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A step to disentangle diversity patterns in Uruguayan grasslands: Climatic seasonality, novel land-uses, and landscape context drive diversity of ground flora

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Abstract

South American grasslands contain extraordinary biodiversity and play a central role in the subsistence of regional agroecosystems. In recent decades, afforestation, followed by the soybean planting boom, have led to drastic land-use changes at the expense of grasslands. Impacts on local biodiversity have remained understudied. We explored the taxonomic richness and ß-diversity of plants of ground layer (excluding trees and shrubs) at different land uses, its interplay at regional scale with environmental heterogeneity, and at local scale with novel land cover types and landscape configurations. We conducted correlation, principal component, NDMS, and SDR analysis to explore variation of taxonomic richness, richness difference, replacement, and similarity of ground flora as response to environmental filters and land use change across Uruguay. We surveyed 160 plots distributed in 10 land cover types, that is, closed and open native forests, different grasslands, crops, orchards, and timber plantations. We observed overlaying regional patterns driven by seasonality of temperature and precipitation, and land cover shaping taxonomic richness at local scale. Landscape configuration affects diversity patterns of native ground flora, which seems to be sustained mainly by the "old growth grassland" species pool. Taxonomic richness of native species decreases with an increase of distance to grassland. Crops and grasslands harbor a higher number of native species in the ground flora than native forests and timber plantations. The introduction of exotics is driven mostly by crops or highly modified pastures. Diversity patterns only partially reflect the ecoregion concept. Expanding the perspective from conservation in purely natural ecosystems to measures conserving species richness in human-modified landscapes is a powerful tool against species loss in the Anthropocene.

KEYWORDS

climatic seasonality, land cover change, landscape metrics, South America, temperate grasslands

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1 | INTRODUCTION

Non-forest ecosystems, such as grasslands or shrublands, are often neglected in conservation frameworks despite their high biodiversity, high endemism, and the key ecosystem services they provide (Henwood, 2010). Grasslands, in particular, are essential to the world's food supply, and play an important role in human well-being especially in regions where cattle ranching is one of the principal economic activities (Overbeck et al., 2015; Veldman et al., 2015). Beside pasture forage, grasslands are crucial for water regulation and freshwater supply, habitat services, erosion control, pollinator health, and carbon sequestration (Bengtsson et al., 2019; Murphy et al., 2016), but remain by far the least protected of the existing biomes (Buisson et al., 2022; Henwood, 2010; Sala et al., 2000; Sala et al., 2001).

In order to conserve natural grasslands, and to adapt management practices, species distribution pattern needs to be understood (Veldman et al., 2015). Since decades, calls for more protection are unlistened and forest restoration efforts additionally threaten grasslands as these forests are also established in natural grassland and savannah ecosystems (Buisson et al., 2022). Our knowledge on grassland restoration processes is still superficial and long-term visions are lacking (Buisson et al., 2022).

As an emblematic example from South America, the “Campos” grasslands cover more than two thirds of Uruguay (Alvarez et al., 2015), and constitute the national landscape of the so called “Patria Gaucha,” as extensive cattle and sheep rearing is the most emblematic economic activity since the European colonialization (Säumel et al., 2023). The success of the economic model depends on the production of meat and fiber, and on the overall functionality of the ecosystem (di Minin et al., 2017). Only 0.2% of Uruguayan Campos are currently protected within the global system of protected areas (Henwood, 2010). In recent decades, many such natural grasslands have been replaced by crops and afforestation (Alvarez et al., 2015; Paruelo et al., 2006). Timber plantations, principally composed of *Eucalyptus* (77%) and *Pinus* (22%), have grown from occupying 4% of the territory in 2000 to more than 6% in 2011, while the area planted with soybeans increased by 2000% between 1991 and 2011 (Alvarez et al., 2015). New approaches of grassland intensification have emerged in response to this silvi- and agricultural expansion (Jaurena et al., 2021) and continue to be at the expense of native grassland diversity. Land-use changes follow different trajectories (Ramírez & Säumel, 2022a). Thus, we expect overlaying effects of agri- and silvicultural expansion at local scale with changing climate and other environmental filters at regional scale.

Although maintaining grassland functions and diversity became a major issue in academic debates in South America (Overbeck et al., 2015; Veldman et al., 2015), we still know far too little about species diversity of Campos grasslands in general and how land use change shapes the diversity of the ground flora at local scale. Existing regional studies on ground flora or herbaceous species are limited to a small number of plots on grasslands under different management strategies (Altesor et al., 1998, 2005; Lezama et al., 2013). This shortage limits Uruguayan conservation planning as the characterization of local ecoregions and the identification of “priority areas for conservation” within these eco-regions were developed without considering ground flora (Brazeiro, 2015), although the later comprise also the grassland species pool. Correspondingly, the ecosystems determined for conservation priority are covering mainly native forests and wetlands, whereas grasslands are subsumed only as an associated ecosystem (Brazeiro, 2015) and remain under-represented in the national system of protected areas compared to their biome-dominating role (Säumel et al., 2023). In contrast, riparian forests, which cover only 6% of the country are much better protected (Ramírez & Säumel, 2022a). For territorial planning, relevant policies and regulations that respond to landscape-specific drivers of change, better insight into grassland biodiversity affected by afforestation, and intensive agriculture at different scales are crucial (Andrade et al., 2015; Altesor et al., 1998; Jobbágy et al., 2006).

In this study, we focus on taxonomic species richness and ß-diversity. The taxonomic richness has been used mainly in the efforts to establish nature protection areas in Uruguay (Brazeiro, 2015; Brazeiro et al., 2020; MVOTMA, 2016; SNAP, 2015). Taxonomic species richness and ß-diversity cover only two facets of biodiversity (Brunbjerg et al., 2018; Craven et al., 2018; Mace, 2004; Moreno et al., 2017; Ricketts et al., 1999) but not functional or genetic diversity. However, “conservation biology is a discipline with a deadline” (Wilson, 2002) and very limited resources to inform decision makers (Ricketts et al., 1999), especially in highly contested landscapes with scarce databases such as Uruguayan grasslands. It is a first step to disentangle the role of environmental gradients, of assignment to ecoregions and to conservation priority ecosystems at regional scale and of changing land uses and related landscape metrics at local scale. We analyze the relationship of exotic and native taxonomic species richness and composition in order to shed light on the floristic quality and the role of exotic species in changing landscapes (Schetter et al., 2013). We aim to identify main factors shaping diversity of ground flora at regional scale through climate and other environmental filters and at local scale where land cover patterns and landscape contexts determine the grassland diversity.

2 | METHODS

2.1 | Study area

The study area is located in the temperate grasslands of the Oriental Republic of Uruguay (34°52′S, 56°10′W), also known as South American Campos (Figure 1a). The climate is humid subtropical. The mean annual temperature ranges between 16 and 20°C with monthly average temperatures ranging between 17°C (April) and 11°C (July). The accumulated precipitation ranges between 1000 and 1500 mm per year with steady rainfall occurring throughout the year. The topography is dominated by low hills and plains, accompanied by a large freshwater network. Dominant soils are phaeozems, leptosols, vertisols, acrisols, and luvisols.

