 modified landscapes at three localities each within *Campos* remnant area, using 9
26 plots of 1 m² per locality. In part of the same localities, arthropod data was sampled
27 to investigate if a potential loss of plant diversity has a cascading effect on other

28 trophic levels. We evaluated ant generic richness, an omnivore group with high
29 levels of plant associations, in respect to a plant community's phylogenetic diversity.
30 We found that species richness, beta-diversity – when disentangled into its species
31 turnover and nestedness components – and phylogenetic diversity of local plant
32 communities responded to the amount of *Campos* in a landscape. We found species
33 poorer, taxonomically more homogenized and phylogenetically less diverse local plant
34 communities in landscapes with less *Campos*. Our results suggest that species loss is
35 nonrandom and can be linked to taxonomic homogenization resulting in ecologically
36 more homogenized plant communities. Furthermore, ant richness responded to the
37 phylogenetic diversity of plant communities, suggesting that effects of habitat loss
38 perpetuate to higher trophic levels. We conclude that the *Campos*' biological diversity
39 is at risk under the current rate of land-use conversion. We emphasize the urgency
40 of a higher representation of the *Campos Sulinos* in conservation units and a more
41 restrictive policy framework for land-use change authorizations in Rio Grande do
42 Sul.

43 **Key words**— *Campos*, species richness, beta-diversity, phylogenetic diversity,
44 trophic cascade, ants, resource diversity

45 Introduction

46 Habitat loss has been, and still is, the greatest threat to global biodiversity (Balmford et al. 2005;
47 Rands et al. 2010). When analyzing the threats to biodiversity, it is important to consider the
48 effects of larger spatial scales on the species composition of local ecological communities (Fahrig
49 2001; Ricklefs 2008). As the amount of natural habitat in anthropologically modified landscapes
50 declines, continuous habitat is usually broken into multiple smaller fragments (Gardner & O'Neill
51 1991) and the average distances between habitat fragments increases (With & Crist 1995). This
52 increases the importance of ecological drift, while recolonization counterbalancing stochastic local
53 extinctions decreases. Moreover, a greater exposure to human land uses is likely to influence
54 community assembly processes in habitat remnants (Mack & D'Antonio 1998).

55 Communities post-habitat loss are in a process of disassembly and assembly, i.e., stochastic
56 and deterministic local species extinction and colonization occur simultaneously (Diamond

57 1975; Connell & Slatyer 1977; Ostfeld & LoGiudice 2003; Zavaleta et al. 2009). Driven by
58 anthropogenic stressors, the species favoured during assembly typically differ from those lost
59 during disassembly (Zavaleta et al. 2009). Favoured species are disturbance tolerant, widely
60 distributed and sometimes cosmopolitan, ruderal or exotic species, whereas the species lost are
61 rare, specialist, endemic or narrowly distributed native species (Naaf & Wulf 2010; Tabarelli
62 et al. 2012). This human induced process of replacement of species types typically leads
63 to biotic homogenization (McKinney & Lockwood 1999; Tabarelli et al. 2012), i.e., reduced
64 beta-diversity (taxonomic homogenization) and/or increased ecological similarity of species
65 (ecological homogenization) (Olden & Rooney 2006). Increased ecological similarity of species
66 may be the result of nonrandom extinctions that are not only restricted to endemic and rare
67 species but to species of particular guilds or evolutionary lineages, in which traits prone to
68 habitat loss are conserved (Heard & Mooers 2000; Winter et al. 2009).

69 If evolutionary lineages of primary producers are lost post-habitat loss, this will likely affect
70 associated mutualists and antagonists as well (Dinnage et al. 2012). For instance, many herbivores
71 show phylogenetic structure in their diets – they feed on groups of closely related genera or
72 species (Ødegaard et al. 2005; Weiblen et al. 2006) – or respond to the diversity of resources, i.e.,
73 plant traits (Armbrecht et al. 2004). Thus, plant biotic homogenization may lead to bottom
74 up effects and/or trophic cascades, in which community reorganization is not only restricted
75 to plants but perpetuates through all trophic levels. Biotic homogenization may thus collapse
76 intricate networks of interactions of various trophic levels, result in taxonomic, ecological and
77 genetic impoverishment and thereby reduce ecosystem functioning and resilience (Olden 2006;
78 Norden et al. 2009; Cadotte et al. 2012; Fraser et al. 2015).

79

80 Given the fast rate of land use change in many regions of the world, including southern Brazil
81 (Overbeck et al. 2015), there is an urgent need to understand at which amount of habitat loss
82 these processes unfold. There is empirical evidence for considerable local extinctions to occur
83 with severe rates of habitat loss, e.g., when the remaining landscape area is below 10 to 30%
84 (Cousins et al. 2003). However, there is few and less coherent information on biodiversity erosion
85 under less dramatic dimensions of habitat loss.

