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Research Paper

What land use better preserves taxonomic and functional diversity of birds in a grassland biome?

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ABSTRACT. The Pampean grassland in South America has been almost completely transformed by human activities and is one of the biomes at the highest conservation risk. Although several land uses are developed in temperate grasslands, studies comparing their impact on bird taxonomic and functional diversity are still missing. We determined what habitat type resulting from human land uses better preserves the assemblage of birds and their functional traits that occur in protected grasslands. We compared taxonomic and functional diversity between protected grasslands and cattle pastures, crop fields, tree plantations, and urban settlements. We surveyed birds and environmental variables in the 5 habitat types using point counts and selected 11 traits to estimate functional diversity. We performed principal component analysis to explore environmental differences between habitat types, ANOVA to compare taxonomic and functional diversity, nonmetric multidimensional scaling to explore relationships between habitat type characteristics and species traits, and similarity percentage analysis to find the bird functional traits that contributed the most to differentiate habitat types. Bird composition and functional diversity in cattle pastures was the most similar to that of protected areas but showed no significant differences with crop fields. In cattle pastures, crop fields, and protected areas, the most frequent species traits were related to narrow ranges and high vulnerability to extinction, whereas urban settlements included traits covering wide ranges or related to impervious areas. When compared with protected areas, land conversion into cattle pastures and some types of agricultural lands resulted in a lower loss of bird species and functional diversity than conversion into tree plantations or urbanized areas. Approximately 35% of species found in protected areas were not recorded in any of the other habitat types. Therefore, we emphasize the need to protect the native habitat. Our findings help with land use planning in the Pampas and other temperate grasslands.

Quelle utilisation des terres préserve au mieux la diversité taxonomique et fonctionnelle des oiseaux dans un biome de prairie?

RÉSUMÉ. Les prairies pampéennes d'Amérique du Sud ont été presque complètement transformées par les activités humaines et constituent l'un des biomes les plus menacés en matière de conservation. Bien que plusieurs utilisations des terres soient développées dans les prairies tempérées, des études comparant leurs impacts sur la diversité taxonomique et fonctionnelle des oiseaux manquent encore. Nous avons déterminé quel type d'habitat résultant de l'utilisation des terres par l'homme préservait au mieux l' 'ensemble des oiseaux et leurs caractéristiques fonctionnelles qui se trouvent dans les prairies protégées. Nous avons comparé la diversité taxonomique et fonctionnelle entre les prairies protégées, les pâturages, les champs cultivés, les plantations d'arbres, et les agglomérations urbaines. Nous avons étudié les oiseaux et les variables environnementales dans les 5 types d'habitat en utilisant des dénombrements ponctuels et en sélectionnant 11 caractères pour estimer la diversité fonctionnelle. Nous avons effectué une analyse en composantes principales pour explorer les différences environnementales entre les types d'habitat, une ANOVA pour comparer la diversité taxonomique et fonctionnelle, une échelle multidimensionnelle non métrique pour explorer les relations entre les caractéristiques des types d'habitat et les traits des espèces, et une analyse du pourcentage de similarité pour trouver les traits fonctionnels des oiseaux qui contribuent le plus à différencier les types d'habitat. La composition en oiseaux et la diversité fonctionnelle dans les pâturages de bovins étaient les plus similaires à celles des aires protégées mais ne présentaient pas de différences significatives avec les champs cultivés. Dans les pâturages, les champs, et les prairies protégées, les caractères les plus fréquents étaient liés à des aires de répartition étroites, et à une forte vulnérabilité à l'extinction, alors que les agglomérations urbaines comprenaient des caractères couvrant de vastes aires de répartition, ou liées à des zones imperméables. Par rapport aux zones protégées, la conversion des terres en pâturages pour bovins et certains types de terres agricoles, a entraîné une perte moins importante d'espèces d'oiseaux et de diversité fonctionnelle que la conversion en plantations d'arbres ou en zones urbanisées. Environ 35% des espèces présentes dans les prairies protégées ne sont répertoriées dans aucun autre type d'habitat. En conséquent, nous insistons sur la nécessité de protéger l'habitat naturel. Nos conclusions aident à planifier l'utilisation des terres dans la Pampa et autres prairies tempérées.

Key Words: *anthropogenic habitats; Argentina; birds; functional diversity; grasslands; taxonomic diversity*

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INTRODUCTION

Habitat conversion attributable to human activities is a major cause of global biodiversity loss (Sala et al. 2000, Foley et al. 2005), especially in temperate climates (Millennium Ecosystem Assessment 2005). Grasslands are one of the most threatened terrestrial ecosystems in the world because of both the replacement of native habitat by agricultural lands and the existence of relatively few protected areas (Hoekstra et al. 2005, Henwood 2010). In South America, the Pampean grassland is an extraordinarily productive land that has been almost completely transformed by human activities over the 20th century (León et al. 1984, Paruelo et al. 2006, Vega et al. 2009), and it is considered at high conservation risk because of agricultural development (Soriano et al. 1991, Sala et al. 2000, Viglizzo et al. 2001). The grassland transformation process in the Pampas started in the 16th century with the introduction of domestic cattle brought by Europeans (Hall et al. 1992). After the 1950s, the native vegetation was rapidly and highly degraded and fragmented because of increasing intensive agriculture (Bilenca and Miñarro 2004), and the land was converted primarily into crop fields and cattle pastures (Facelli et al. 1989, Miñarro and Bilenca 2008). Also, urban settlements were established or further developed in the region, and financial incentives promoted commercial plantations of exotic eucalypt (*Eucalyptus* spp.) and pine (*Pinus* spp.; Brizuela et al. 2003, Galindo Leal and de Gusmão Câmara 2003). Currently, the Pampean region shows an agricultural matrix and supports one of the highest rates of land use change in the world (Paruelo et al. 2006, Baldi and Paruelo 2008). Previous studies have shown that the loss and degradation of grasslands because of anthropogenic land use have negative effects on terrestrial vertebrates (Ceballos et al. 2010, Davidson et al. 2012), including birds (Goriup 1988, Stotz et al. 1996, Donald et al. 2006, Askins et al. 2007). In the Pampas, there is evidence that the populations of several resident grassland birds have declined markedly (Azpiroz et al. 2012).

An increasing number of studies have analyzed biodiversity in both native and anthropogenic habitats and landscapes, resulting from different human land uses, to better understand the changes in natural communities caused by human activities that modify large extensions of land (e.g., Renjifo 2001, Benton et al. 2003). However, the biodiversity in natural and anthropogenic habitats at the regional or interregional scales has been less explored (but see Allen and O'Connor 2000, Catterall et al. 2010, Filloy et al. 2015), and studies considering several land uses are even more infrequent and are conducted mostly in forest biomes (Petit et al. 1999, Tylianakis et al. 2006, Zurita and Bellocq 2012, Phillips et al. 2017). Furthermore, few studies have analyzed how land use changes the assemblage of species and their functional traits (Luck et al. 2013, Bregman et al. 2016).

Previous studies conducted in many ecosystems including grasslands have documented the impacts of land use on bird taxonomic richness (e.g., Chamberlain and Fuller 2000, Verhulst et al. 2004, Waltert et al. 2004, Piha et al. 2007) and community composition (e.g., Perkins et al. 2000, McMaster and Davis 2001, Bennett et al. 2004). In recent years, however, species are also perceived as a collection of individuals with phenotypic and behavioral traits that determine where they can occur, how they interact with each other, and the species contribution to ecosystem functioning (McGill et al. 2006). Thus, researchers have become increasingly interested in the diversity of species traits related to life history, i.e., clutch size and body mass, and ecosystem functioning, i.e., distance of seeds dispersed and predation rate. Functional diversity was first defined by Tilman (2001) as the value and range of species traits that influence the way ecosystems operate, and later expanded by Petchey et al. (2004) to represent the diversity of traits related to life history and functions. The study of biodiversity is not limited to species richness and has incorporated functional diversity to understand the responses of species to environmental changes (Schleuter et al. 2010, Cadotte et al. 2011), the process of assemblage formation (Petchey et al. 2007, Cornwell and Ackerly 2009), and how species diversity relates to ecosystem function (Norberg et al. 2001, Petchey et al. 2004, Suding et al. 2008). Furthermore, by measuring and understanding functional diversity, we can make better conservation and restoration decisions (Cadotte et al. 2011); for example, we can predict functional community structure to anticipate the potential loss of ecosystem services and detect disturbance impacts before species loss and extinctions occur (Cardinale et al. 2012, Mouillot et al. 2013). Environmental conditions and anthropogenic disturbances influence functional diversity (Vandewalle et al. 2010, Villéger et al. 2010, Luck et al. 2013), which is particularly relevant for birds because they play a wide variety of ecological functions and are sensitive to habitat changes (Cody 1985, Sekercioglu 2006).