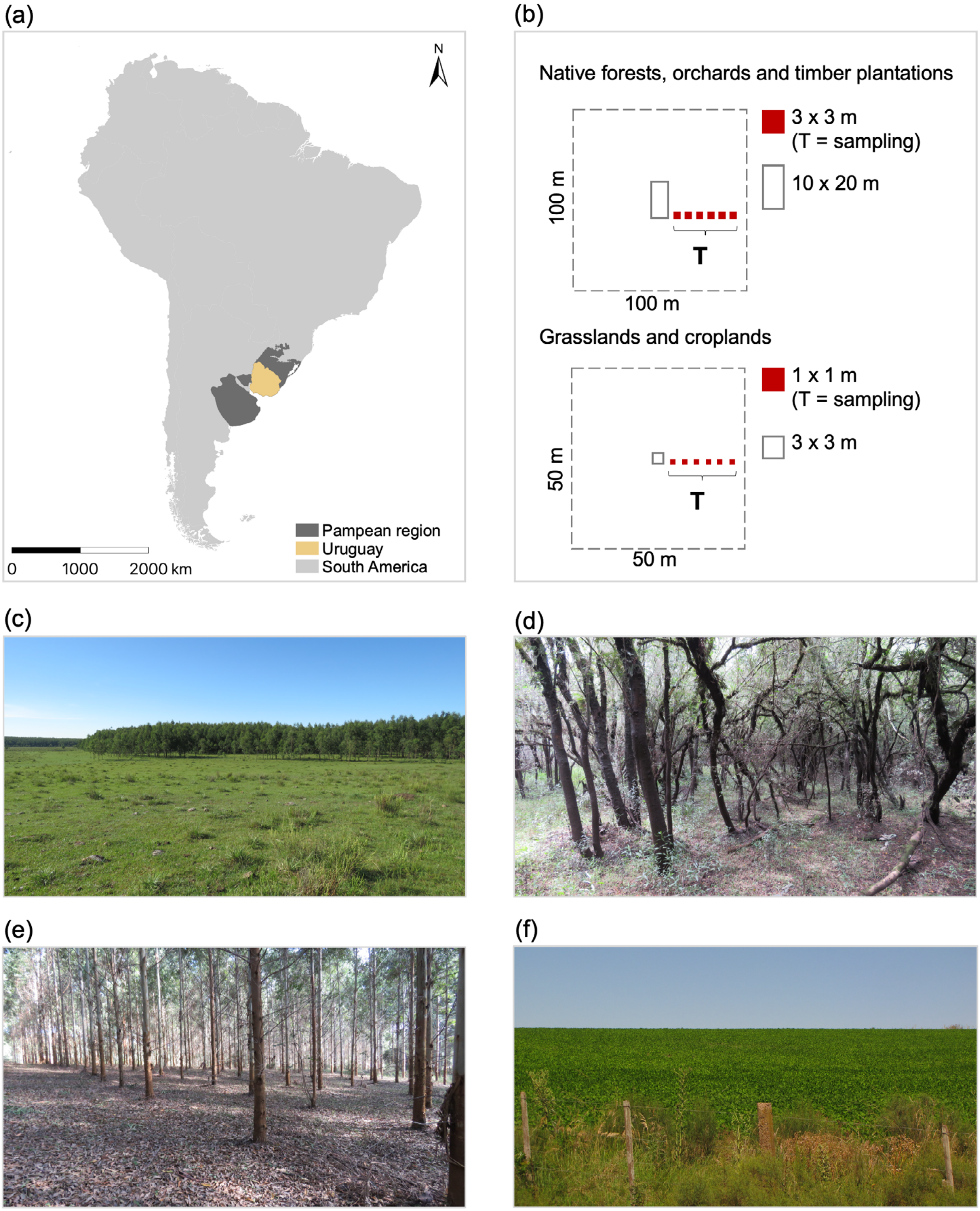

FIGURE 1 Study region within South America (a), sampling design (b), and main land use types across Uruguay: grassland (b); native riparian forests (c), 5–7 years old *Eucalyptus* plantation (d), and soybean crops (e).

Uruguay has been divided into seven ecoregions (Brazeiro, 2015): Cuenca Sedimentaria del Oeste (CSO), Cuesta Basáltica (CB), Cuenca Sedimentaria Gondwánica (CSG), Escudo Cristalino (EC), Sierras del Este (SE), Graben de la laguna Merín (GLM), and Graben del Santa Lucía (GSL; Figure 2a). The ecoregion approach uses relatively coarse biogeographic divisions of a landscape (Ricketts et al., 1999), which has been used in Uruguayan conservation efforts mainly prioritizing geomorphological and edaphic structures, intersected by information on taxonomic species richness for woody species, fish, amphibians, reptiles, birds, and mammals from different local experts. Based on this, "priority ecosystems for conservation" have been determined (Brazeiro, 2015). The CSO is a sedimentary basin along the Uruguay River next to the border with Argentina, which covers about 22,000 km^2 between 5 and 160 m asl. Agri- and silvicultural land-uses on profound brunosoles are dominating. The CB is an extensive basaltic plateau dominated by natural pastures covering 42,000 km^2 ranging between 20 and 400 m asl, which is inclined toward the Uruguay River. The CSG covers about 33,000 km^2 between 90 and 380 m asl in the Northeastern Uruguay and has a large variety of soils (e.g., brunosoles, vertisoles, litosoles). During the last decades, large timber plantations are expanding on previously extensively used grasslands, The EC covers about 27,000 km^2 between 0 and 190 m asl in the Southwestern Uruguay with brunosoles. The traditionally dominating grassland with dairy and livestock production experience an ongoing agricultural intensification by crops and timber monocultures. The SE cover about 26,000 km^2 between 0 and 500 m asl in the Southeastern Uruguay with a dominance of livestock and timber production on more superficial and stonier brunosoles. The GLM covers about 16,000 km^2 between 0 and 40 m asl in the Eastern Uruguay with a dominance of livestock and agricultural production on profound brunosoles. The GSL covers about 9000 km^2 between 0 and 120 m asl in the South of Uruguay with a dominance of horti- and agricultural production on profound brunosoles including also the agglomeration of Montevideo.

Grasslands including prairies and palm groves currently occupy about 71% of the Uruguayan territory (Alvarez et al., 2015). Management varies from primary grasslands with no visible human influence to highly modified pastures fertilized or "improved" through (often non-native) forage species for higher livestock production (Modernel et al., 2016). In the last decades, stimulated by governmental policies and financial incentives, over 10% of the grassland has been transformed to cropland, orchards, and timber plantations (Alvarez et al., 2015). This expansion of cash crops and forestry has led to the displacement of traditional livestock activities and changed many economic, socio-cultural, and environmental aspects of rural life (e.g., Säumel et al., 2023). Even though the precipitation regime is not a limiting factor in the establishment of woody species, native forests cover only about 6% of Uruguay, and there is little evidence of recent forest expansion. Native riparian forests, commonly with a dense canopy, are found along rivers and streams on poorly drained soil, while native park forests, characterized by an open canopy, can be distinguished as a transitional formation between riparian forests and grasslands (Pozo & Säumel, 2018).

2.2 | Sampling design

First, we randomly selected monitoring sites across the country. Then we contacted landowners to explore their willingness to establish a monitoring site. If the owner agreed, plot selection was stratified by land cover type. We sampled the species of the ground flora in 160 plots at 44 monitoring sites distributed across the country (Figure 2a; Supporting Information Figure A1; Supporting Information Table A2), covering the main land cover types (Figure 1b–f) including: native forests, grasslands, orchards, croplands, and timber plantations. Our survey also covers highly modified land-uses to explore their potential role as refugia or replacement habitats for grassland species. We categorized 10 land cover subtypes according to our field observations: closed native forest (Fc with 80%–100% canopy cover), open native forest (Fo with 10%–20% canopy cover), primary grasslands (Gp, without grazing), low intensity secondary grassland (Gl; with sporadic grazing and low animal charge), high intensity secondary grassland (Gh; grazing with high animal charge), crops (Ca), fruit orchard (Co), *Eucalyptus* plantation (<4 years; PEy), *Eucalyptus* plantations (>8 years; PEo), old pine plantations (>8 years; Pp). Only 1% of the crops and 60% of orchards are irrigated (MGAP, 2018).

Elevation across sites ranged from 0 to 215 m above sea level, with a maximum slope of 27° (Supporting Information Table A4). Within each plot, six subplots following a transect from the center to the edge of the plot were established (Figure 1b). Subplots in grasslands and croplands consisted of 1 × 1 m quadrats, while in native forests, orchards and timber plantations, subplots consisted of 3 x 3 m quadrats.

Plant survey were performed during two field campaigns from December 2015 to April 2016, and from October to December 2016 to cover the whole growing season. Ground flora included all plants under 1.5 m, excluding shrubs and trees. All species of the ground flora at the subplot level were identified in situ or, if