86 Due to their fertile soils and favourable topographic features the temperate grassland biome
87 has become the most extensively modified ecosystem by man (Henwood 1998). The grasslands

88 of South Brazil, Argentina and Uruguay are jointly one of the largest temperate grasslands
89 regions in the world and the most extensive in South America (Soriano et al. 1991). In Brazil's
90 southernmost state, Rio Grande do Sul, these grasslands are named *Campos Sulinos* or simply
91 *Campos* (Lindman 1906). While harbouring high levels of biodiversity – estimates reach a total
92 number of 3000 grassland plant species (Boldrini 1997) – and endemism, the *Campos* of Rio
93 Grande do Sul have lost 50% of their original distribution in only 35 years from 1970 to 2005
94 due to agri- and silvicultural expansion (Cordeiro & Hasenack 2009). This contrasts with a low
95 protection level: A negligible percentage of 2.58% of *Campos* area is protected in Rio Grande do
96 Sul (T. Brandão et al. 2008). In fact, Brazil's Pampa biome, i.e the *Campos* in the southern half
97 of Rio Grande do Sul State, presents the highest Conservation Risk Index of all Brazilian biomes
98 (Overbeck et al. 2015).

99

100 Here we used data from a large-scale biodiversity survey carried out in the *Campos* of Rio
101 Grande do Sul and investigated different aspects of community organization. We hypothesized
102 that slight levels of habitat losses – i.e., up to 50%, the current overall level of landscape change
103 in the region – may already lead to locally species poorer plant communities. We then asked if
104 this species loss may be due to taxonomic homogenization because of altered community assembly
105 post-habitat loss. For this, we disentangled overall beta-diversity into its antithetic species gain
106 (turnover) and species loss (nestedness) components. We expected a decline of species turnover
107 and a simultaneous increase of nestedness in response to habitat loss. Further, we addressed
108 plant community composition from an evolutionary perspective. We expected ecologically more
109 similar local plant communities due to nonrandom species loss, thus a decrease in phylogenetic
110 diversity (Nee & May 1997), measured at the basal nodes and at the tips of the plant community's
111 phylogeny. Given the shared evolutionary history of particular plant clades with their mutualists
112 and antagonists, we expected more habitat and/or feeding niches for consumer communities
113 in phylogenetically more diverse plant communities. We used ants as model system since they
114 comprise high levels of association with plants, benefiting both from plant-derived food resources
115 and also herbivore insects as prey (Mayer et al. 2014). We expected declines in ant richness if
116 plant evolutionary lineages are lost post-habitat loss.

117 **Methods**

118 **Study Region**

119 Climate in the *Campos Sulinos* region in Rio Grande do Sul is humid subtropical with warm
120 summers and no pronounced dry seasons (mostly Koeppen's Cfa, at higher altitudes Cfb (Alvares
121 et al. 2013)). An existing sampling unit network of the *Campos* from Brazil's National System
122 of Research on Biodiversity (Sistema Nacional de Pesquisa em Biodiversidade, SISBIOTA) was
123 used to study the effect of landscape habitat amount on local biodiversity. SISBIOTA sampling
124 units cover the natural distribution of the *Campos* (based on do RADAMBRASIL, IBGE (1986)).
125 Here we focussed on sampling units located in Rio Grande do Sul with more than 50% *Campos*
126 habitat. Landsat 5 satellite images (from 2009) for the entire territory of Rio Grande do Sul were
127 georeferenced to identify and evaluate the spatial distribution of land use/cover types. CartaLinx
128 was used for visual interpretation and ArcView GIS 3.2 for mapping of land use/cover types.
129 A total of 24 landscape sampling units with more than 50% *Campos* area was selected from
130 SISBIOTA (Fig. 1).

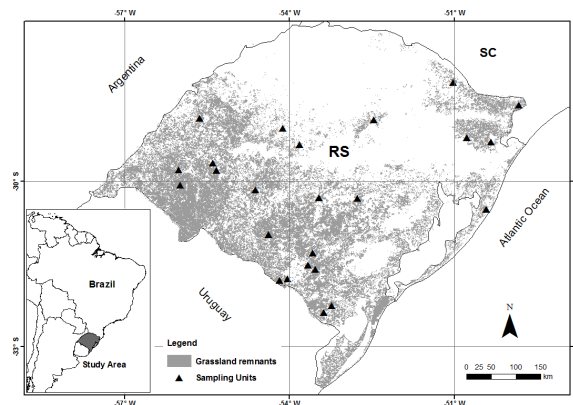


Figure 1 – Location of the 24 landscape sampling units (more than 50% remaining *Campos* area) in Rio Grande do Sul.