The richness and composition of bird assemblages, hereafter referred to as taxonomic diversity, in a given anthropogenic habitat type depend primarily on how land use alters the natural environmental filters imposed on the regional species pool. Environmental filters are abiotic conditions and resources that exclude species with nonviable physiological or ecological limits, defined by functional traits, to enter or persist in a community (Mayfield et al. 2010, Kraft et al. 2015). Thus, it is expected that different anthropogenic habitat types, such as crop fields, tree plantations, and urban centers, alter environmental filters in different ways, resulting in different biological assemblages. For example, in grassland ecosystems, the soil temperature is lower in tree plantations but higher in cattle pastures than in the native habitat; similarly, the soil compaction is higher in cattle pastures but lower in crop fields, promoting different changes in biological communities (Hobbs et al. 2006, Mayfield et al. 2006, Ricotta et al. 2008).

The resulting assemblage in each anthropogenic habitat type will be composed of species sharing functional traits that make them tolerant to the new abiotic conditions and resource availability (Kraft et al. 2015). Habitat types that are very different from the natural habitat lead to major changes of the natural environmental filters. Therefore, our working hypothesis is that the detrimental effects of land use on native biological communities depend on the environmental similarity between the native and the human-modified habitats (Filloy et al. 2010, Diniz-Filho et al. 2011). Because birds are sensitive to vegetation structure (MacArthur and MacArthur 1961), it is expected that habitat types preserving the vegetation structure of the natural habitat, at least partially, will better conserve the taxonomic and functional diversity of the native regional pool (Gascon et al. 1999, Zurita and Bellocq 2010). In contrast, it is expected that habitat types that drastically change features of the original habitat will lead to major loss of native species richness and functional diversity (Naeem and Wright 2003, Flynn et al. 2009, Mayfield et al. 2010). To give useful conclusions about changes in biodiversity and ecosystem functions and solve conservation problems, current research encourages the simultaneous study of different facets of diversity (Naeem et al. 2012). Although several land uses are developed in temperate grasslands, studies comparing simultaneously their impact on taxonomic and functional diversity are still missing. Understanding the response of taxonomic and functional diversity to several anthropogenic habitat types in grasslands such as the Pampas will contribute to land use planning and wildlife conservation.

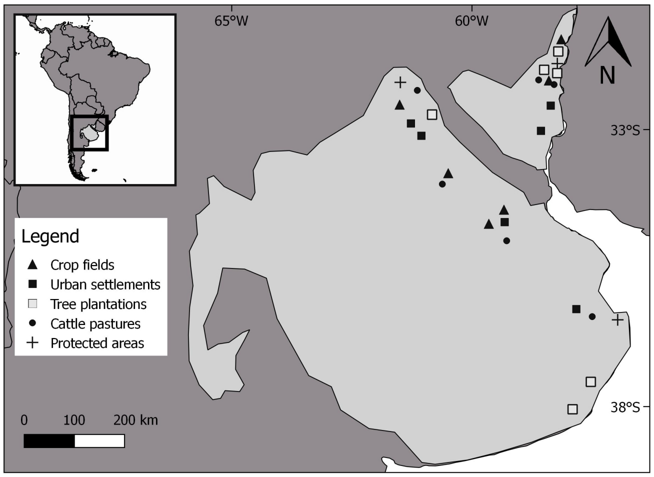
We compare for the first time in temperate grasslands, taxonomic diversity, i.e., species richness and species composition similarity, and functional diversity, i.e., bird trait diversity and trait composition similarity, between protected areas (grasslands considered as the reference habitat type) and four extended anthropogenic habitat types, i.e., crop fields, cattle pastures, tree plantations, and urban settlements, to find out what habitat type better preserves the assemblage of selected bird species and functional traits that occur in protected grasslands. Based on our working hypothesis, we posited that, environmentally, cattle pastures would be the most similar to natural grasslands, because they have a monostratified vegetation structure, i.e., the herbaceous stratum, and relatively low human intervention. Although crop fields are also monostratified, they are exposed to mechanical and chemical treatments that deeply influence vegetation structure and species composition. We also hypothesized that tree plantations and urban settlements would be the most different from natural grasslands because of the high canopy and impervious coverage, respectively. Then, we predicted that species richness and functional diversity of birds would be the highest in cattle pastures followed by crop fields, tree plantations, and urban settlements. Furthermore, we predicted that habitats showing less drastic differences with protected areas, such as cattle pastures, would have the highest taxonomic and functional similarities. We also explored relationships between different habitat type characteristics and species traits and expected that each habitat type would have a set of species with traits related to the vegetation structure; for example, we predicted that species with generalist traits, such as omnivorous diet, nesting in various sites, or cosmopolitan distribution, would be more frequent in habitat types with the highest environmental differences with the natural habitat. To test our predictions, we first compared environmental similarity, species richness, and functional diversity between protected grasslands and the different anthropogenic habitat types. Then, we compared taxonomic and functional similarities among habitat types; and finally, we explored the ordination of habitat types based on species traits.

METHODS

Study design

To analyze the relationship of taxonomic and functional diversity with habitat type, we surveyed birds and registered environmental variables in protected grasslands and 4 anthropogenic habitat types, i.e., cattle pastures, crop fields, tree plantations, and urban settlements, resulting from different land uses in the Pampean region of Argentina. We selected a total of 27 study sites (Fig. 1), 6 sites per anthropogenic habitat type and 3 in protected areas, the only natural reserves available in the region. Each study site was approximately 20 ha in size, and sites were at least 2 km apart to ensure different local bird communities. We recorded vegetation coverage and stratification to characterize the habitat at each study site and to estimate the environmental similarity between protected grasslands and each anthropogenic habitat type. We selected 11 functional traits and estimated functional diversity and functional similarity for each study site. Selected traits were as follows: diet, foraging substrate, body size, clutch size, nesting habitats, migratory status, amplitude of habitat use, primary habitat, sensitivity to human disturbance, abundance, and distribution (for more details, see Appendix 1).

Fig. 1. Location of the 27 sampling sites (different symbols for each habitat type) in the Pampean region of Argentina (light gray).



Study area and land uses

The Pampean region covers approximately 444,990 km^2 (30°48′ 5″ to 38°58′47″ from N to S and 56°42′25″ to 66°33′37″ from W to E). It has temperate climate, with mean annual temperature and precipitation ranging between 13°C and 17°C and between 800 and 1100 mm/yr, respectively. The region was originally dominated by grasses such as *Paspalum, Axonopus, Stipa, Bromus,* and *Piptochaetium* (Landi et al. 1987), and trees were absent; however, currently, small and isolated woodlots are often found in cattle shelters, windbreaks, farms, or towns.

We selected the main land uses of the region, i.e., agriculture, livestock, forestry, and urbanization, that resulted in the 4 most extended habitat types: crop fields, cattle pastures, tree plantations, and urban settlements. Crop fields represented the main crops produced in the region: soybean, wheat, and corn. Cattle pastures were areas with spontaneous vegetation, i.e, no seeded pastures, composed primarily of grasses and secondarily of herbaceous dicots, supporting a moderate grazing pressure of 0.7-0.6 animals/ha. Tree plantations were commercial eucalypt plantations (mainly *Eucalyptus grandis*), 7 to 10 years of age, used primarily for lumber and board production. Urban settlements were typical cities of the region holding 14,000-60,000 inhabitants, where the impervious area, i.e, buildings, houses, and paved roads, increased from the rural to the core urban zone (Garaffa et al. 2009). The 3 protected areas were El Palmar National Park (82 km²; 31°51′11″ S, 58°19′2″ W), Campos del Tuyú National Park (30 km²; 36°21′00″ S, 56°52′00″ W), and the Federico Wildermuth private natural reserve (13 km²; 32°00′33″ S, 61°24′30″ W).

Bird survey and environmental variables

In each of the selected study sites, we established 10 observation points systematically from a random starting point. All points were located at least 200 m away from a different habitat type. The shortest distance between observation points was 150 m because that is the minimum distance recommended to avoid double counting (Bibby et al. 1998). In urban areas, points were located every 2 blocks (200 m) in the city centers, at the street intersections, and at least 1 block apart from green areas. Birds were surveyed using the point-count technique with a fixed 50-m radius (DeGraaf et al. 1991, Ralph et al. 1996). Observation points were visited once during the breeding season (September to November), from sunrise to 4 h after sunrise on sunny days with calm wind. At each observation point, all birds seen or heard were identified and recorded during a 5-min period. To increase reliability of species identification, bird surveys were made simultaneously by 2 trained independent observers at each observation point, and bird songs were recorded with a digital recorder (Zoom H4next Handy Recorder) at all observation points during the 5-min period. Identities for recorded songs were verified by comparing them with published recordings (Xeno-canto Foundation 2018). Birds flying overhead were disregarded.

Environmental variables related to soil and vegetation coverage and structure were measured at each observation point: percentage coverage of trees, shrubs, herbaceous vegetation (including grasses, dicots, and crops), bare soil, leaf litter, and impervious areas and grass height. We considered crops as the herbaceous vegetation stratum because our objective was to conduct a general characterization of vegetation structure. At each observation point, we randomly established three 1-m² quadrats within an area of 50-m radius centered at each observation point and visually estimated coverage of shrubs, herbs, bare soil, and leaf litter following Braun-Blanquet (Mueller-Dombois and Ellenberg 1974). Values from the 3 quadrats were averaged for each observation point. To estimate tree coverage and impervious areas, we used satellite images, establishing a circle of 50-m radius centered at each observation point. For each environmental variable, values obtained from the 10 observation points were averaged for each study site.