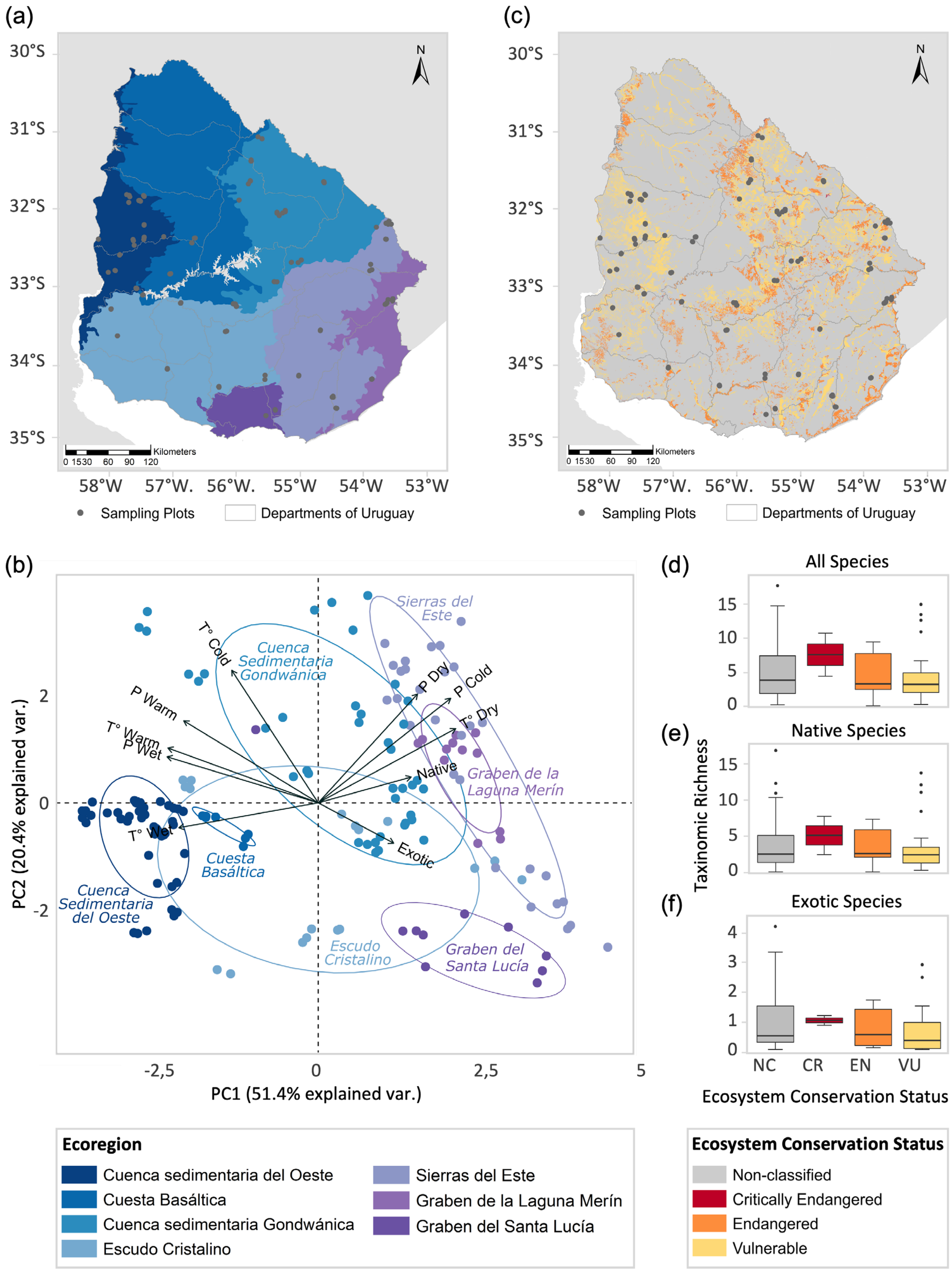

FIGURE 2 Legend on next page.

necessary, taken to the herbarium of the Museo Nacional de Historia Natural del Uruguay for taxonomic classification. Voucher specimens were used for identification. Less than 5% of the individuals have been identified only at a genus level and were not further considered for the analysis. Species were identified by origin as native or exotic species (LFF, 2010; MVOTMA-MGAP-SNAP, 2011).

The total number of ground flora species was determined by calculating the cumulative number of species that occurred in the six subplots. To eliminate the effect of area sampled between plots, the taxonomic richness (St) per area was calculated as $\mathrm{St} = n_i/ln\mathrm{A}_i$, where n_i is the number of species per plot and $ln\mathrm{A}_i$ is the natural logarithm of the total area (m^2) of study. St was calculated separately for native ($\mathrm{St}_{\mathrm{Nat}}$) and exotic ($\mathrm{St}_{\mathrm{Exo}}$) species. Finally, plots were classified according to their spatial distribution within the seven ecoregions and within the priority ecosystems for conservation in Uruguay based on Brazeiro (2015) (Figure 2).

2.3 | Environmental and landscape variables

To explore patterns of ground flora as a response to the environmental heterogeneity and the landscape context, we used site-specific environmental and landscape metrics as variables (Supporting Information Tables A3 and A4). Climatic variables were extracted for each plot from the WorldClim v.1.4 database (Fick & Hijjmans, 2017) with a resolution of $30\mathrm{s} = 0.93\ \mathrm{km}^2$ due to the scarcity of meteorological stations in Uruguay. This database is widely used in other regional studies (e.g., Toranza et al., 2016). We included the mean temperature and precipitation during the wettest, driest, warmest, and coldest quarter to test potential associations to the variance of taxonomic richness and the relevance to capture the climate variability and seasonality of the region, site elevation (meter above sea level) and slope (°). Elevation was obtained from the Digital Elevation Model from the governmental server (DINAMA, 2020) and slope was determined using ArcGis v.10.3.1. We extracted values of elevation and slope using the central point of each plot.

Variables regarding landscape matrix were calculated based on land cover maps obtained through the classification of a set of Landsat 5 TM and Landsat 8 OLI satellite images. The acquisition dates were between December 2015 and January 2016 (Supporting Information Table A1). We used Landsat 5 when Landsat 8 had a cloud cover percentage over 10%. For this, images were first atmospherically and geographically corrected using the land surface method (Moran et al., 1992) and dark object saturation (Chavez Jr, 1996) in Matlab (The Mathworks Inc., Natick, MA; for details see Ramírez & Säumel, 2022b). The resulting raster images have a spatial resolution of 30 m, and reveal different land covers, including timber plantations, native forest, grassland, and cropland (see detail in Ramírez & Säumel, 2022b).

To quantify the surrounding landscape of each plot, we created circular buffers with a radius of 1 km from the central point of each plot. Each buffer was used to extract land-cover maps that were later used as the basis for the calculation of spatial metrics using ArcGis v.10.3.1 (ESRI, 2016). When the distance between plots was less than a km, land cover maps overlapped. All individual circular land cover maps were used to compute landscape metrics using FRAGSTATS version 4.2 (McGarigal et al., 2012), including different spatial levels of analysis. At the landscape level, we quantified the Shannon's diversity for each thematic land cover maps. At class level, which account landscape metrics considering the identity of the cover, we calculated the total land cover area and number of patches by land cover type. We also measured the landscape configuration and connectivity as the median Euclidean nearest-neighbor distance and the aggregation index by land covers. The Euclidean distance was determined as the distance from patch to nearest neighboring patch of the same class type, based on the shortest edge-to-edge distance. For landscape units for which the Euclidean distance could not be computed

FIGURE 2 Location of the 160 sampling plots across the ecoregions of Uruguay (a). Limits of the local ecoregions were adapted from Brazeiro (2015): Cuenca Sedimentaria del Oeste (CSO), Cuesta Basáltica (CB), Cuenca Sedimentaria Gondwánica (CSG), Escudo Cristalino (EC), Sierras del Este (SE), Graben de la laguna Merín (GLM), and Graben del Santa Lucía (GSL). Principal Component Analysis results (b) based on climatic variables and taxonomic species richness grouped by ecoregion. Native: Native Species Richness; Exotic: exotic species richness; $\mathrm{T°}_{\mathrm{warm}}$: mean temperature − warmest quarter (°C); $\mathrm{T°}_{\mathrm{cold}}$: mean temperature − coldest quarter (°C); $\mathrm{T°}_{\mathrm{wet}}$: mean temperature − wettest quarter (°C); $\mathrm{T°}_{\mathrm{dry}}$: mean temperature − driest quarter (°C); $\mathrm{P}_{\mathrm{warm}}$: precipitation − warmest quarter (mm); $\mathrm{P}_{\mathrm{cold}}$: precipitation − coldest quarter (mm); $\mathrm{P}_{\mathrm{wet}}$: precipitation − wettest quarter (mm); $\mathrm{P}_{\mathrm{dry}}$: precipitation − driest quarter (mm). For details see Table 1. Map of the threatened ecosystems in Uruguay adapted from Brazeiro (2015) (c), taxonomic richness (St) of all species (d; $\mathrm{St}_{\mathrm{All}}$), native species (e; $\mathrm{St}_{\mathrm{Nat}}$), and exotic species (f; $\mathrm{St}_{\mathrm{Exo}}$) per ecosystem category. Proposed categories are abbreviated as follows: critically endangered (CR), endangered (EN), vulnerable (VU), and information not available (N/C). Median, first and third quartile, max, min, and outliers are given in (d–f). See Supporting Information Table A14.