131 Landscape sampling units were delimited to approximately 2 x 2 km. Within each landscape
132 sampling unit three local sampling units (70 x 70 m) were established inside the boundary of
133 *Campos* remnants. The distribution of local sampling units within each landscape sampling
134 unit followed judgement by botanists and operational criteria (presence of natural grassland,
135 accessibility and permission). The average condition of these three local sampling units is to

136 represent a local community in the respective landscape. Since there was a strong negative
137 correlation between *Campos* area and agricultural area ($r = -0.798$), we used *Campos* area as
138 predictor variable and not *Campos* loss, as the latter references to differing amounts of original
139 *Campos* area and as other non-natural land uses might also play a role, in addition to agricultural
140 area.

141 **Data collection**

142 **Vegetation data** Data collection took place from 2011 to 2013 during spring and early summer.
143 Vegetation data, confined to angiosperms, was sampled in each landscape sampling unit, recorded
144 in 9 plots of 1 x 1 m, systematically allocated in a grid of 3 x 3 with 17 m spacing, in each
145 local sampling unit. Species were identified in the field, unidentified species were collected for
146 subsequent identification with the help of bibliography, consultation of the ICN Herbarium (Porto
147 Alegre, Brazil).

148 **Arthropods** Sampling of arthropods was carried out in 14 landscape sampling units during
149 spring and summer of 2011 and 2012. Sampling occurred between 09:30am and 4:30pm under
150 sunny and dry weather conditions. Each local sampling unit was sampled by sweeping the
151 grassland vegetation with a net (50 cm large; 0.1 m²) along four transections, totaling about 120
152 pendulum sweeps. Arthropods were stored in containers with alcohol 70% and brought to the
153 lab, where all ants (Formicidae) were sorted and identified to genera.

154 **Quantitative Analysis**

155 **Species Richness** All quantitative analyses were performed in R version 3.3.2 (R Core Team
156 2014). To estimate species richness for each of the three local sampling units, we calculated Chao
157 2 (Chao 1987; Colwell & Coddington 1994) for occurrence data from multiple samples ($n = 9$)
158 using `specpool` in package `vegan` (Oksanen et al. 2015). Values were averaged for the landscape
159 sampling unit. Chao 2 was regressed on landscape *Campos* area (%).

160 **Beta-Diversity** Multiple site dissimilarity and its partitioning into turnover and nestedness
161 components were calculated for each of the three local sampling units ($n = 9$) using the package
162 `betapart` (Baselga & Orme 2012) and averaged for the respective landscape sampling unit. The

163 dissimilarity measures used were multiple site versions of the Sørensen dissimilarity index (β_{SOR}),
164 and their turnover (Simpson index of dissimilarity, β_{SIM}) and nestedness (nestedness resultant
165 index of dissimilarity, β_{SNE}) components (Baselga 2010). These measures were regressed on
166 landscape *Campos* area (%).

167 **Phylogenetic Diversity** A hypothesized phylogenetic tree for the plant species occurring in
168 the sampled area was constructed using the Phylomatic tree version R20031202 software (Webb &
169 Donoghue 2005) with the Angiosperm Phylogeny Group classification III (APG III 2009). Branch
170 lengths to the phylogenetic tree were assigned using the branch length adjustment function BLADJ
171 of the Phylocom version 4.2 software package (Webb et al. 2008), creating a pseudochrono-gram
172 with branch lengths based on clade ages reported by Wikström et al. (2001).
173 The phylogenetic structure was calculated using the Standardized Effect Sizes for Mean Pairwise
174 Distance (SES MPD) and Mean Nearest Taxon Distance (SES MNTD). These indices quantify
175 how strongly the phylogenetic relatedness of a set of co-occurring species deviates from a null
176 expectation. SES MPD measures the overall distance of taxonomic clades present in a community
177 and is strongly influenced by branch lengths at the deepest nodes of the phylogeny and as such
178 sensitive to replacement of taxa that differ in broad taxonomic placement. SES MNTD provides
179 a measure of the average distances between each species and its nearest phylogenetic neighbour in
180 the community. SES MNTD is sensitive to replacement of closely related taxa and is much less
181 sensitive to changes at the basal nodes of the phylogeny. If phylogenetic distance is assumed a
182 proxy of ecological similarity, i.e., closely related species exhibit similar traits (trait convergence)
183 (Webb 2000), SES MNTD is a proxy of how ecologically similar two co-occurring species are
184 and SES MPD is a proxy of the ecological similarity of an entire community. SES MPD and
185 SES MNTD were calculated with the package `picante` (functions `ses.mpd` and `ses.mntd`) by
186 comparing the observed phylogenetic relatedness to a null model that randomly draws species
187 while keeping sample species richness constant (null model "`richness`" in `picante`) (Kembel
188 et al. 2010). The phylogenetic structure was calculated for each of the three local sampling
189 units and averaged for the respective landscape sampling unit. SES MPD and SES MNTD were
190 regressed on landscape *Campos* area (%).