Selection of functional traits

We selected 11 functional traits, and their categories, related to species life history, based on previous studies on bird functional diversity or responses to habitat replacement (Cofre et al. 2007, Feeley et al. 2007, Petchey et al. 2007, López-Lanús et al. 2008, Flynn et al. 2009, Vandewalle et al. 2010, Leveau 2013, Corbelli et al. 2015). We considered ecological traits, e.g., main foraging substrate, habitat amplitude, sensitivity to human disturbance, and distribution, and life-history traits, e.g., diet, body mass, and clutch size (see Table A1.1 in Appendix 1). The selected traits are relevant to understand how bird species may respond to environmental changes and how each species affects ecosystem function (Luck et al. 2013). Following the usual protocol for standardization of the trait matrix (e.g., Holmes et al. 1979, Jaksić and Medel 1990, Petchey and Gaston 2002), all traits were treated as categorical, and each category was binary: we assigned 0 or 1 depending on whether the species presented each category of the trait. Traits with multiple states, such as diet, were subdivided, and each state was treated as a single binary trait. For example, if a species feeds primarily on insects and seeds, we assigned 1 to both "insectivore" and "granivore," and 0 to the rest of the feeding categories. All trait categories were mutually exclusive, i.e., only one category of each trait was 1, except "diet," "foraging substrate," and "nesting habitat." Trait information was taken from Narosky et al. (2010), De la Peña (2013, 2016), Del Hoyo et al. (2016), BirdLife International (2018), and López-Lanús et al. (2008).

Data analyses

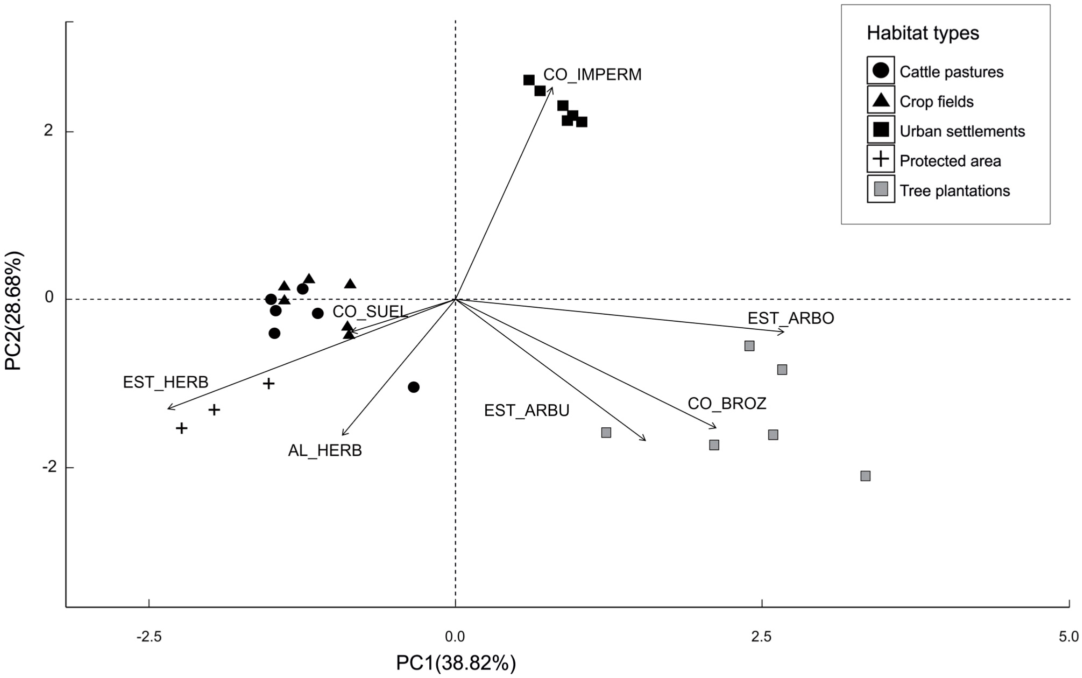
Based on survey data and functional trait values, we built 3 matrices: (1) sites by environmental variables, (2) sites by species abundance, and (3) species by traits. To build the site by environmental variables matrix, we calculated the average value, from the 10 observation points, of each environmental variable at each study site, obtaining a matrix with 27 × 7 dimensions. The site by species abundance matrix was built by adding species abundance recorded at the 10 observation points for each study site, obtaining a matrix with 27 × 92 dimensions because we recorded a total of 92 bird species. Finally, the species by traits matrix had 92 × 55 dimensions because we selected a total of 55 trait categories for each species (see Table A1.1 in Appendix 1 and Table A4.1 in Appendix 4).

Environmental variables and taxonomic and functional diversity

To explore environmental differences between habitat types, we performed a principal component analysis (PCA) on environmental variables at each sampling site (Legendre and Legendre 2012) using the "rda" function of the "vegan" package (Oksanen et al. 2016, R Core Team 2018). Because environmental variables were measured at different scales and units, we standardized them using the standard deviation to render scale-free and dimensionless variables (Legendre and Legendre 1998).

Species richness was obtained by pooling the 10 point counts and calculating the number of different bird species present in each study site (Magurran 2004). We used the "diversityresult" function in the R package "BiodiversityR" (Kindt and Coe 2005, R Core Team 2018). To estimate functional diversity (FD), we used the multidimensional functional dispersion index (FDis) developed by Laliberté and Legendre (2010). FDis is the mean distance of the multidimensional trait space of individual species to the centroid of all species, and it allows for the use of relative abundances. This index is unaffected by species richness, is not strongly influenced by outliers, can include any number and type of traits, and can be computed from any distance or dissimilarity measure (Anderson et al. 2006). To estimate FDis, we first calculated the species by species distance matrix from the species by traits original matrix using the Jaccard method ("vegdist" function in the R package "vegan") because it is suitable for categorical data and omits double zeros (Legendre and Legendre 2012, R Core Team 2018). Then, we calculated FDis for each study site with the "FD" package based on the species by species distance and the sites by species matrices (Laliberté and Legendre

Fig. 2. Biplot representing the first (PC1) and second (PC2) axes of principal component analysis, showing ordination of sites according to environmental variables measured in cattle pastures, crop fields, urban settlements, protected areas, and tree plantations. Environmental variables are percentage coverage of trees (TREE_STR), shrub (SHRUB_STR), herbs (HERB_STR), bare soil (SOIL_CO), leaf litter (LITT_CO), impervious surface (IMP_CO), and grass height (HERB_HEIGHT).



2010, R Core Team 2018). Finally, we tested for significant differences of the species richness and FDis values among habitat types using ANOVA and post hoc multiple comparisons, previously testing assumptions of normality and homogeneity of variances.

We calculated the similarity of bird assemblages between each anthropogenic habitat type and the pool of species recorded in our surveys of protected areas that represent a subset of the regional grassland species pool, based on both species composition and functional traits. For species composition, i.e., taxonomic similarity, we obtained the Jaccard index of similarity among study sites, i.e., 1 minus dissimilarity, using the "betapart" R package (Baselga and Orme 2012, R Core Team 2018). To estimate functional similarity, we first calculated a functional similarity among species matrix using the Jaccard similarity measure in the R package "vegan." Second, we used the functional similarity matrix and the unweighted pair-group clustering method using arithmetic averages to build a dendrogram that represented the trait similarity between species (Petchey and Gaston 2002). Third, we used the sites by species presence/absence matrix and the trait similarity dendrogram to calculate the functional Sorensen's index (FSor). FSor is an indicator of the function shared between two communities (Swenson et al. 2011) and is analog to the phylogenetic metric PhyloSor, which is in the R package "Picante" (Kembel et al. 2010). The obtained taxonomic and functional similarity values (Jaccard similarity and FSor) were compared among habitat types using ANOVA and post hoc multiple comparisons; assumptions of normality and homogeneity of variance were previously tested.

Bird traits and land uses

A nonmetric multidimensional scaling (NMDS), with the Horn index in the R package "vegan," was used to ordinate land uses based on the similarity of the functional trait assemblages. We first constructed the sites by traits presence/absence matrix by using the sites by species and the species by traits matrices. NMDS was developed with the "metaMDS" function in the R package "vegan" (Oksanen et al. 2016, R Core Team 2018). This function adds trait scores to the site ordination; to improve the visualization, we show an NMDS for each group of traits, i.e., feeding habits, breeding, habitat use, and vulnerability (see Table A1.1 in Appendix 1).

We used the similarity percentage (SIMPER) analysis to find the bird functional traits that contributed the most to differentiate habitat types (Clarke 1993). The SIMPER function performs pairwise comparisons of groups of sampling units and finds the average contributions of each variable to the average overall dissimilarity, ranking all variables according to the average contribution. We used the sites by traits presence/absence data matrix to perform SIMPER analysis. For each pairwise comparison of habitat types, we selected the top 10 traits that best discriminated between land uses. The total number of traits obtained was 23, because many of them were repeated in the comparisons; we show these traits in a separate NMDS.