TABLE 1 Descriptive statistics on total taxonomic richness (St) observed in different ecoregions (see Figure 2a and Section 2) and land-use types.

		n	Area sampled (m^2)	Taxonomic richness (St) observed: Mean ± SE	Min	Max
Ecoregion						
Cuenca Sedimentaria del Oeste (CSO)		44	1542	2.61 ± 0.28	0.29	8.06
Cuesta Basáltica (CB)		7	138	3.79 ± 0.70	1.67	6.48
Cuenca Sedimentaria Gondwánica (CSG)		41	1158	3.77 ± 0.49	0.15	14.6
Escudo Cristalino (EC)		18	444	5.32 ± 0.81	0.54	10.7
Sierras del Este (SE)		29	892	7.45 ± 0.79	1.63	17.5
Graben de la Laguna Merín (GLM)		12	264	7.67 ± 0.97	3.34	14.6
Graben del Santa Lucía (GSL)		9	288	6.75 ± 0.90	0.68	9.82
Land use type						
Native Forest	Closed native forest (Fc)	29	1566	2.72 ± 0.32	0.41	8.56
	Open native forest (Fo)	13	702	4.8 ± 0.70	1.07	8.54
Grassland	Primary grassland (Gp)	20	120	6.94 ± 1.01	1.88	17.5
	Low intensity secondary grassland (Gl)	28	166	6.54 ± 0.79	1.25	14.6
	High intensity secondary grassland (Gh)	20	120	6.43 ± 0.76	1.88	12.1
Agriculture	Croplands (c)	12	72	3.27 ± 0.43	0.93	5.38
	Orchard (o)	3	162	7.8 ± 1.71	4.72	10.6
Timber plantations	*Eucalyptus* plantation (<4 years) (Ey)	10	540	3.38 ± 0.93	0.64	8.90
	Eucalyptus plantations (>8 years) (Eo)	20	1008	3.19 ± 0.66	0.15	8.39
	Old *Pinus* plantations (>8 years) (Po)	5	270	2.29 ± 0.13	0.36	4.47

Note: The mean and the corresponding standard error (S.E.) is given based on the number of species per plot and the total class area sampled (in total 160 plots covering 4726 m^2).

because they did not contain any patch, or presented only one patch of the focal class, we assumed a distance of 2015 m (hypothetical distance from a cell center located outside the landscape unit). The aggregation index (He et al., 2000) was determined as the number of joins or like adjacencies involving a determined class, divided by the maximum possible number of like adjacencies of the corresponding class (McGarigal et al., 2012). When the aggregation index could not be computed due to the absence of the focal class in the landscape unit, we assumed a value of zero. This index illustrates the frequency with which different pairs of patches from a same land-cover type appear side-by-side on the landscape (McGarigal et al., 2012). Finally, at the patch level, we identified single patches on which the vegetation samples were performed and quantified the patch size and patch isolation as the patch area and distance to grassland. Here, distance to grassland was calculated separately in ArcGIS, as the distance from a single sampling plot to the nearest neighboring patch of grassland in the landscape unit, based on point-to-edge distance.

2.4 | Data analysis

Differences of taxonomic richness (St) between ecoregions, land cover types, and within priority ecosystems for conservation were analyzed using the Kruskal–Wallis test. For pairwise post-hoc multiple comparisons, we used the Mann–Whitney *U*-test with Bonferroni correction. The correlation and relationships of climatic and landscape metrics with taxonomic richness were evaluated using Spearman-rank correlations and generalized linear models, respectively.

To further illustrate the variation of taxonomic richness (St), landscape, and environmental predictors across ecoregions and land cover types in Uruguay, we performed a principal component analysis with climatic variables including St to cluster and visualize patterns in ground flora richness. Analyses were performed in R using the packages “vegan,” “rstatix,” and “stats” (Kassambara, 2020; Oksanen et al., 2016; R Core Team, 2021).

We explored the ground flora diversity patterns across and within the ecoregions and different land cover types by performing SDR-simplex analysis (Podani & Schmera, 2011) calculating three complementary indices measuring similarity based on Jaccard index, relative richness difference, and species replacement for all pairs of sites using the function beta.div.com of the package *adespatial* in R (Dray et al., 2022). We displayed the indices in triplots (Podani & Schmera, 2011).

To understand differences in community composition between land cover types, we performed a nonparametric multidimensional scaling (NMDS) based on Jaccard dissimilarity index between land cover types across and within different ecoregions using the function *metaMDS* of the package *vegan* in R (Oksanen et al., 2016). The NMDS was performed based on presence/absences matrices of species.

To evaluate composition differences between land cover types, we run a permutational multivariate analysis of variance over distances matrices based on Jaccard index (Anderson, 2017) using the function *Adonis2* of the package *vegan* in R (Oksanen et al., 2016). Dissimilarity pairwise multiple-comparisons between land cover types were evaluated using adjusted *p*-values with Bonferroni correction using the function *pairwiseAdonis* of the package *vegan* in R (Oksanen et al., 2016).

3 | RESULTS

A total of 10,223 plant individuals were registered, belonging to 733 species, 82 families, and 358 genera. We identified 565 native species from 76 families and 294 genera and 112 exotic species from 29 families and 84 genera. Less than 5% of the individuals could only be identified at the genus level. One belongs to a genus with almost non-native species, whereas the other belongs to a genus with mostly native species.

3.1 | Ground flora richness and composition depending on ecoregion

We revealed significant differences in taxonomic richness (St) between ecoregions ($X^2 = 48.42$, $p < .001$). CSO harbors significantly lower St compared to the GSL, GLM, and SE (Figure 3a). CSG has a significantly lower St than GLM and SE. A similar pattern was observed when accounting only for $\mathrm{St}_{\mathrm{Nat}}$ (Figure 3b), with CSO and CSG supporting a significantly lower $\mathrm{St}_{\mathrm{Nat}}$ than GLM and SE. Across all plots, $\mathrm{St}_{\mathrm{Nat}}$ and $\mathrm{St}_{\mathrm{Exo}}$ species richness was positively correlated, but is not significant when considering only plots within the ecoregions CB, CSG, GSL, and GLM (Supporting Information Table A5). GSL had a significantly higher $\mathrm{St}_{\mathrm{Exo}}$ compared to CSO and CSG (Figure 3c).

Regarding the variation of community composition, the SDR analysis revealed a high richness difference, dissimilarity, and replacement of species between plots across the whole country and within each ecoregion (Figure 4). Half of all species are replaced across sites. In average over all ecoregions, only 4% of the species are common between sites (Figure 4a). Similarity of species composition is lowest in the Western ecoregions (CSO, CB, CSG; 5–9%; Figure 4b–d) and highest in the ecoregion around Montevideo (GSL, 15%; Figure 4h).

3.2 | Ground flora richness and community composition depending on land cover

We found variation in the taxonomic richness of the ground flora ($\mathrm{St}_{\mathrm{All}}$) across all land cover types ($X^2 = 41.0$, $p = .005$). Primary grasslands showed the highest cumulative number of species and timber plantations the lowest values per plot. All types of grasslands harbor a significantly higher $\mathrm{St}_{\mathrm{All}}$ compared to closed native forests (Figure 3d). $\mathrm{St}_{\mathrm{Nat}}$ was significantly higher in primary grasslands plots compared to plots covered by closed native forests and crops (Figure 3e), while closed native forest exhibited a significant lower $\mathrm{St}_{\mathrm{Exo}}$ than crops and secondary grassland with a high grazing intensity (Figure 3f).

We found a significant variation of ground flora composition comparing the four main land cover types (i.e., native forests, grasslands, crops, and timber plantation) across all ecoregions for all species and for native and exotic species, separately (Supporting Information Table A6). We observed the same pattern for CSO in the West, CSG in the North-East and for SE in the East of Uruguay, when including all and native species of ground flora. Composition of exotic species differs between timber plantations and other land cover types, between grasslands and crops in CSO and between native forests and grasslands in CSG and SE. Composition of ground flora of native forests within the other ecoregions do not differ significantly (Supporting Information Table A10).

The SDR analysis revealed a high richness difference, dissimilarity, and replacement of species between plots across all different land cover types (Figure 5). In average, more than the half of all species are replaced and only 6%–8% of the species are common between sites in most land use types, except in timber plantations with about 40% of replacements. Similarity of ground flora is lowest in old timber plantations (Figure 5h–j) and highest in crops or orchards (Figure 5f,g). We found variation of species composition across the 10 different land cover