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

198 **Regressions** We applied robust inferential methods, which perform well with relatively small
199 sample sizes, where data often slightly departs from normality assumptions. Robust methods
200 mitigate the effect of single influential data points and heteroscedasticity, i.e., whereas ordinary
201 least square regression breaks down quickly when error distributions are heavy-tailed, robust
202 regression does not. Robust regression was performed as implemented by `lmrob` of the package
203 `robustbase` (Rousseeuw et al. 2015). The Robust Wald Test was used for an analysis of variance
204 (`anova`), comparing the model with estimates for intercept and landscape *Campos* amount to
205 the model with the intercept estimate only. Effect size r was calculated for each regression.
206 Confidence intervals of r were obtained via Fisher's z-transformation and classified following
207 Cohen's effect size benchmarks (Cohen 1977).

208 **Results**

209 **Species Richness** We found that local species richness was significantly related to landscape
210 *Campos* area (%). Landscapes with little *Campos* cover had locally less species than those
211 landscapes with a high proportion of *Campos* ($df = 22$, adjusted $R^2 = 0.18$, $p = 0.022$) (Fig. 2
212 and Tab. 1).

213 **β -diversity** Only when overall beta-diversity (β_{SOR}) was disentangled into its species turnover
214 (β_{SIM}) and nestedness (β_{SNE}) components, the effect of landscape *Campos* area (%) on floristic
215 heterogeneity was revealed. Landscape *Campos* area (%) significantly explained variation of
216 the multiple-site dissimilarity indices β_{SIM} and β_{SNE} . Whereas Sørensen dissimilarity (β_{SOR})
217 remained constant ($df = 22$, adjusted $R^2 = 0.06$, $p = 0.141$), β_{SIM} increased ($df = 22$, adjusted

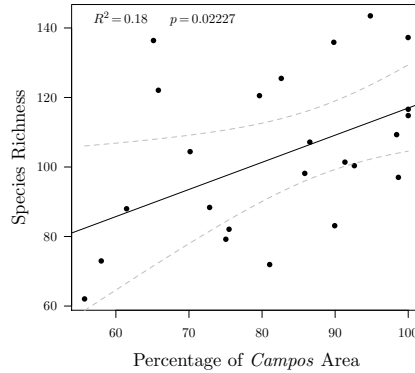


Figure 2 – Relationship between local species richness and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries.

218 $R^2 = 0.12$, $p = 0.043$) and β_{SNE} decreased ($df = 22$, adjusted $R^2 = 0.26$, $p = 0.002$) with
 219 landscape *Campos* area (%) (Fig. 3 and Tab. 1).

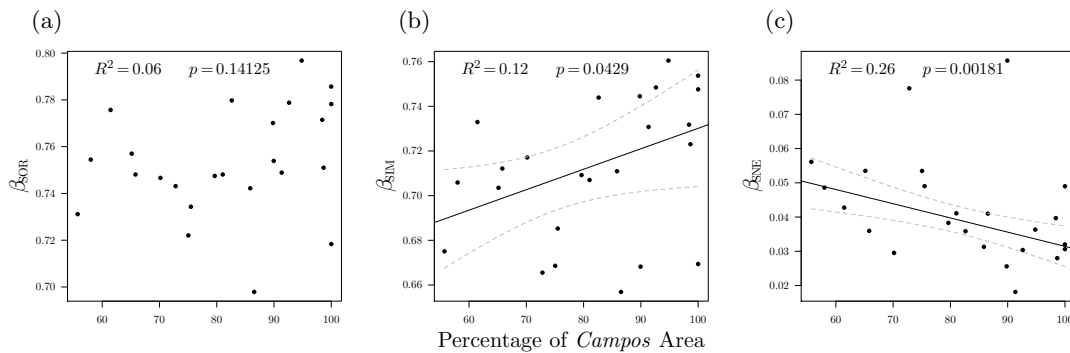


Figure 3 – Relationship between local floristic heterogeneity ((a) β_{SOR} , (b) β_{SIM} , (c) β_{SNE} multiple site dissimilarities) and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries.