RESULTS

In the 27 sites surveyed (3 protected areas and 6 of each anthropogenic habitat type), we recorded a total of 2773 individual birds belonging to 93 species: 333 individuals from 46 species in protected areas, 787 individuals representing 50 species in cattle pastures, 392 individuals from 33 species in crop fields, 360 individuals from 34 species in tree plantations, and 901 individuals from 24 species in urban settlements. Approximately 35% of species found in the protected areas were not recorded in any of the other habitat types (Appendix 3).

The PCA, used to explore environmental differences between habitats, ordered sites by habitat type (Fig. 2). The first and second axes explained 38.8% and 28.7% of the variation in environmental variables among sites, respectively. Urban settlements and tree plantations were located at the upper and bottom right quadrants of the biplot, respectively, whereas cattle pastures, crop fields, and protected grasslands were on the left side with the latter taking the bottom quadrant. Protected areas were characterized by high coverage of tall grasses, whereas both cattle pastures and crop fields were characterized by intermediate values of herbaceous plants and bare soil coverage. Tree plantations were associated with high coverage of trees, shrubs, and leaf litter, and urban settlements were associated with impervious areas. Cattle pastures and crop fields were the most similar to protected grasslands.

Protected areas and cattle pastures showed the highest richness values, although with nonsignificant differences with crop fields. Also, we found no difference between species richness in protected areas and tree plantations. Species richness in crop fields and tree plantations was intermediate, and urban settlements showed the lowest values, but with nonsignificant differences with tree plantations and crop fields (Table 1, Fig. 3). Results showed a gradient of decreasing functional diversity (FDis) between habitat types (Fig. 4). Protected areas showed the highest FDis values followed by tree plantations, cattle pastures, and crop fields, although with nonsignificant differences. In urban areas, functional diversity was significantly lower than that in the other habitat types (Table 2, Fig. 4).

Table 1. Multiple comparisons of means (Tukey contrasts) of richness between habitat types. Habitat types are urban settlements (US), cattle pastures (CP), crop fields (CF), tree plantations (TP), and protected areas (PA). $P < 0.05$; asterisk (*) indicates significant differences.

Habitat Types Comparison	*t* Value	*P*
US versus CP	−4.483	0.0016*
US versus CF	−1.546	0.5426
US versus PA	−3.661	0.0106*
US versus TP	−1.159	0.7716
CP versus CF	−2.937	0.0526
CP versus PA	0.000	1.0000
CP versus TP	−3.324	0.0227*
CF versus PA	−2.398	0.1516
CF versus TP	−0.386	0.9949
TP versus PA	−2.714	0.0831

Table 2. Multiple comparisons of means (Tukey contrasts) of functional diversity (FDis) between habitat types. Habitat types are urban settlements (US), cattle pastures (CP), crop fields (CF), tree plantations (TP), and protected areas (PA). $P < 0.05$; asterisk (*) indicates significant differences.

Habitat Types Comparison	*t* Value	*P*
US versus CP	−4.467	0.0015*
US versus CF	−3.395	0.0194*
US versus PA	4.817	<0.001*
US versus TP	5.327	<0.001*
CP versus CF	−1.072	0.8171
CP versus PA	1.17	0.766
CP versus TP	0.86	0.9072
CF versus PA	2.045	0.2762
CF versus TP	1.932	0.3281
TP versus PA	−0.467	0.9894

Fig. 3. Averages of species richness values in different habitat types of the Pampean grasslands. Vertical lines show standard deviations. Different letters indicate significant differences ($P < 0.05$) between pairs of habitat types: results of multiple comparisons of means (Tukey contrasts) of richness between habitat types.

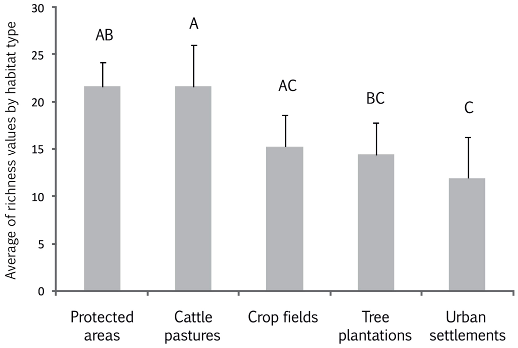
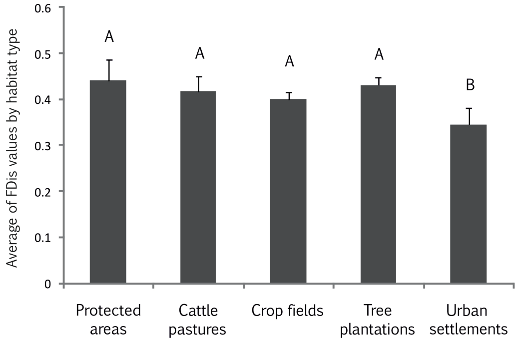


Fig. 4. Averages of functional diversity values (FDis index) in different habitat types of the Pampean grasslands. Vertical lines show standard deviations. Different letters indicate significant differences ($P < 0.05$) between pairs of habitat types: results of multiple comparisons of means (Tukey contrasts) of FDis between habitat types.



Species composition and functional similarities of birds with respect to protected areas differed between anthropogenic habitat types ($F_{3,20} = 6.152$, $P < 0.005$ for species composition similarity and $F_{3,20} = 10.28$, $P < 0.0003$ for functional similarity; Tables 3 and 4). Cattle pastures tended to be more similar to protected areas than crop fields, although the difference was nonsignificant, followed by tree plantations and urban settlements. Differences in 1 minus Jaccard and FSor values between tree plantations and crop fields were not significant. Species composition similarity between urban settlements and protected areas was the lowest, although not significantly different from crop fields and tree plantations. Functional similarity in urban settlements was the lowest and significantly differed from cattle pastures and crop fields, but it was not significantly different from tree plantations (Figs. 5 and 6).

Table 3. Results of multiple comparisons of means (Tukey contrasts) of species composition similarity (1 − Jaccard) between habitat types and protected areas. Acronyms are as given in Table 1. $P < 0.05$ indicates significant differences.

Comparisons	*t* Value	*P*
CP-PA versus CF-PA	−1.590	0.4061
CP-PA versus US-PA	−3.979	0.0039*
CP-PA versus TP-PA	−3.124	0.0253*
CF-PA versus US-PA	2.389	0.1117
CF-PA versus TP-PA	1.534	0.4371
TP-PA versus US-PA	−0.855	0.8276

Table 4. Results of multiple comparisons of means (Tukey contrasts) of functional similarity (FSor) between habitat types and protected areas. Acronyms are as given in Table 1. $P < 0.05$ indicates significant differences.

Comparisons	*t* Value	*P*
CP-PA versus CF-PA	1.892	0.2626
CP-PA versus US-PA	5.444	<0.001*
CP-PA versus TP-PA	2.888	0.04164*
CF-PA versus US-PA	3.552	0.0099*
CF-PA versus TP-PA	0.995	0.75362
TP-PA versus US-PA	−2.556	0.08118

The NMDS analysis ordered sites by habitat type, separating tree plantations and urban settlements from the other habitat types, indicating that similarity in species trait assemblages in tree plantations and urban settlements was different from that of crop fields, cattle pastures, and protected areas. Each habitat type was characterized by the occurrence of traits related to habitat characteristics: for example, generalist traits in urban areas, foraging and nesting in trees and shrubs in tree plantations, and nesting on grasses or ground in protected areas, cattle pastures, and crop fields (Figs. A2.1 to A2.4 in Appendix 2). Bird species with a specific diet, e.g., frugivore, carnivore, and invertebrate diet, were more frequent in protected areas, cattle pastures, and some crop fields. In addition, protected areas, cattle pastures, and some crop fields were characterized by the occurrence of species that forage in the air or water, show some migratory status, and nest in trees and shrubs (Figs. A2.1, A2.2, and A2.4 in Appendix 2), and species with wetlands as primary habitats (Fig. A2.3 in Appendix 2).

Fig. 5. Averages of species composition similarity values (1 − Jaccard) between each habitat type and protected areas of the Pampean grasslands. Vertical lines show standard deviations. Different letters indicate significant differences ($P < 0.05$) between pairs of habitat types: results of multiple comparisons of means (Tukey contrasts) of 1 minus Jaccard between habitat types.