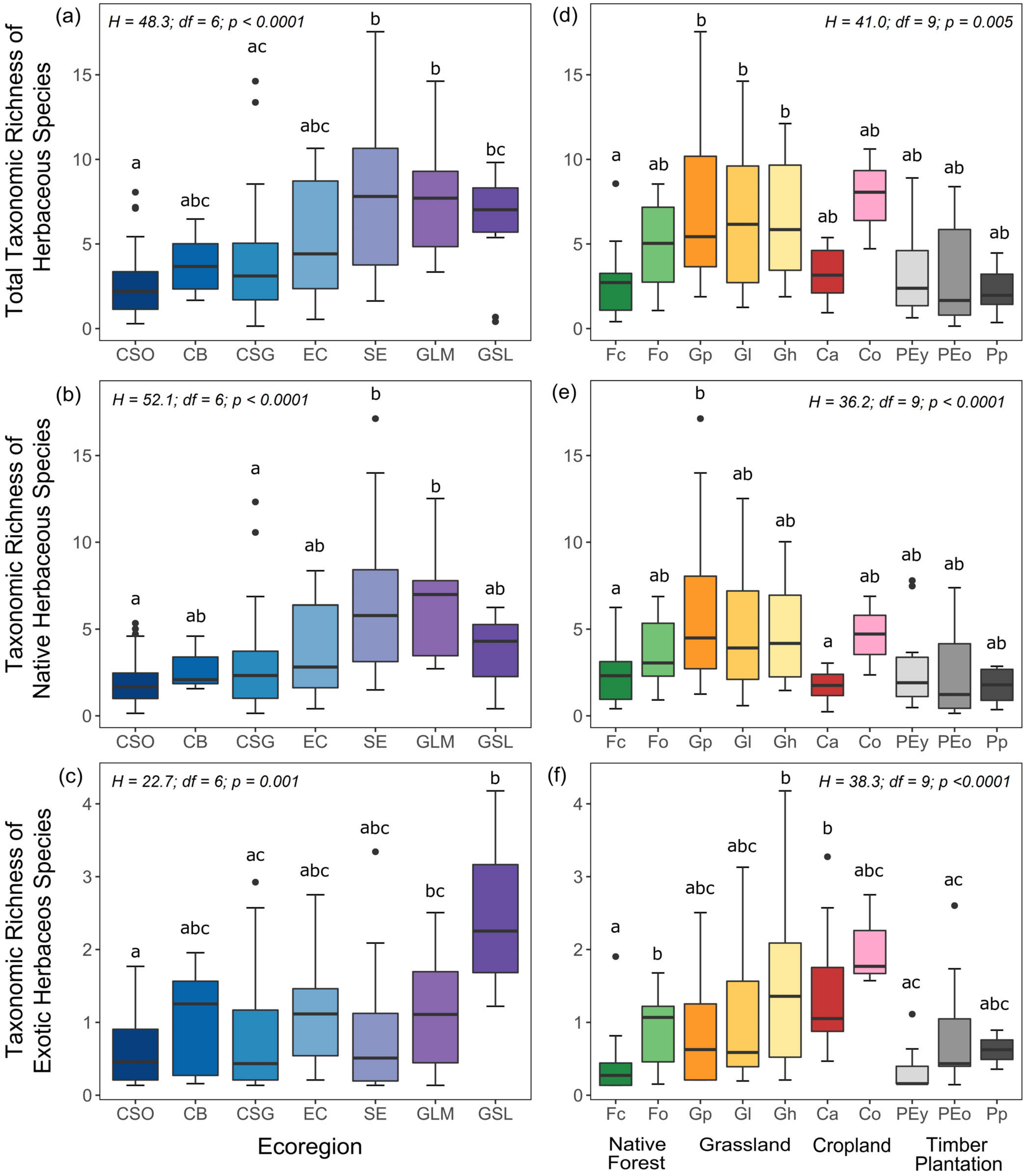

FIGURE 3 Taxonomic species richness (St) of the ground flora per ecoregions (left) and land-use classes (right). The ecoregions are Cuenca Sedimentaria del Oeste (CSO), Cuesta Basáltica (CB), Cuenca Sedimentaria Gondwánica (CSG), Escudo Cristalino (EC), Sierras del Este (SE), Graben de la Laguna Merín (GLM), and Graben del Santa Lucía (GSL). See the geographic location of each región in Figure 2a. Land-use types are closed native forest (Fc), open native forest (Fo), primary grasslands (Gp), low intensity secondary grassland (Gl), high intensity secondary grassland (Gh), crops (Ca), Fruit orchard (Co), *Eucalyptus* plantation (<4 years; PEy), *Eucalyptus* plantations (>8 years; PEo), old pine plantations (>8 years; Pp). Figures (a) and (d) show the taxonomic species richness of the ground flora, independent of their origin (St_{all}). Figures (b) and (e) show the taxonomic species richness of native ground flora and Figures (c) and (f) show the taxonomic species richness of exotic ground flora. Different letters represent significant differences between groups ($p < .05$). Median, first and third quartile, max, min, and outliers are given.

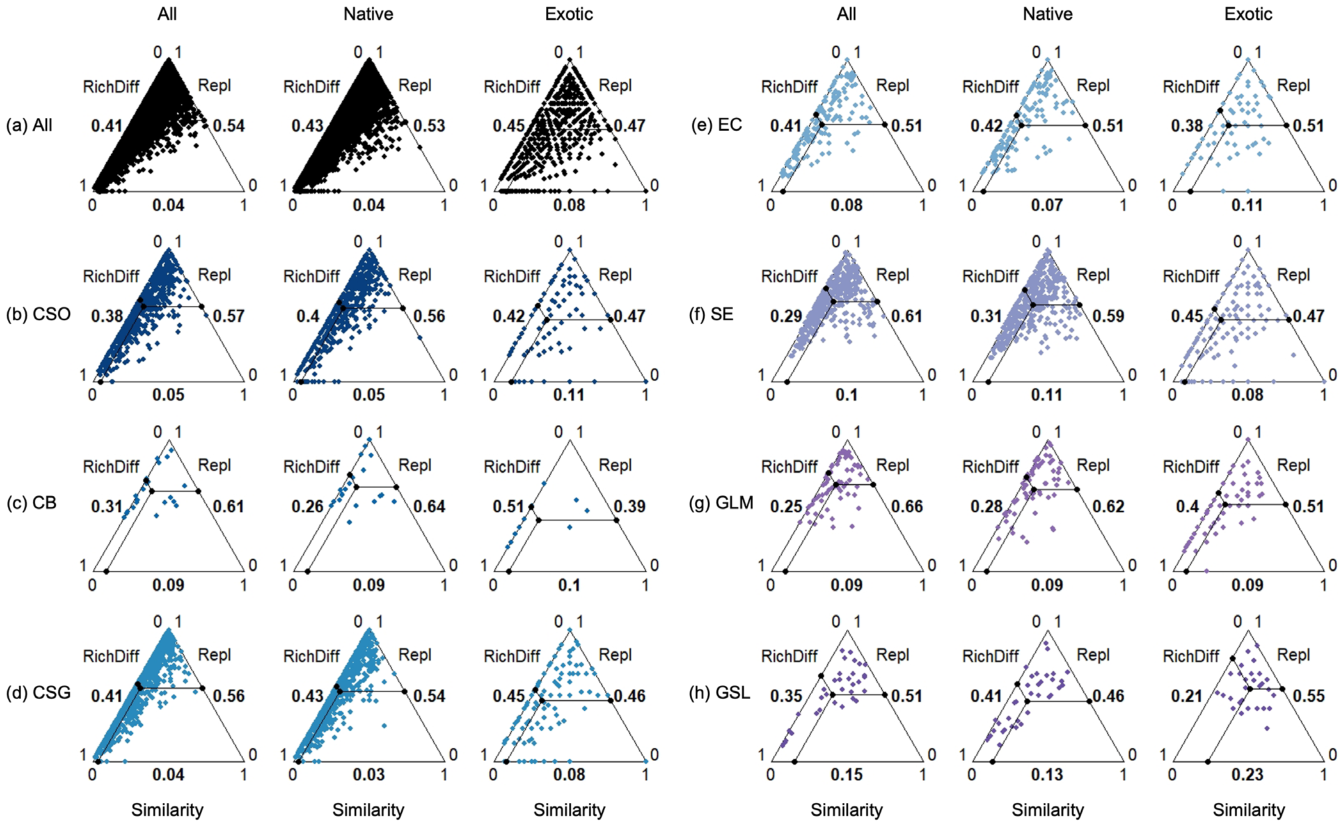

FIGURE 4 Species richness, replacement, and similarity of ground flora communities presented as SDR simplex triplots for all plots across Uruguay (a) and for the seven ecoregions (see Figure 2a). Ecoregions are Cuenca Sedimentaria del Oeste (CSO), Cuesta Basáltica (CB), Cuenca Sedimentaria Gondwánica (CSG), Escudo Cristalino (EC), Sierras del Este (SE), Graben de la laguna Merín (GLM), and Graben del Santa Lucía (GSL). The edges of the triplots represent, respectively: Species replacement (Repl); Richness difference (RichDiff), and Similarity. Dots represent pairs of sites.

types for all species and for native and exotic species, separately (Figure 6, Supporting Information Table A11). These differences between land cover types can be revealed also for native species composition (Figure 6; Supporting Information Table A12). There are less land cover pairs with different exotic species composition (Figure 6, Supporting Information Table A12).

3.3 | Taxonomic species richness within priority ecosystems for conservation

A quarter of all our sampled plots were located within areas classified as threatened ecosystems in Uruguay (Figure 2c). Plots in the areas categorized as critically endangered ecosystems sustain in average a higher taxonomic richness among native (St_{Nat}; $\mu_{\text{Nat}} = 5.26 \pm 0.7$) than among exotics species (St_{Exo}; $\mu_{\text{Exo}} = 1.09 \pm 0.2$). The same hold for plots in areas classified as endangered ($\mu_{\text{Nat}} = 3.84 \pm 1.0$, $\mu_{\text{exo}} = 0.86 \pm 0.3$) or as vulnerable ($\mu_{\text{Nat}} = 3.36 \pm 0.6$, $\mu_{\text{exo}} = 0.73 \pm 0.1$; Figure 2d–f). However, there was no statistical difference in St_{all} found in the plots located within threatened ecosystems compared to St_{all} observed on plots not assigned a conservation priority category ($X^2 = 0.581$, $p = .44$).