220 **Phylogenetic Diversity** Landscape *Campos* area (%) was significantly related to the overall
 221 distance of taxonomic clades present in a local community, measured by SES MPD ($df = 22$,
 222 adjusted $R^2 = 0.18$, $p = 0.049$), as were the average distances between each species and its nearest
 223 phylogenetic neighbour in the community, measured by SES MNTD ($df = 22$, adjusted $R^2 = 0.5$,
 224 $p \leq 0.001$) (Fig. 4 and Tab. 1). Local plant communities were increasingly phylogenetically
 225 clustered in landscapes with less *Campos* area (%).

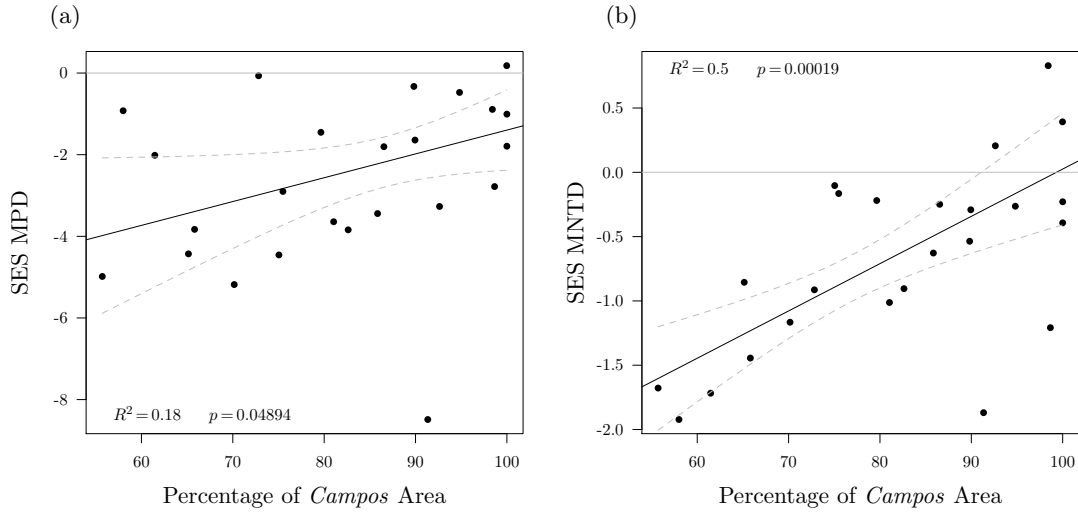


Figure 4 – Relationship between local phylogenetic relatedness ((a) SES MPD: standard effect size for mean pairwise distance, (b) SES MNTD: standard effect size for mean nearest taxon distance) and landscape *Campos* area (%). Hatched lines represent the 95% confidence boundaries.

Tabela 1 – Parameter estimates with standard errors, test statistics and effect sizes with 95% confidence intervals for the relationship between landscape *Campos* area (%) and species richness (Chao 2), beta-diversity (β_{SOR}) and beta-diversity components (turnover β_{SIM} and nestedness β_{SNE}), and phylogenetic diversity (SES MPD and SES MNTD) of local plant communities.

	<i>Dependent variable:</i>					
	Chao 2 (1)	β_{SOR} (2)	β_{SIM} (3)	β_{SNE} (4)	SES MPD (5)	SES MNTD (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)
Constant	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	0.216	0.097	0.160	0.291	0.217	0.520
Adjusted R^2	0.180	0.056	0.122	0.259	0.182	0.498
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

226 **Trophic Cascade** SES MPD, being more sensitive to the overall distance of taxonomic clades
 227 present in a community and to replacement of taxa that differ in broad taxonomic placement, did
 228 not significantly explain variation in ant generic richness ($df = 12$, adjusted $R^2 = 0$, $p \leq 0.259$).
 229 SES MNTD, a measure sensitive to replacement of closely related taxa and much less sensitive
 230 to changes at the basal nodes of the phylogeny, significantly predicted generic richness of ant
 231 ($df = 12$, adjusted $R^2 = 0.31$, $p \leq 0.012$) (Fig. 5 and Tab. 2).