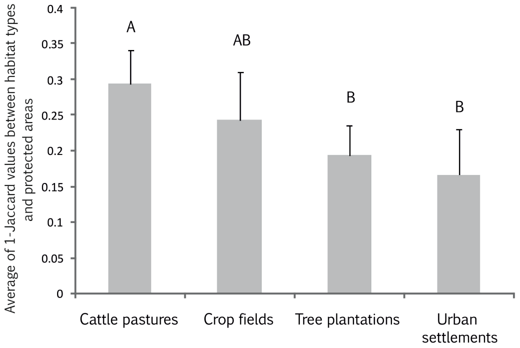
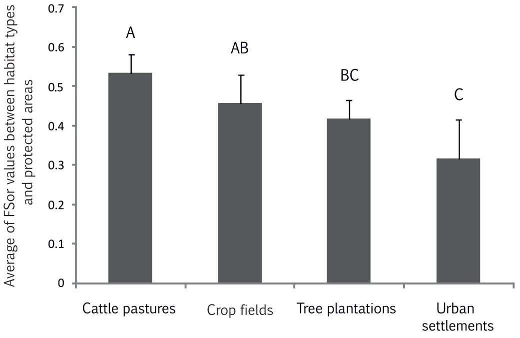
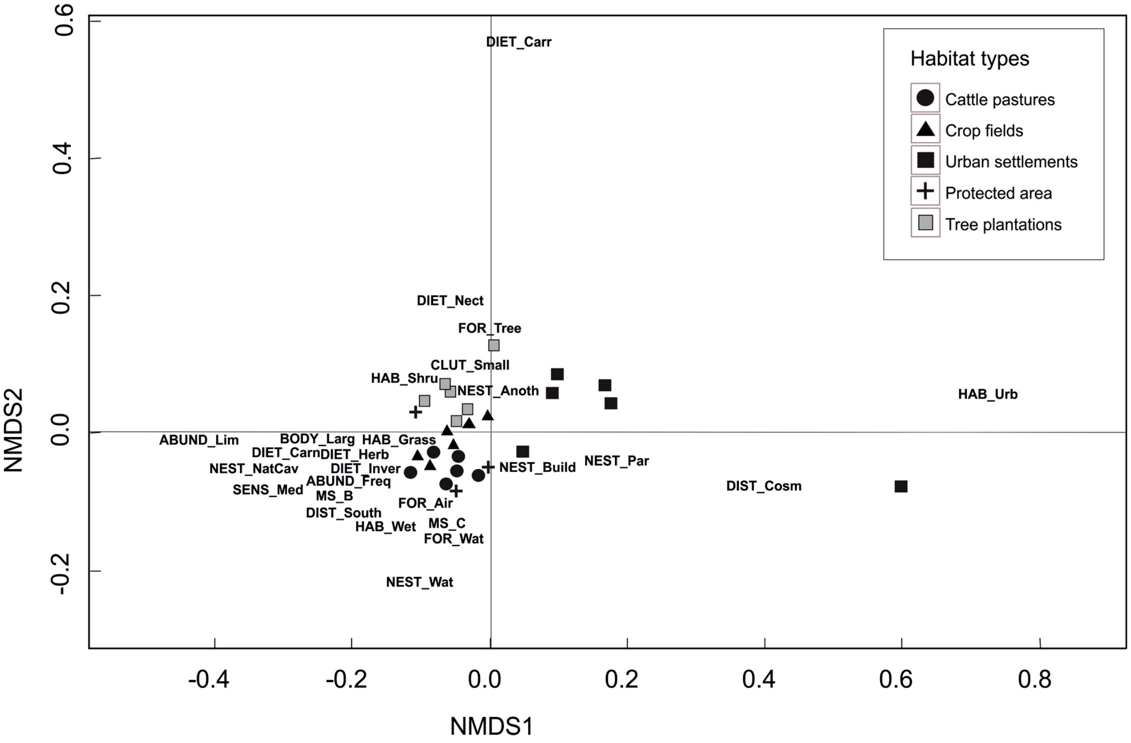


Fig. 6. Averages of functional similarity values (FSor) between each habitat type and protected areas of the Pampean grasslands. Vertical lines show standard deviations. Different letters indicate significant differences ($P < 0.05$) between pairs of habitat types: results of multiple comparisons of means (Tukey contrasts) of FSor between habitat types.



Results of the SIMPER analysis highlighted the primary traits contributing the most to differentiate land uses (Fig. 7). In urban settlements, common traits included those covering wide ranges or related to impervious areas, such as cosmopolitan distribution, urban areas as primary habitat, parasitic breeding such as laying eggs in the active nests of other species, and nesting in inactive nests of other species. In contrast, in cattle pastures, crop fields, and protected areas, the most frequent species traits were related to narrow ranges and high vulnerability to extinction, such as medium sensitivity, i.e., species is not in short-term danger but is vulnerable if habitat destruction continues; migratory status;

Fig. 7. Nonmetric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits. The function adds traits scores to the site ordination. Only 23 traits resulting from SIMPER (similarity percentage) are shown. Acronyms of categorical traits are given in Appendix 1.



foraging in the air and water; nesting in vegetation on water; herbivorous and carnivorous diet; and large body size.

DISCUSSION

We are the first to simultaneously compare bird taxonomic and functional diversities between the natural habitat and the different types of anthropogenic habitats in a grassland biome, providing new insights into grassland bird communities in general and into the Pampean region of South America in particular. The observed species richness, species composition similarity, functional trait diversity, and functional similarity of bird assemblages in cattle pastures were the closest to those observed in protected grasslands, followed by crop fields, tree plantations, and urban settlements. Although previous studies have emphasized the relevance of cattle pastures, as opposed to other anthropogenic habitat types, for the conservation of grassland bird species in North America (Askins et al. 2007), South America (Azpiroz et al. 2012), and the Pampean region (Codesido and Bilenca 2011), our work extends the relevance to the conservation of bird functional traits. Therefore, we emphasize the need to protect the native habitat, because none of the studied anthropogenic habitat types is able to support all the diversity of native grasslands.

Our results show that livestock is better than other land uses to preserve more grassland birds and their traits. Low to moderate rates of cattle grazing (0.4 to 0.7 animals/ha) may promote vegetation growth, favoring the diversity and abundance of invertebrates and seeds, thus providing food supply for invertebrate- and seed-eating birds (Gibson et al. 1992, Perkins et al. 2000, Fontana et al. 2016). Also, moderate grazing rates may provide grass coverage and height similar to those of natural grasslands, as found in the rangelands of North America (Peterjohn 2003). Furthermore, pastures may offer horizontal and vertical structural diversity for birds nesting on the ground, such as the Burrowing Owl (*Athene cunicularia*; Pairo et al. 2017), or on grasses, such as the Great Pampa-Finch (*Embernagra platensis*), the Brown-and-yellow Marshbird (*Pseudoleistes virescens*), the Hudson's Canastero (*Asthenes hudsoni*), and the Greater Rhea (*Rhea americana*; Codesido et al. 2013). Also, grazing management could be used in the restoration of seminatural grasslands (WallisDeVries et al. 1998). Grazing has been considered the most practical option to reverse the decline of northern European grasslands (Pykälä 2003), and cattle have been considered as ecosystem engineers for the conservation of semiarid rangelands of the western North American Great Plains (Derner et al. 2009). Based on our results and other studies, it is recommended in land use planning for bird conservation to prioritize cattle grazing over other land uses in the Pampean grasslands and, presumably, in other grasslands of the world as well.

Although many studies have documented a decline in the abundance and number of grassland bird species because of agriculture (Peterjohn and Sauer 1999, Donald et al. 2001, Canavelli et al. 2004, Azpiroz et al. 2012), we found that bird communities in crop fields showed relatively high taxonomic and functional similarities relative to protected grasslands. Our work was designed at the scale of land use (agriculture), pooling the most abundant crop fields of the study area. For example, soybeans, corn, and wheat were included in agricultural sites to represent agricultural use rather than restricting the findings to only one type of crop. However, agricultural practices and the structure of crop fields may have different effects on birds. Some fields with high and dense crop cover may serve as refuges from predators and extreme weather conditions and provide abundant food resources (Wilson et al. 2005); for example, large flocks of the White-browed Meadowlark (*Sturnella superciliaris*), a grassland species, usually forage in croplands (Belton 1994). During our spring surveys, crops were primarily soybean, a summer crop with low height during our surveys, and mature wheat, a winter crop harvested in late spring to early summer, and about 1 m in height during our surveys, which may offer a tall herbaceous vegetation stratum. Therefore, mature wheat fields could have contributed to the relatively high environmental similarity between crop fields and protected areas. Weyland et al. (2014) also found a large group of grassland birds, e.g., the Spotted Nothura (*Nothura maculosa*), the White-browed Meadowlark, and so on, positively associated with wheat coverage; it is possible that wheat crop fields offer some environmental conditions, such as tall vegetation and low soil compaction, that may be more consistent than cattle pastures with the ecological niches of grassland birds. Also, habitat structure showed higher seasonality in agricultural lands than in cattle grazing sites. In agricultural lands, there are periods over the year, after harvesting and before seeding, with low vegetation coverage. In the Pampean region, the traditional rotation management between crops and cattle pastures has been replaced mainly by the rotation between different crops, i.e., soybean, wheat, and maize, and, further, soybean monoculture system. Agricultural intensification and expansion to soybean monocultures were induced by the use of the direct sawing technique, transgenic seeds, and agrochemicals such as insecticides, herbicides, fungicides, and fertilizers (Baldi and Paruelo 2008). Previous studies revealed that intense agriculture was more detrimental to the avian community than pastoral farming in the Pampean region (Verhulst et al. 2004, Filloy and Bellocq 2007).