3.4 | Environmental variables and taxonomic richness

Eight climatic variables plus two species richness variables of the two first principal components preserved about the 72% of the total variation across all sites (Figure 2b; Supporting Information Table A14). Across all plots, the elevations were not significantly associated with St (Table 2). We found a positive correlation between slope and St_{All} and St_{Nat} and a negative association between slope and St_{Exo} and total St for the plots of CB, and a positive association between elevation and total St in EC, and between elevation and St_{Exo} in SE (Supporting Information Table A5). Most of our climatic variables are negatively associated to St_{all}, St_{Nat}, and St_{Exo}, with the exception of the mean temperature and precipitation during the driest quarter and the precipitation during the coldest quarter. The mean temperature during the wettest quarter had a negative

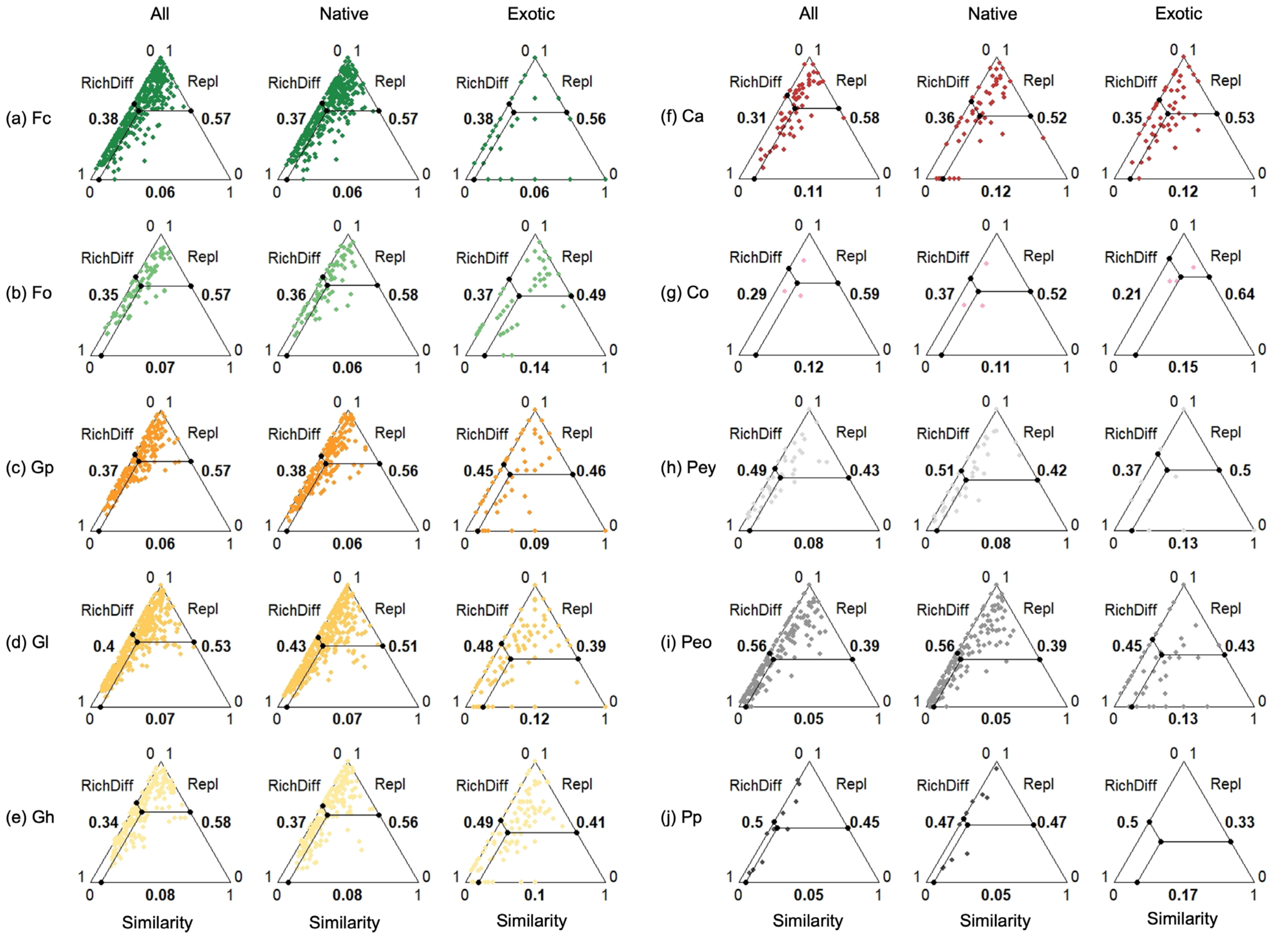

FIGURE 5 Species richness, replacement, and similarity of ground flora communities presented as SDR simplex triplots for all plots per land cover typ: closed native forest (a, Fc), open native forest (b, Fo), primary grasslands (c, Gp), low intensity secondary grassland (d, Gl), high intensity secondary grassland (e, Gh), crops (f, Ca), Fruit orchard (g, Co), *Eucalyptus* plantation (<4 years) (h, PEy), *Eucalyptus* plantations (>8 years) (i, PEo), old pine plantations (>8 years) (j, Pp). The edges of the triplots represent, respectively: Species replacement (Repl); Richness difference (RichDiff) and Similarity. Dots represent pairs of sites.

correlation to the St_{Nat} ($r_s = -.53$), while the mean temperature during the warmest quarter had the strongest association to the St_{Exo} ($r_s = -.33$; Table 2).

3.5 | Landscape variables and taxonomic richness

At the landscape level, the Shannon diversity index of landscape composition showed a significant negative correlation to St_{Nat}, St_{Exo}, and St_{All} (Table 2).

At the class level, most structural metrics that are related to land use changes from extensive grasslands to other more intensive uses such as an increase in grassland and timber plantation patch numbers, an increase of distance between grassland patches, increase of timber plantation area and its aggregation (Table 2) are negatively correlated to taxonomic diversity of native and all species (St_{Nat}, St_{All}). St declines with increasing total area, aggregation and the number of patches of both timber plantations and native forests. In contrast, increasing total area, aggregation, and patch number of croplands are positively correlated to taxonomic species richness. In contrast, the majority of landscape composition metrics exhibited a significant association to the St_{Exo} (Table 2).

Finally, at the patch level (i.e., patch where the plots were localized), larger patch area, a higher proximity to grassland and a higher distance to native forest patches, is correlated with higher taxonomic species richness (Table 2). Patch area did not significantly differ between land cover classes ($X^2 = 158.39$, $p = .38$) nor ecoregions ($X^2 = 153.73$, $p = .49$), as expected by the random distribution of sampling plots.