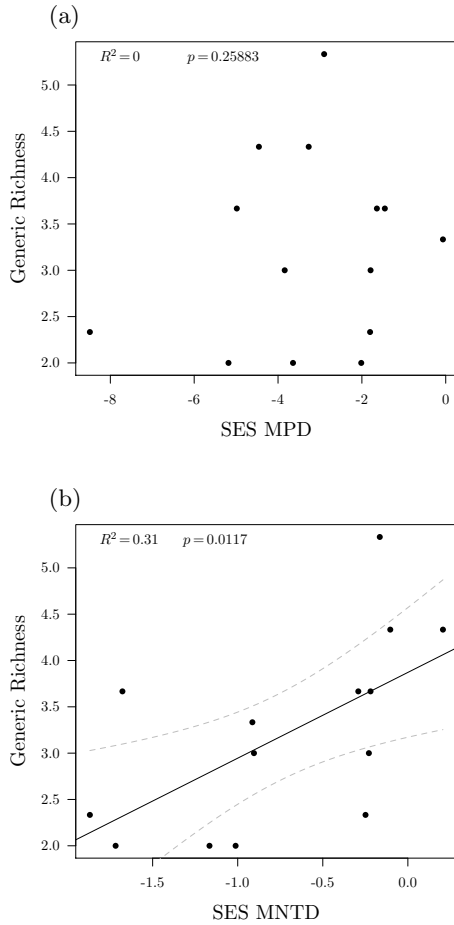


Tabela 2 – Parameter estimates with standard errors, test statistics and effect sizes with 95% confidence intervals for the relationship between plant phylogenetic diversity (SES MPD, SES MNTD) and ant generic richness.

	<i>Dependent variable:</i>	
	(1)	(2)
SES MPD	0.087 (0.073)	
SES MNTD		0.926* (0.312)
Constant	3.465*** (0.348)	3.871*** (0.321)
Observations	14	14
R^2	0.030	0.365
Adjusted R^2	0	0.312
Res. SE ($df=12$)	1.201	0.843
Wald	1.405	8.821**
Effect size r	0.32	0.65
95% CI of r	0.07, 0.86	0.53, 0.98

Figure 5 – Relationship between local ant generic richness and phylogenetic diversity ((a) SES MPD and (b) SES MNTD) of local plant communities. Hatched lines represent the 95% confidence boundaries.

232 Discussion

233 Using data from the South Brazilian grasslands that in recent years have been subjected to
234 extensive land-use changes, we show that landscape habitat amount explains variation in species
235 richness, beta-diversity components and phylogenetic diversity of local plant communities. Our
236 results suggest that local plant communities respond to even slight landscape habitat loss ($\leq 50\%$).
237 We found species poorer (Fig. 2 and Tab. 1), more homogenized (Fig. 3 and Tab. 1) and
238 phylogenetically less diverse (Fig. 4 and Tab. 1) local plant communities in landscapes with less
239 *Campos* habitat. Ants, a taxa with high levels of plant associations (or interactions), responded
240 to changes in plant community phylogenetic structure (Fig. 5 and Tab. 2). This suggests that
241 effects of habitat loss may perpetuate to higher trophic levels.

242 **Species Richness** Species poorer local plant communities in landscapes with less *Campos*
243 amount may be the result of at least four processes (i) stochastic local extinctions due to smaller
244 population sizes (Orrock & Watling 2010), (ii) lower recolonization rates due to decreased habitat
245 connectivity (Haddad et al. 2015), (iii) taxonomic homogenization, as generalist species that are
246 widely distributed in the changed landscape replace more specialist grassland species (Tabarelli
247 et al. 2012) and (iv) nonrandom local extinctions, i.e., particular evolutionary lineages are more
248 prone to effects of habitat loss (Nee & May 1997; Winter et al. 2009) leading to ecological
249 homogenization. All here suggested processes are likely to account in orchestrated fashion to
250 observed pattern. To regard underlying processes in more detail, we investigated beta-diversity
251 and phylogenetic diversity metrics. Beta-diversity may detail on whether observed species loss is
252 stochastic (increased beta-diversity (Segre et al. 2014)) or rather due to "winner-loser" replacement
253 (decreased beta-diversity). Measures of phylogenetic diversity may support whether species loss
254 is stochastic or nonrandom (Nee & May 1997; Purvis et al. 2000), thereby furthermore allowing
255 inference about ecological homogenization (Cavender-Bares et al. 2009).

256 **Beta-Diversity** If overall beta-diversity, which remained unaltered by landscape habitat amount,
257 were not disentangled into its species turnover and nestedness components, we would have errone-
258 ously concluded that local floristic variation remained similar across landscapes with differing
259 habitat amount. However, the correlation between *Campos* amount and overall beta-diversity
260 components, species turnover and nestedness, were both significant with medium effect sizes. Spe-

261 cies turnover decreased with decreasing landscape habitat amount, whereas nestedness increased
262 (Fig. 3 and Tab. 1), suggesting taxonomically more homogenized local plant communities in
263 landscapes with less *Campos*.