Tree plantations differed from natural grasslands in vegetation structure, species composition, and functional diversity. Many studies have documented that tree plantations developed in natural grasslands alter water and soil (Jobbágy and Jackson 2004, Silveira and Alonso 2009) and affect biodiversity (Brockerhoff et al. 2008, Buscardo et al. 2008). Nonnative tree plantations have replaced cattle raising in some grasslands of southeastern South America (Overbeck et al. 2007, Baldi and Paruelo 2008), resulting in negative effects on several threatened grassland birds (Di Giacomo and Krapovickas 2001, Azpiroz et al. 2012, Fontana et al. 2016). The replacement of grasslands with tree plantations may result in the local loss of some species traits related to grasslands as primary habitat and to some ecosystem functions. Consequently, our results provide evidence against the promotion of forestry in the Pampean grasslands.

Urbanization imposes a powerful environmental filter to native grasslands, changing deeply the original environmental conditions and disrupting the natural vegetation dynamics (Williams et al. 2005). Our results showed that urban settlements were the most different habitat type relative to natural habitats regarding vegetation structure, species composition, and functional diversity. Furthermore, this habitat type held the lowest species richness and functional diversity among other land uses in the Pampean grasslands. Low species richness and functional diversity in urban areas have been previously documented for birds (Ortega-Álvarez and MacGregor-Fors 2009, Pauw and Louw 2012, Leveau et al. 2015). High levels of urbanization reduce bird species richness (Chace and Walsh 2006, Faeth et al. 2011) and functional diversity because environmental filters allow only the persistence of species with traits to tolerate urban constraints (Petchey and Gaston 2007, Croci et al. 2008).

Understanding the relationship between species traits and environmental characteristics is essential to predict community responses to land use and allows us to make suitable conservation decisions (Hausner et al. 2003). Our site ordination based on the similarity of the functional trait assemblages was consistent with habitat type characteristics; in general, each habitat type was characterized by a set of species with traits related to vegetation structure. However, we also found some traits related to the heterogeneity of habitat types, for example, “nesting in trees” in protected areas. Grasslands in protected areas may have a few isolated trees, shrubs, or small woodlots of *Celtis tala* (Cabrera 1976). Furthermore, in cattle pastures we found bird assemblages with some traits related to aquatic habits, such as foraging in water, nesting in vegetation on water, and having wetlands as primary habitat, in sites located in the southern Pampean region, i.e., the Flooding Pampa, characterized by very slight slopes and poor water drainage resulting in water accumulation during periods of abundant rainfall (Miñarro and Bilenca 2008). Our results indicate that keeping isolated woodlots in cattle pastures and farmland, which offer opportunities for birds holding tree-related traits, and temporary ponds in cattle pastures, which could support greater abundance of wetland birds that forage in these zones as well as in grasslands (Canevari et al. 1991, Codesido et al. 2012), will enhance the conservation of bird functional diversity.

As expected, in urban settlements we found bird assemblages composed of species characterized by generalist traits because these species can tolerate urban constraints. In city parks of France, Lizée et al. (2011) also found bird assemblages with omnivorous species that nest on buildings and have high egg production. Croci et al. (2008) found that the presence of sedentary and widely distributed bird species was related to urban areas in Switzerland and France, and Silva et al. (2016) found higher abundance of habitat generalist birds in urban than in periurban areas of southern Chile. The environmental filters imposed by urbanization prevent the establishment of many native species, i.e., urban avoiders, holding specific traits such as long-term migrants, diet specialists, e.g., exclusively feeding on arthropods, or traits that indicate high sensitivity to human disturbances, e.g., nesting on the ground (Seress and Liker 2015).

Many studies have proposed that the presence of certain traits based on foraging substrate, diet, and nest-site preferences in the local assemblage may be used as indicators of habitat alteration (Hausner et al. 2003, Schulze et al. 2004, Vandewalle et al. 2010). For land uses in the Pampas, in addition to the presence of species with traits related to vegetation structure, other traits that contributed the most to differentiate habitat types, highlighted by the SIMPER analysis, may be good indicators of environmental change. Our results showed that land uses that preserve bird functional diversity of natural grasslands, at least partially, will support species holding traits related to narrow ranges and high or medium vulnerability to extinction rather than traits covering wide amplitudes or indicating low vulnerability. Only 1% of the original grassland is conserved in public protected areas in the region, and many threatened grassland birds are found on private lands (Azpiroz et al. 2012). Grassland conservation helps not only to preserve functional traits but also to protect species that are at conservation risk, because the native habitat has many species that were not found in the studied anthropogenic habitat types.

CONCLUSION

We used multiple facets of diversity to understand community responses to environmental changes caused by human activities developing in one of the terrestrial biomes at the greatest conservation risk. We found that cattle pastures and urban settlements had the lowest and highest negative effect, respectively, on the species community and functional trait assemblage of native birds in the Pampean grasslands. We predict that the land use ranking of increasing negative impact of human activities in the Pampean grasslands of Argentina, i.e., cattle pastures, crop fields, tree plantations, and urban settlements, will remain true for other temperate grasslands. We hypothesize, however, that such ranking will change when the same human activities develop in forest biomes, because environmental similarity between anthropogenic habitat types and the natural habitat will also change (Filloy et al. 2010, Corbelli et al. 2015, Santoandré 2017).

Responses to this article can be read online at:
http://www.ace-eco.org/issues/responses.php/1293

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Appendix 1

Table A1.1 Trait data used in this study.

MAIN GROUP/TRAIT TYPE		ABBREVIATION	DESCRIPTION	REFERENCES
FEEDING/DIET	Frugivore	DIET_Frug	This trait indicates position in food web and it provides information about ecosystem services such as population regulation of invertebrate and vertebrate species, pollination and seed dispersal.	Sekercioglu 2006 Cofre et al. 2007 Petchey et al. 2007 Flynn et al. 2009 Vandewalle et al. 2010 Luck et al. 2012, Leveau 2013 Salgado-Negret and Paz 2015 Corbelli et al. 2015
	Granivore	DIET_Gran		
	Carnivore	DIET_Carn		
	Carrion	DIET_Carr		
	Herbivore	DIET_Herb		
	Insectivore	DIET_Insec		
	Another invertebrates	DIET_Inver		
	Omnivore	DIET_Omn		
	Nectarivore	DIET_Nect		
FEEDING/FORAGING SUBSTRATE	Ground	FOR_Grou	This trait indicates where birds conduct their activities. Species with particular foraging behaviour might be impacted by environmental change.	Martin & Possingham 2005 Petchey et al. 2007 Flynn et al. 2009 Luck et al. 2012 Leveau 2013 Salgado-Negret and Paz 2015 Corbelli et al. 2015
	Shrub	FOR_Shru		
	Trees	FOR_Tree		
	Air	FOR_Air		
	Water	FOR_Wat		
	Forage throughout	FOR_Thro		
	Ground	FOR_Grou		
	Shrub	FOR_Shru		
	Trees	FOR_Tree		
FEEDING/BODY SIZE	Less 100 gr	BODY_Small	Body size is strongly related to a range of other traits in birds including metabolic rate, foraging behaviour, longevity and home-range size.	Cofre et al. 2007 Feeley et al. 2007 Petchey et al. 2007 Flynn et al. 2009 Vandewalle et al. 2010 Luck et al. 2012 Salgado Negret and Paz 2015 Corbelli et al. 2015
	100-500 gr	BODY_Med		
	More 500 gr	BODY_Larg		

Appendix 1

Table A1.1 continued.

BREEDING/CLUTCH SIZE	One egg	CLUT_Small	Species with low reproductive rates (e.g. small clutch size, infrequent breeding and low annual productivity) and low survival rates are less resilient to environmental change (i.e. have a reduced capacity to recover from disturbances) than those with high rates.	Cofre et al. 2007 Petchey et al. 2007 Luck et al 2012 Corbelli et al. 2015
	Two to three eggs	CLUT_Med		
	More than three eggs	CLUT_Larg		
BREEDING/NESTING HABITATS	Ground	NEST_Grou	This trait indicates sensitivity to different habitat changes that affect the nesting habitats' availability.	Sekercioglu 2006 Vandewalle et al.2010 Luck et al 2012 Leveau 2013
	Water	NEST_Wat		
	Grass	NEST_Gras		
	Shrub	NEST_Shru		
	Trees	NEST_Tree		
	Natural cavities	NEST_NatCav		
	Nest of another species	NEST_Anoth		
	Parasitic	NEST_Par		
	Various	NEST_Var		
	Buildings or human constructions	NEST_Build		
BREEDING/MIGRATORY STATUS	Resident	MS_R	This trait might influence large-scale cycling of nutrients and the delivery of services across broad regions and determines	Cofre et al. 2007 López-Lanús et al. 2008 Luck et al. 2012 Leveau 2013 Corbelli et al.
	Migratory A	MS_A		

Appendix 1

Table A1.1 continued.