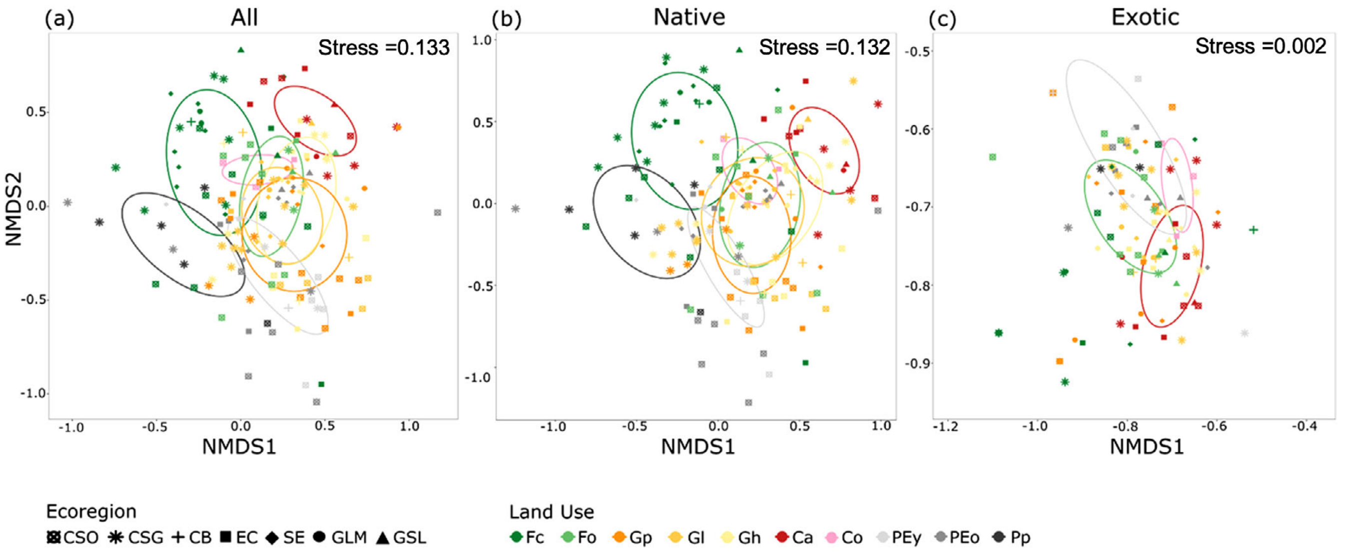

FIGURE 6 Non-parametric multidimensional scaling (NMDS) based on Jaccard dissimilarity index for all species (a), native species (b), and exotic species (c) between plots in different ecoregions (coded by legend symbols; Cuenca Sedimentaria del Oeste [CSO], Cuesta Basáltica [CB], Cuenca Sedimentaria Gondwánica [CSG], Escudo Cristalino [EC], Sierras del Este [SE], Graben de la laguna Merín [GLM], and Graben del Santa Lucía [GSL]) and at different land-uses (coded by colors; closed native forest [Fc], open native forest [Fo], primary grasslands [Gp], low intensity secondary grassland [Gl], high intensity secondary grassland [Gh], crops [Ca], Fruit orchard [Co], *Eucalyptus* plantation [<4 years; PEy], *Eucalyptus* plantations [>8 years; PEo], old pine plantations [>8 years; Pp]). Colored ellipses indicate 95% confidence intervals fitted into the spatial ordination. For permutational multivariate analysis of variance results regarding composition differences between land-uses see Supporting Information Table A11.

4 | DISCUSSION

Our study presents data on the taxonomic species richness (St) and species composition of ground flora from a systematic survey of 160 sampling plots covering the large variety of land-uses in the Campos region. We provide insights how diversity patterns of ground flora are associated at the regional scale to environmental gradients, and how these patterns are shaped at the local scale by different land cover types and landscape configurations. As Andrade et al. (2015) suggested, the impact of conversion from grasslands to other land-uses is likely to be greater than management changes to enhance productivity.

4.1 | High diversity of ground flora at regional scale

Species composition of ground flora is characterized by a high species turnover across the whole country and also within the ecoregions (Figures 3 and 4). Our data show a greater overall taxonomic richness in ecoregions of the South-Eastern compared to the Western Uruguay. We observed also a significant longitudinal increase of the native species richness, higher similarity, and nestedness from West (CSO) to East (SE). A similar pattern has been reported for woody species (Haretche et al., 2012; Zuloaga et al., 2008). However, we expected a major degree of nestedness within the ecoregions as biogeographic studies of woody species have revealed that the Uruguayan flora is located in a transition zone between the floristic realms of southern Brazil and northeastern Argentina (Grela, 2004; Haretche et al., 2012; Oliveira-Filho et al., 2015).

As also demonstrated by other grassland studies (e.g., Peng et al., 2022), our results indicate that though climate is overlooked in the identification of ecoregions, seasonality of temperature and precipitation plays a crucial role in shaping the diversity pattern of temperate grasslands. The divergence between the South-East (SE, GLM) with higher taxonomic richness and North-west (CSO, CB) with lower taxonomic richness is mainly correlated with the temperature and precipitation during the warmest and wettest quarter, and by the precipitation during the coldest and driest quarter of the year (Table 2).

4.2 | High richness of native and exotic species in changing landscapes

In general, we did not find a contrasting association of exotics or native species richness to the climatic variables.

TABLE 2 Slopes of generalized linear model for estimated species richness of ground flora (taxonomic richness values × 10 and Shannon × 10) of all species versus environmental and landscape metrics and Spearman rank correlation (r_s) between the taxonomic species richness of ground flora (including all species, native and exotic species separately) across all plots and climatic and environmental variables (A) and landscape variables (B).

	Taxonomic richness (St)					
	All species (St_{All}) Slope (GLM)	**Native species (St_{Nat})**	**Exotic species (St_{Exo})**	**All species (St_{All}) r_s (Spearman)**	**Native species (St_{Nat})**	**Exotic species (St_{Exo})**
A: Climatic and environmental variables						
Elevation (m)	−1E-4	−4E-4	−4E-4	.01	−.01	−.02
Slope (°)	.01***	.02***	−.04***	−.04	.12	−.04
Mean temperature – warmest quarter (°C; T° warm)	−.33***	−.34***	−.35***	−.49***	−.49***	−.33***
Mean temperature – coldest quarter (°C; T° cold)	−.15***	−.07***	−.39***	−.21**	−.17*	−.21**
Mean temperature – wettest quarter (°C; T° wet)	−.07***	−.08***	−.05***	−.51***	−.53***	−.29***
Mean temperature – driest quarter (°C; T° dry)	.07***	.08***	.07***	.33***	.34***	.19*
Precipitation – Warmest quarter (mm; P warm)	−.01***	−.01***	−.01***	−.38***	−.36***	−.28***
Precipitation – coldest quarter (mm; P cold)	.01***	.01***	4E-3***	.38***	.41***	.15
Precipitation – wettest quarter (mm; P wet)	−.01***	−.01***	−.02***	−.42***	−.41***	−.28***
Precipitation – driest quarter (mm; P dry)	.01***	.01***	.01***	.18*	.18*	.04
B: Landscape variables						
Landscape level						
Shannon diversity index	−.07***	−.09***	−.03**	−.19*	−.20*	−.13
Class level						
Total area of grassland (ha)	2E-3***	3E-3***	−2E-3***	.07	.07	−.08
Grassland (GL) patch number	-3E-3	−.01***	.03***	−.05	−.06	.08
Median Euclidean distance between GL (m)	−3E-3***	−5E-3***	3E-4	−.07	−.11	.08
Aggregation index of grasslands	7E-3***	.01***	−.02***	.08	.08	−.04
Total area of native forest (ha)	−4E-3***	−4E-3***	−5E-3***	−.22**	−.17*	−.26***
Native forests (NF) patch number	−0.02***	−.02***	−.03***	−.14	−.13	−.20*
Median Euclidean distance between NF (m)	3E-4***	3E-4***	4E-4***	.25**	.18*	.33***
Aggregation index of native forests	−6E-3***	−6E-3***	−6E-3***	−.12	−.08	−.12
Total area of cropland (ha)	2E-3***	9E-4***	5E-3***	.19*	.10	.48***
Crop patch number	0.05***	.04***	.09***	.24**	.19*	.35***
Median Euclidean distance between crops (m)	−1E-4***	<1E-4	−4E-4***	−.16*	−.09	−.36***

(Continues)

TABLE 2 (Continued)

	Taxonomic richness (St)					
	All species (St_{All}) Slope (GLM)	Native species (St_{Nat})	Exotic species (St_{Exo})	All species (St_{All}) r_s (Spearman)	Native species (St_{Nat})	Exotic species (St_{Exo})
Aggregation index of croplands	1E-3***	2E-4	8E-3***	.09	.02	.29***
Total area of timber plantation (ha)	−2E-3***	−2E-3***	−4E-3***	−.18*	−.13	−.30***
Timber plantations (TP) patch number	−.04***	−.04***	−.07***	−.29***	−.24**	−.42***
Median Euclidean distance between TP (m)	3E-4***	3E-4***	4E-4***	.24**	.20*	.35***
Aggregation index of timber plantations	−5E-3***	−5E-3***	−.01***	−.19*	−.14	−.26***
Patch level						
Patch area (ha)	3E-3***	3E-3***	2E-3***	.28***	.27***	.10
Distance to grassland patch (m)	−4E-3***	−4E-3***	−2E-3***	−.39***	−.37***	−.21
Distance to native forest patch (m)	4E-4***	4E-4***	5E-4***	.23**	.17*	.21**

Note: Details are given in the Supporting Information Tables A7–A9.
***$p < .001$; **$p < .01$; *$p < .05$.

Both are associated with the same climatic factors and are linearly correlated, similar to the neighboring flooding pampas (Perelman et al., 2007). Higher slope and elevation tend to reduce exotic richness in the North-West. Here, land-use change to crops occurs in the plains, whereas hilly sites remained untouched. In SE, where change of land cover also reaches higher elevations, exotic richness increases significantly with elevation, so other factors such as low land prices may be more important drivers of change. As expected, the exotic species richness is high in GSL, a small ecoregion with highest landscape diversity (Brazeiro, 2015) and the agglomeration of Montevideo (Figure 3c). Urbanization drives worldwide species richness through a high diversity of habitats per area, and also through a higher number of species introduced intentionally or non-intentionally by humans (Cilliers et al., 2008). The similarity of exotic species composition is higher in GSL compared to other ecoregions (Figure 4), suggesting the introduction of a similar set of predominately ornamentals or commercially used species. Here, exotics contribute to floristic homogenization, although this impact remains small in ground flora communities with such a high turnover. Among the exotics, 18 species are categorized as invasive (Masciadri et al., 2021).