264 The pattern of decreased turnover and increased nestedness is generally attributed to the per-
265 sistence and proliferation of disturbance tolerant, abundant and/or widespread species, and the
266 extinction of narrowly distributed species with small populations. However, a greater exposure
267 to anthropogenic land uses may also increase the propagule pressure of exotic species and thus
268 the potential of biological invasions (Mack & D'Antonio 1998). Exotic species establishment and
269 spread may then additionally account for taxonomic homogenization. A recent study using data
270 from the same sampling network in Rio Grande do Sul showed that the four most problematic
271 alien species invading natural grasslands respond positively to decreasing *Campos* cover in the
272 surrounding landscape (Guido et al. 2016). This makes a case that observed taxonomic homo-
273 genization may in part be due to a few highly-resilient exotic species replacing multiple rare,
274 specialist species – in our study 24 species were identified as exotic (classification according to
275 Rolim et al. (2015)). Upon establishment, exotic species may disperse and proliferate in remnant
276 habitat, thereby establishing a gradient of occurrence probability being highest closer to habitat
277 edge (With 2002), increasing nestedness and decreasing turnover.

278 That taxonomic homogenization of grassland communities at the focal spatial scale, i.e., within
279 a locality, may occur as a result of exotic species proliferation finds empirical support from
280 exotic-dominated prairie grasslands, which – when compared to native grasslands – reveal lower
281 beta-diversity locally (Martin & Wilsey 2015).

282 **Phylogenetic Diversity** We found that landscape *Campos* amount significantly explained
283 variation in local phylogenetic diversity. We investigated phylogenetic structural changes at
284 basal branches (SES MPD) and tips (SES MNTD) of the focal phylogeny. Both SES MPD
285 and SES MNTD declined with landscape *Campos* amount (Fig. 4 and Tab. 1). This suggests
286 that local extinctions occur nonrandomly in landscapes with less habitat amount: particular
287 evolutionary lineages erode leading to phylogenetic clustering. There is growing evidence that
288 phylogenetic diversity, and niche differentiation is positively related to primary productivity in
289 plant communities (Cadotte et al. 2008). A loss of evolutionary history may thus affect facets of
290 ecosystem functioning. Moreover, as greater evolutionary diversity buffers ecosystems against

291 environmental variation, a loss of evolutionary information may ultimately result in decreased
292 ecosystem resilience (Cadotte et al. 2012).

293 Albeit currently compiled, there was yet no sufficient amount of trait data available for the
294 majority of sampled plant species. Therefore, we did not investigate the phylogenetic signal of key
295 functional traits. However phylogenetic conservation of ecologically important traits is common in
296 plants (Futuyma & Agrawal 2009; Wiens et al. 2010). Under the assumption of trait conservatism,
297 we can hypothesize that certain traits are selected for by the effects of landscape habitat loss,
298 for instance a specific agricultural disturbance regimen, land-use history and management may
299 select for species with high seed production and specific leaf area (Dinnage et al. 2012). Further
300 research should investigate whether there is a reducible identity of particular functional traits that
301 subjects plants to local extinction in disturbed environments. This link to functional diversity
302 may potentially enable predicting trajectories in other systems undergoing habitat loss and
303 fragmentation.

304 **Trophic Cascade** As phylogenetic diversity of the local plant community declines, we found
305 that ant generic richness follows. While not related to SES MPD, ant generic richness responded
306 to SES MNTD (Fig. 5 and Tab. 2). Formicidae is a family having thus a comparably low
307 taxonomic rank. Its taxonomic associations to plants are likely restricted to a range of closely
308 related genera or species, i.e., ants rather responds to changes at the tips (SES MNTD) than to
309 changes at the basal nodes (SES MPD) of the phylogeny. Although the model estimates the loss
310 of only up to 2 ant genera in phylogenetically less diverse plant communities, this represents a
311 diversity loss of 50% and may further have magnified effects on ant species richness.

312 Since (i) the strong relationship of SES MNTD to landscape *Campos* amount suggests with
313 habitat loss species pertain to fewer genera in plant communities, and (ii) ants responded to this
314 loss of lineage diversity, we infer that niche dimensions of ants are locally lost in landscapes with
315 less *Campos* amount. For instance, sampled genera such as *Pseudomyrex*, *Myrmelachista* and
316 *Cephalotes* that have specialized nesting requirements (C. R. Brandão et al. 2012) may respond
317 to the loss of specific evolutionary lineages, whereas sampled genera with broader niches, such as
318 *Camponotus* or *Pheidole*, may respond to phylogenetic diversity as proxy for resource diversity
319 (Armbrecht et al. 2004).