	Migratory B	MS_B	seasonal change in community composition.	2015
	Migratory C	MS_C		
HABITAT/NUMBER OF HABITATS USED	One to three	NHU_Small	Habitat generalists are more resilient to environmental change as they can choose from a variety of habitats, than those which are specialist.	López-Lanús et al. 2008 Luck et al. 2012 Corbelli et al. 2015
	More than three	NHU_Big		
HABITAT/PRIMARY HABITAT	Forest	HAB_Forest	This trait is closely related to the principal habitat where the different species can be found. This includes human modified habitats.	Stotz et al. 1996 Cofre et al. 2007 Feeley et al. 2007 López-Lanús et al. 2008 Vandewalle et al. 2010 Corbelli et al. 2015
	Shrub	HAB_Shru		
	Rural areas and towns	HAB_Rur		
	Urban areas	HAB_Urb		
	Wetlands	HAB_Wet		
	Grassland	HAB_Grass		
	No primary habitat	HAB_Many		
VULNERABILITY/ SENSITIVITY TO HUMAN DISTURBANCE	Favorable	SENS_Fav	This trait is related to the way in which the different species react to the anthropic processes of modification, replacement and pollution of environments. Some might benefit from human disturbance or be affected by it in a low, medium or high intensity.	Stotz et al 1996 López-Lanús et al. 2008 Cobelli et al. 2015
	Low	SENS_Low		
	Medium	SENS_Med		
	High	SENS_High		
VULNERABILITY/ ABUNDANCE	Common	ABUND_Com	Population abundance is	Stotz et al. 1996

Appendix 1

Table A1.1 continued.

	Frequent	ABUND_Freq	strongly related to the species' risk of extinction.	Cofre et al. 2007 Feeley et al. 2007 López-Lanús et al. 2008
	Limited	ABUND_Lim		
VULNERABILITY/ DISTRIBUTION	Cosmopolitan	DIST_Cosm	Species with very restricted distributions have higher risk of extinction than those with broader ones.	Gillespie 2002 Cofre et al. 2007 Feeley et al. 2007 López-Lanús et al. 2008
	Neotropical	DIST_Neo		
	South America	DIST_SouAme		
	South of South America	DIST_South		

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Table A1.1 continued.

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Appendix 2

Figures of non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits.

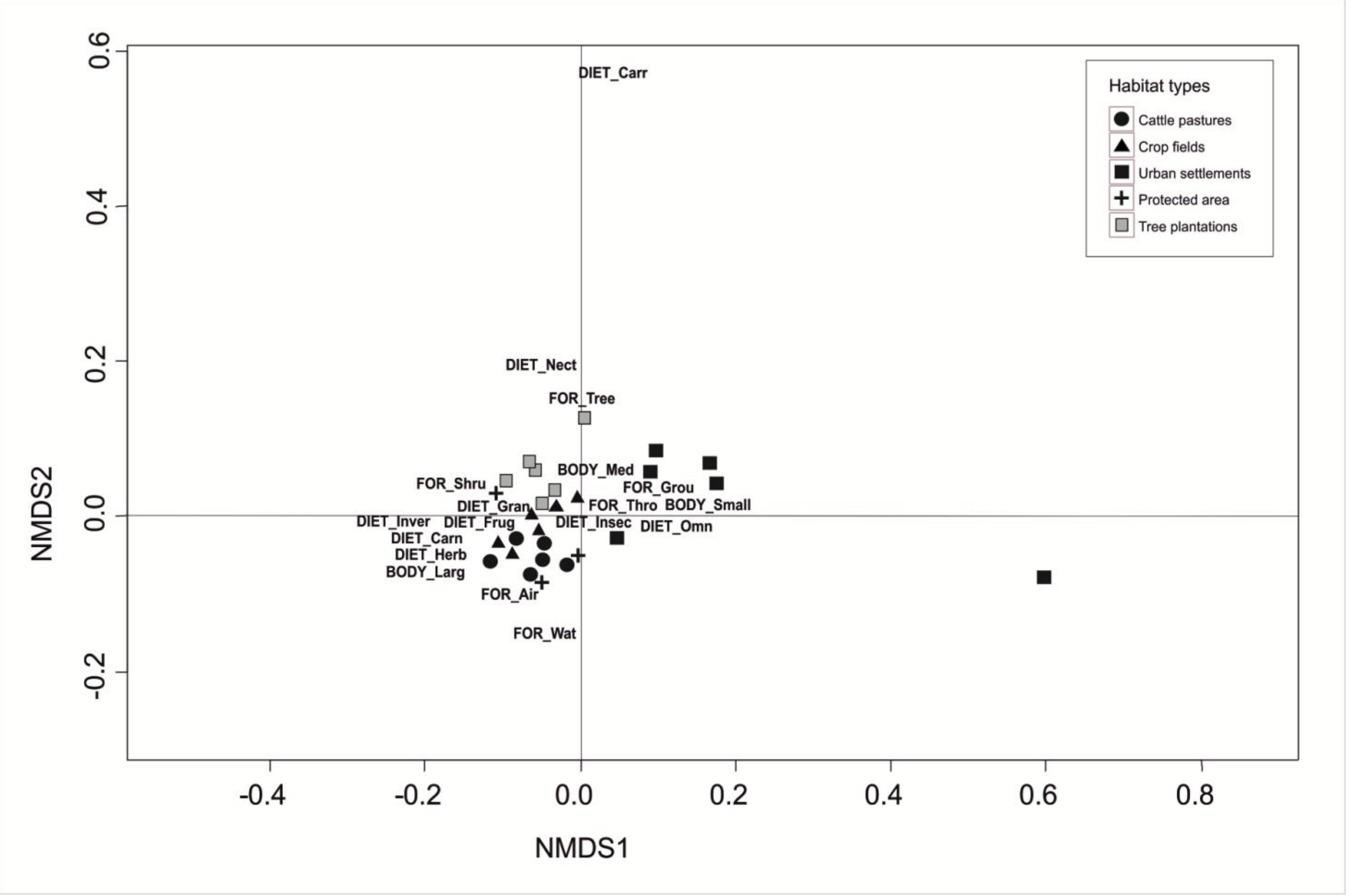

Fig. A2.1. Non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits. The function adds traits scores to the site ordination. Traits groups are shown in four separated figures. This figure corresponds to feeding habits. Acronyms of categorical traits are in Appendix 1.

Appendix 2

Figures of non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits.

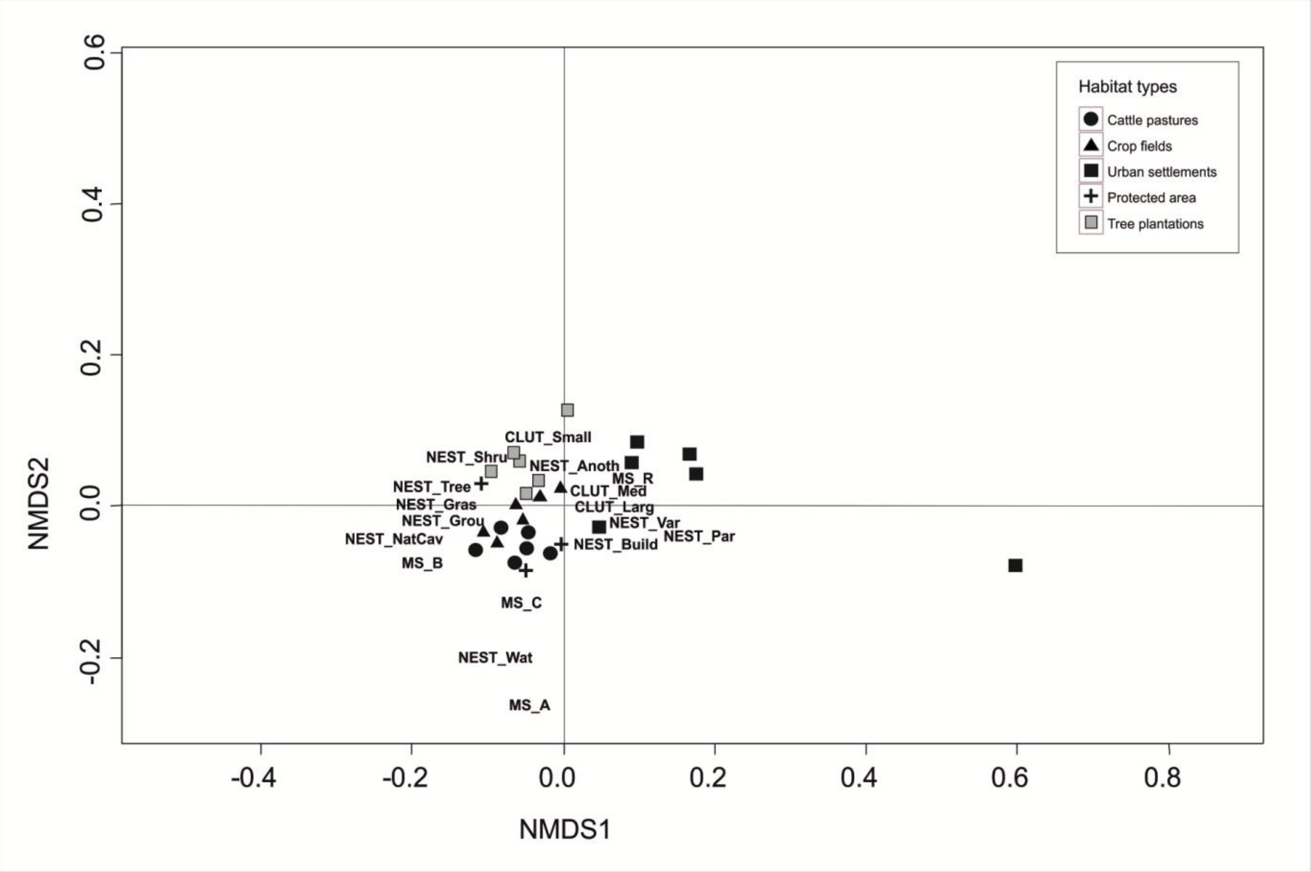

Fig. A2.2. Non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits. The function adds traits scores to the site ordination. Traits groups are shown in four separated figures. This figure corresponds to breeding habits. Acronyms of categorical traits are in Appendix 1.