4.3 | Land-use shape diversity at local scale

We observed that the overall species richness is higher in open ecosystems compared to those with closed canopies. The St_{Nat} of ground flora within riparian forests is significantly lower than in grasslands or park forests. Open ecosystems such as grassland types, young plantations, and the park forests share the native species pool of old grasslands. The presence of native trees in these open forests enhances overall species abundance beneath the trees supporting multi-taxon diversity (Bernardi et al., 2016; Pozo & Säumel, 2018, 2022).

Our results indicate different drivers of exotic species introduction, for example, open ecosystems with higher disturbance levels provide establishment opportunities for exotic species. Most of them have been introduced unintentionally with agriculture and livestock. The risk of further homogenization within the invasive floras across the temperate grasslands have been highlighted previously (Fonseca et al., 2013). We demonstrate that timber plantations and native riparian forests harbor almost no exotic species in the ground flora, although it has been demonstrated that afforestation with exotic trees across the region considerably can alter the diversity of grassland communities (Souza et al., 2012;

Zaloumis & Bond, 2011). A study in the northern Uruguay (Six et al., 2014) found no differences among grassland sites and *Eucalyptus* plantations stands during their early establishment. Different management strategies in afforestation sites such as the stand density, rotation, canopy structure, among others, further shape species richness (Six et al., 2014). During the planting phase of grassland afforestation, ground flora species are directly eliminated by the standard use of pesticides (Pozo & Säumel, 2018). In later stages of stand development, light is a limiting factor for the establishment of the ground flora (Abreu & Durigan, 2011), along with water competition (Nosetto et al., 2005).

Besides the disappearing ground flora at plantation sites, crops and afforestation have an indirect effect on grassland diversity by promoting land-use intensification at local scale. Reduced land availability pressures farmers to higher stocking rates, and increased grazing, mowing, or fertilization regimes on remaining grasslands in the region (Jaurena et al., 2021). This intensified management impoverishes the soil seed banks, which in turn can drive the loss of native species of the ground flora and, by favoring the establishment of other exotic species, lead to a diversity homogenization (Gossner et al., 2016).

Overgrazing is one of the main drivers of reduced species diversity (Altesor et al., 1998, 2005; Overbeck et al., 2007). The reduction of livestock diversity and the focus on few high yield breeds also reduce species diversity (Wang et al., 2019). Although several measures to increase productivity have been supported by the local government to combat the "Tsunami of soja," the impact on the depletion of ground flora diversity is similar in crops and highly modified pastures. Among the most common measures are grassland fertilization, overseeding with fast-growing species, and crop–pasture rotation systems (Jaurena et al., 2021; Modernel et al., 2016).

The cropping and grazing systems cause a significant loss of diversity due to the initial land clearance, land rotation, soil tillage, soil erosion, and the input of pesticides (Altesor et al., 2005; López-Mársico et al., 2015). While there is a significant reduction of native species richness at sites under crop cultivation, and a minor decrease in plots under different grazing intensities, the mean total richness remains constant across primary grasslands and secondary grasslands of low and high intensity. This pattern is mainly driven by the richness of exotic species in these areas. Cattle grazing enhances the local community richness by promoting exotic plants (Chaneton et al., 2002; Lezama et al., 2013). Their introduction is driven mostly by intensified used open landscapes (crops or highly modified pastures). Exotic grass invasions are dependent on the native species diversity and proximity to cultivated areas (Seabloom et al., 2013).

4.4 | Landscape configuration matters at local scale

New land use modes drive landscape diversity but not taxonomic species richness (Table 2). Landscape configuration is correlated with patterns of richness of native ground flora in Uruguay, mainly sustained by the "old growth grassland" species pool, which deserve more attention (Overbeck et al., 2007; Veldman et al., 2015). Native species richness decreases with increasing fragmentation and patchiness of grassland and distance to grassland. This suggests that a shorter distance to grassland patches in the landscape facilitates the dispersal of ground flora.

Interestingly, land-use change to crops has divergent impacts on species richness compared to afforestation. In general, while a greater extent of afforestation and a higher number and clustering of timber patches increases landscape diversity and fragmentation at the expense of native species richness, the increasing number of crop patches and the presence of crops in the neighboring land-uses increases the richness of both natives and exotic species. A higher number of native species finds a refuge in these open landscapes along the field edges or paths that are categorized as "segetal weeds" in the landscapes that have passed through the land-use change over centuries and hosted crops, although they stem from non-cultivated adjacent habitats such as heathlands, riverbanks, sand dunes (Fonderflick et al., 2020).

Distance to native forests enhances species richness (Table 2). A higher exotic richness of the ground flora is promoted by a more distant dispersion of native forest and timber plantations patches, respectively. Exotic species richness decreases if cropland patches are more distantly distributed, or if timber plantations' patches are more contiguous in the landscape. Thus, the currently observed expansion of native forests at landscape scale, driven by different factors such as changes in precipitation or livestock density (Anadón et al., 2014; Bernardi et al., 2019), reduces the taxonomic richness of ground flora (both native and exotic species). In the transition from the forest edge to the open grassland, numerous factors (e.g., elevation, soil, tree density, flooding frequency, or climate) determine the grassland community structure (Bernardi et al., 2016). In contrast to crops, native forests and timber plantations function as barriers within the landscape and disrupt important ecosystem processes such as seed dispersal and pollination, for example, by wind in an originally almost forestless landscape (Ramírez & Säumel, 2022b; Ramos et al., 2020), while the park forests as a transition zone between native riparian forests and open grasslands can support zoochory (Manning et al., 2006; Pozo & Säumel, 2022).

4.5 | Conserving species richness in priority ecosystems or at landscape scale?

Critically endangered ecosystems harbor twice the number of both native and exotic species compared to the other ecosystem categories (Figure 2e,f). The first indicates their intrinsic value to harbor species diversity, the latter their vulnerability to invasion by exotics. Thus, for this category, our richness patterns coincide with the proposed priority for conservation (Brazeiro, 2015), assuming that these ecosystems have to be protected. However, about three quarters of our plots are located in ecosystems without assigned conservation priority status, and ground flora richness in those does not differ from those found within priority ecosystems for conservation. The overall methodology for selection of the proposed priority per area remained unclear (Brazeiro, 2015), we assume that species richness is only one criterion. There are also other approaches to assess and standardize species richness from different ecosystems and sample efforts (e.g., Chao & Jost, 2012; Roswell et al., 2021). Beyond taxonomic richness, other attributes such as phylogenetic and functional diversity determine multifunctionality and add valuable guidance to restoration efforts (Le Bagousse-Pinguet et al., 2019). Independently from these limitations, our results highlight that expanding the perspective from conservation in purely natural ecosystems to measures for conservation of species richness in human-modified landscapes and replacement habitats is a powerful measure against species loss in the Anthropocene (Johnson et al., 2017).

Uruguayan grasslands, locally referred to as "campo natural," have a long history as socio-ecological systems and need a holistic reading as cultural landscapes (Säumel et al., 2023) that can be described as semi-natural when used extensively and deserve more conservation efforts at landscape scale. In general, edaphic and geomorphologic settings determine the presence of native forests and grasslands both as potential natural vegetation cover that would exist at a given location if not impacted by human activities or changing climate. Though there is criticism of the static character of this theoretical construct (Rull, 2015), it can serve as a baseline for raising public awareness on human impact and as the basis to define re-naturalization goals in the grassland biome (Hengl et al., 2018).

5 | CONCLUSIONS

In general, we observed a high species turnover across all sites independently from geographical distances between them. Seasonality of temperature and precipitation defines the regional species pool of ground flora, which should be considered in classification of ecoregions. Changing land cover and landscape contexts shape species richness at local scale, for example, native species richness decreases with disaggregation and patchiness of grassland. Open ecosystems including crops harbor a higher richness of both native and exotic ground flora compared to native forests and timber plantations both acting as environmental filters and dispersal barriers also for neighboring land uses. Our focus on the diversity of the ground flora from more conserved to highly modified ecosystems contributes to the development of strategies for both management and conservation of the temperate grassland at landscape scale beyond conservation reserves and black and white perspectives on these highly contested landscapes (Jaurena et al., 2021; Veldman et al., 2015). We are convinced that the concept of "old growth grasslands" (Veldman et al., 2015) has the potential to put the "grasslands at the core" in the Campos region, although differently from Jaurena et al. (2021).

AUTHOR CONTRIBUTIONS

Ina Säumel: Conceptualization; methodology; investigation; supervision; resources; funding acquisition; writing—review and editing. **Leonardo R. Ramírez**: Methodology; validation; formal analysis; investigation; data curation; visualization; writing—review and editing. **Julia Santolin**: Formal analysis; investigation; data curation; writing—original draft. **Karla Pintado**: Formal analysis; data curation; visualization; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials. We also prepared a Data in Brief publication related to this manuscript (see file Supporting information "Appendix").

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