320 We argue that the loss of more distantly related plant species (SES MPD decreases with landscape

321 *Campos* amount, too) is likely to affect the host range of a variety of herbivores. Regarding the
322 link between plant phylogenetic diversity and plant productivity, a decrease in productivity
323 may reduce resource volumes for herbivores and consequently their abundance, affecting then
324 predators and parasitoids (Dinnage et al. 2012). While we here elaborate on only a single taxa
325 of higher trophic hierarchy, future research should investigate if broader taxonomic levels, e.g.,
326 birds, amphibians or mammals, respond to habitat loss in the *Campos Sulinos* too, and at what
327 focal spatial scale. For instance, grassland specialist birds may be more reliant on *Campos* cover
328 at larger spatial scales and this would have important implications for conservation.

329

330 **Conclusions**

331 We conclude that species loss, taxonomic homogenization and the loss of phylogenetic diversity of
332 plant communities of the *Campos Sulinos* may occur at even slight habitat loss scenarios, and
333 that changes in plant community structure may perpetuate to higher trophic levels. Our results
334 suggest that species loss can be linked to taxonomic homogenization, in which species are replaced
335 and go extinct nonrandomly, leading to ecologically more similar plant communities. Since losses
336 of phylogenetic information are linked to declines of ecosystem functions, e.g., plant productivity,
337 and since greater evolutionary diversity buffers ecosystems against environmental variation, we
338 ultimately expect that ecosystem resilience, not only in respect to environmental change but also
339 when recovering from a different land use, may decrease. We here provide empirical evidence
340 that the biological diversity of the *Campos Sulinos* is at risk under the current rate of land-use
341 conversion. We emphasize the urgency of a higher representation of the *Campos Sulinos* in
342 conservation units and a more restrictive policy framework for land-use change authorizations in
343 Rio Grande do Sul.

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Conclusões Finais

Conclui-se que a perda de espécies, a homogeneização taxonômica e a perda de diversidade filogenética de comunidades vegetais de *Campos Sulinos* podem ocorrer mesmo em consequência de perdas moderadas de habitat e que mudanças na estrutura da comunidade vegetal podem perpetuar para níveis tróficos mais altos. Nossos resultados sugerem que a perda de espécies pode ser atribuída à homogeneização taxonômica, na qual as espécies são substituídas e extintas de forma não-aleatória, levando a comunidade vegetal ecologicamente mais semelhante. Como as perdas de informação filogenética estão ligadas a declínios das funções dos ecossistemas, e.g., a produtividade das plantas, e como uma maior diversidade evolutiva amortece os ecossistemas contra variações ambientais, esperamos que a resiliência do ecossistema, não somente com relação à alteração ambiental, mas também quando recupera-se após conversão do uso do solo, pode diminuir. Aqui fornecemos evidências empíricas de que a diversidade biológica dos *Campos Sulinos* está em risco sob a atual taxa de conversão de uso do solo. Ressaltamos a urgência de uma maior representação dos *Campos Sulinos* em unidades de conservação no Rio Grande do Sul.

Apêndices

Locais de amostragem

Unidade SISBIOTA Nº	Município	Latitude	Longitude
10	Candiota	-31.511	-53.664
11	Dom Pedrito	-30.955	-54.379
13	Júlio de Castilhos	-29.320	-53.814
14	Aceguá	-31.797	-54.173
15	Aceguá	-31.767	-54.030
17	Palmares do Sul	-30.500	-50.421
19	Cachoeira do Sul	-30.297	-52.766
20	Alegrete	-29.778	-56.014
21	Alegrete	-30.058	-55.985
22	Vacaria	-28.194	-51.018
23	São Francisco de Paula	-29.193	-50.769
24	São José dos Ausentes	-28.615	-49.827
25	Pinheiro Machado (Torrinhas)	-31.305	-53.572
26	Pinheiro Machado (Sul)	-31.588	-53.531
28	São Borja	-28.852	-55.633
31	Jaguarão	-32.377	-53.370
32	Arroio Grande	-32.255	-53.225
34	São Gabriel	-30.148	-54.618
35	Alegrete	-29.665	-55.384
36	Alegrete	-29.799	-55.317
37	São Francisco de Paula	-29.149	-50.279
38	Caçapava do Sul	-30.292	-53.457
39	Tupanciretã	-29.035	-54.123
40	Soledade	-28.872	-52.462

Análise Filogenética: Arquivo Newick

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448)seedplants:75.000000;



Figure 6 – Phylogenetic tree of the plant species sampled in SISBIOTA in Rio Grande do Sul.