Appendix 2

Figures of non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits.

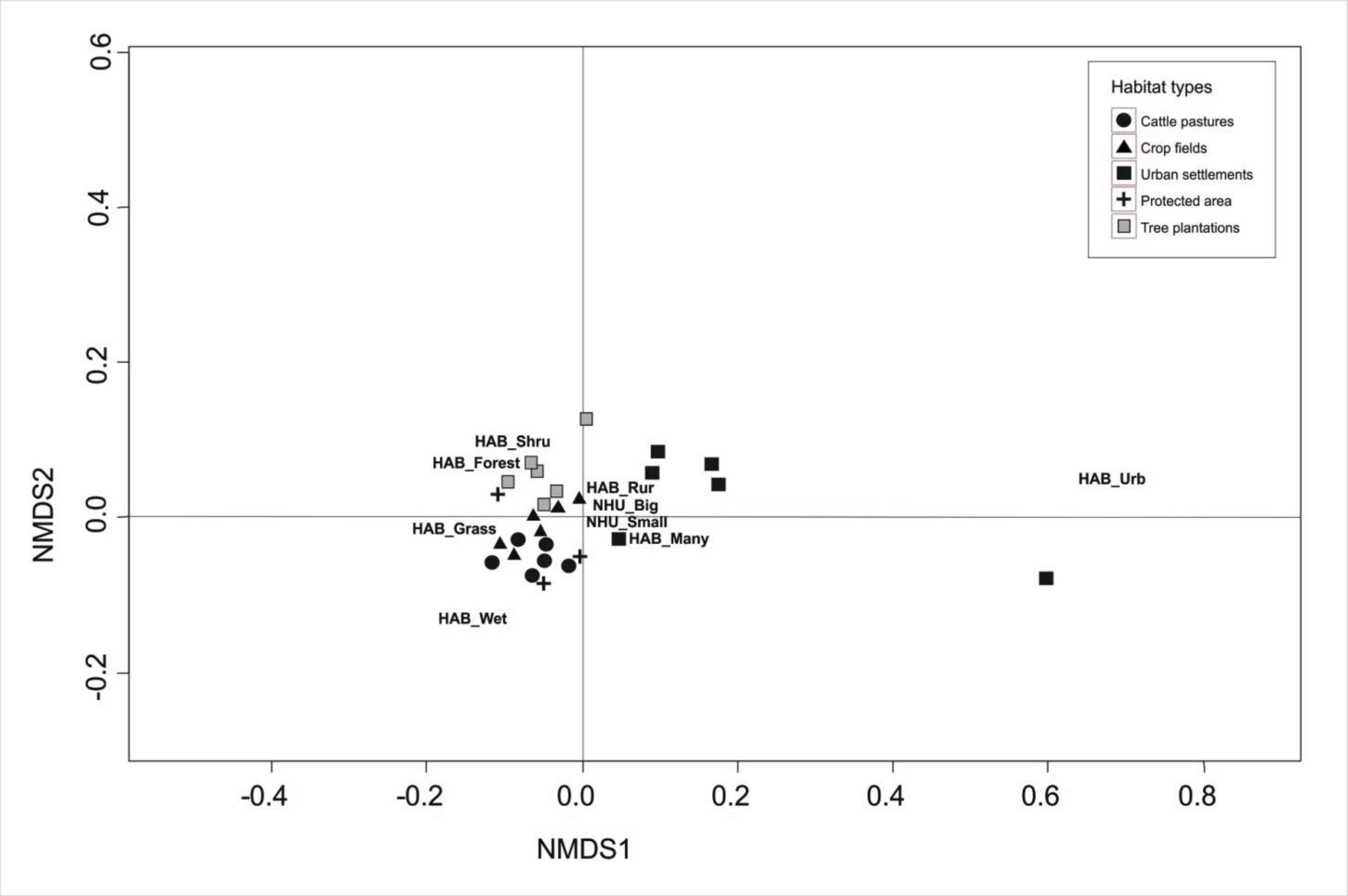

Fig. A2.3. Non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits. The function adds traits scores to the site ordination. Traits groups are shown in four separated figures. This figure corresponds to habitat use. Acronyms of categorical traits are in Appendix 1.

Appendix 2

Figures of non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits.

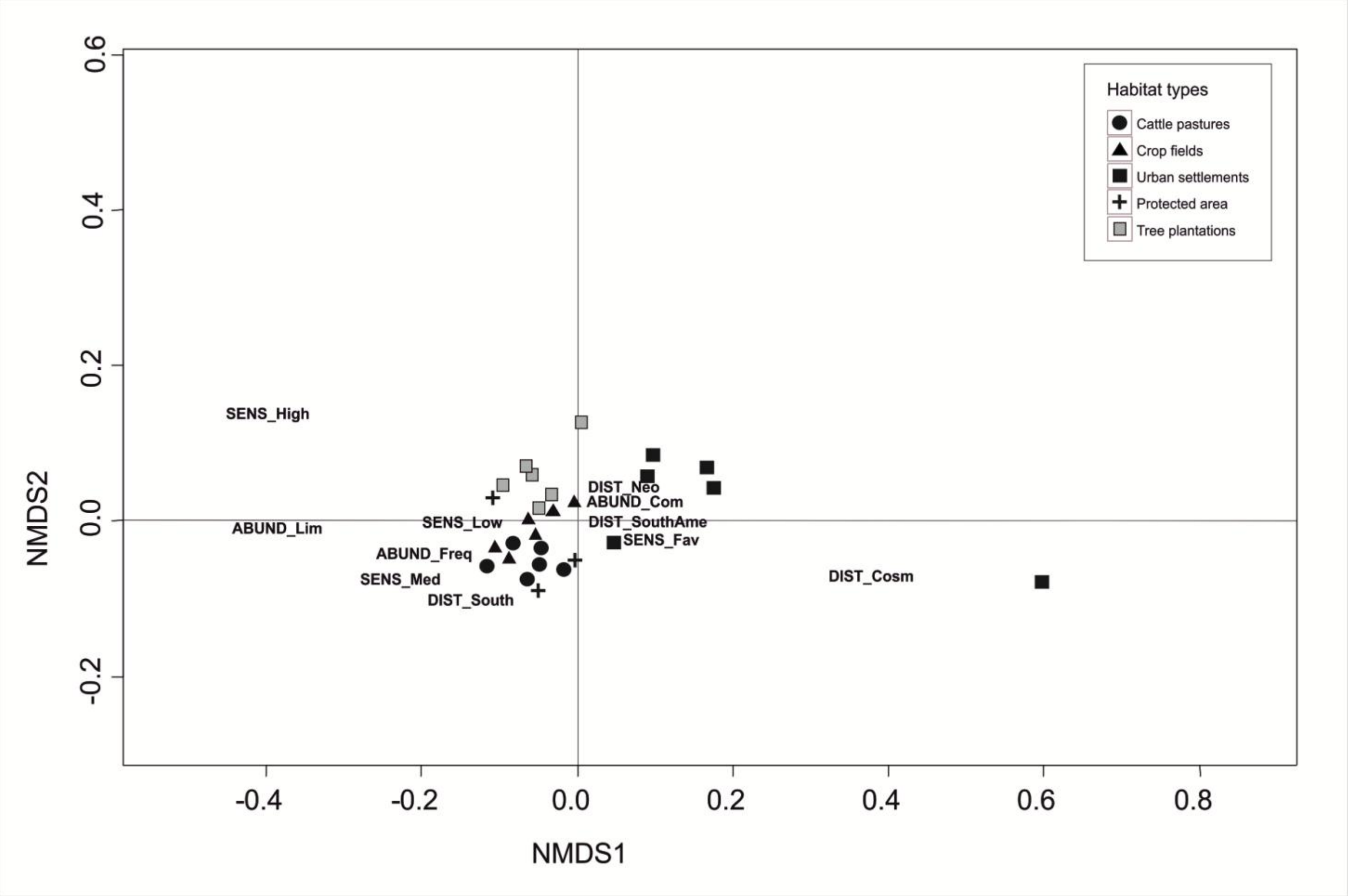

Fig. A2.4. Non-metric multidimensional scaling (NMDS) analysis of habitat type sites and protected areas based on the similarity of traits. The function adds traits scores to the site ordination. Traits groups are shown in four separated figures. This figure corresponds to vulnerability. Acronyms of categorical traits are in Appendix 1.

Appendix 3. Table of number of study sites in each habitat type where the species was detected

Please click here to download file 'appendix3.xlsx'.

Appendix 4. Table of species and traits
