



Avian community response to a novel environment: Commercial forestry in the Campos grasslands of South America

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ARTICLE INFO

Keywords:

Afforestation
Bird assemblages
Ecological novelty
Exotic tree plantations
Forest management
Uruguay

ABSTRACT

Establishing commercial tree plantations in native grassland ecosystems introduces a different structural and functional vegetation cover type, with expected implications for biodiversity. To better understand biodiversity responses to afforestation, we conducted a resource-use study with birds as a focal group, during the 2013–2014 breeding season in the Northern Campos grasslands of Uruguay. We sampled birds in native environments and plantations of loblolly pine (*Pinus taeda*) and flooded gum (*Eucalyptus grandis*) at different rotation stages. We recorded 103 species during 1,573 visits (10-min, 50-meter radius point counts) to 570 stratified sampling units. Native grasslands and forests exhibited greater diversity and had greater variability in species composition than structurally homogeneous plantations. Avian communities in plantations had distinct species combinations and relative abundances not found in native conditions. Avian communities in older plantations were more similar to native forests while those of newly-planted stands were more like grasslands. However, plantations were dominated by habitat generalists and some forest-dependent species, with negligible use by grassland specialist birds. Our results suggest the best conservation opportunities for grassland-dependent birds in afforested systems of the Campos of Uruguay may depend on diverse landscape-level measures rather than stand-level management practices. Albeit our research constituted a comprehensive assessment of bird taxonomic alpha and beta diversity, research on complementary diversity facets and multi-scale resource selection and demographic studies are needed to better understand the fitness implications for conserving and managing grassland birds in afforested landscapes.

1. Introduction

Land-use change represents a major driver shaping diversity and structure of ecological communities from local to global scales (Newbold et al., 2016, 2015). Commercial forestry is increasing worldwide to meet demands for forest products, economic returns, carbon sequestration, forest restoration, and reforestation initiatives (Chazdon and Laestadius, 2016; Nepal et al., 2019; Payn et al., 2015). Where commercial tree plantations are established in native grassland-dominated ecosystems (Veldman et al., 2015a), i.e., afforestation, this replacement introduces different structural and functional vegetation cover types, potentially compromising grassland-dependent species and communities, ecosystem functions, and services (Bond, 2016; Fernandes et al., 2016;

Veldman et al., 2015b, 2015c; Zaloumis and Bond, 2016).

Globally, where tree plantations replace pastures or agricultural lands in locations that were originally forests, properly managed plantations, particularly those of native tree species, have shown to diminish the negative consequences of native forest loss and enhance use by forest-dependent species (Calviño-Cancela, 2013; Demarais et al., 2017; Felton et al., 2010; Law et al., 2014; Volpato et al., 2010). Furthermore, studies across North America have shown that managed plantations where both young and open-forest conditions are maintained in the landscape benefit bird species dependent on early-seral, open vegetation stages (Ellis and Betts, 2011; Evans et al., 2021; Greene et al., 2016; Iglay et al., 2012; King and Schlossberg, 2014). Commercial forestry, where management considerations reflect the dynamics of native ecosystems,

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may represent an opportunity for forest biodiversity conservation (Brockerhoff et al., 2008). Notwithstanding, a proper assessment of the value of plantations to biodiversity requires recognizing the original system being replaced, whether forest, savannah, or grassland, along with the wildlife communities that depend on the ecological conditions provided by the native ecosystem (Brockerhoff et al., 2008; Felton et al., 2010; Filippi-Codaccioni et al., 2010; Stephens and Wagner, 2007).

Temperate grasslands are the most modified ecosystems globally and exhibit the greatest disparity between the degree of threat and formal protection among continental biomes (Carbutt et al., 2017; Henwood, 2010; Hoekstra et al., 2005). Among temperate grassy biomes, the Río de la Plata grasslands (RPG) of southeastern South America stands out as the most extensive grassland ecosystem in the Neotropical Region, encompassing nearly 700,000 km² in southern Brazil, Uruguay, and eastern Argentina (Paruelo et al., 2007; Soriano et al., 1992) (Fig. 1). Cattle grazing and agriculture have been the most dominant and traditional land use in the RPG since early European settlement (Baldi and Paruelo, 2008; Paruelo et al., 2007). However, in recent decades, there has been a notable expansion of large-scale commercial forestry in the Campos sub-region of the RPG, mainly in areas originally devoted to cattle grazing in Uruguay and southern Brazil, where the larger areas of natural and semi-natural grasslands remain (Azpiroz et al., 2012b; Overbeck et al., 2007; Vega et al., 2009).

The expansion of afforestation across the RPG has been facilitated by international market forces, suitable tree growth rates, high economic returns, and national land-use policies (Overbeck et al., 2007; Redo et al., 2012). In Uruguay, implementation of subsidies and tax incentives for investors and the identification of “soils of forest priority” (~20% of

the country) has led to a rapid expansion of the forestry sector (Céspedes-Payret et al., 2009; Mendell et al., 2007). Similar incentives were implemented in southern Brazil (Overbeck et al., 2007). As a result, >1.5 million hectares of Campos grasslands have been planted with pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.). Of this total, approximately one million hectares were planted in Uruguay (Brazeiro et al., 2020; Gautreau, 2014). Thus, tree plantations represent a novel ecosystem in the Campos grasslands of northern Uruguay (Geary 2001, Six et al. 2014), where afforestation represents over 50–60% of vegetation cover in many areas (Brazeiro, 2015). Furthermore, commodity prices and market trends indicate that scenarios of further afforestation expansion in the country are likely (Brazeiro et al., 2020).

Establishing tree plantations on native grasslands replaces open, grass-dominated environments with monocultures of non-native, fast-growing trees (Phifer et al., 2017; Veldman et al., 2015b). Therefore, afforestation represents a novel, high-contrast environment for plant and animal communities adapted to open environments that naturally present low tree cover (e.g., native tree cover in Uruguay is < 4%; Overbeck et al. 2007; Bernardi et al. 2016; Mourelle et al. 2017). Across the RPG, the large-scale conversion of native grasslands has been identified as the major driver of declining grassland-dependent biodiversity (Azpiroz et al., 2012b; Brazeiro et al., 2020; Medan et al., 2011; Overbeck et al., 2007). Biodiversity comparisons across alternative land uses are generally scarce in the region, yet some current studies have reported that afforestation may affect native biodiversity more negatively than traditional land uses, namely cattle grazing, pasture, and agriculture (Pretelli et al., 2018; Vaccaro et al., 2019).

Despite the expansion of commercial forestry in the Campos grasslands, research on afforested landscapes has been limited, with birds being one of the most studied groups to date (Azpiroz et al., 2012b). However, major gaps remain in understanding the effects of commercial forestry on avian diversity and assemblage structure. Reports on bird responses to grassland afforestation in the RPG have assessed eucalyptus plantations within a narrow range of age classes and most have not directly evaluated changes to habitat structure (Brazeiro et al., 2018; Dias et al., 2013; Filloy et al., 2010; Jacoboski et al., 2019, 2016b; Phifer et al., 2017; Vaccaro et al., 2019). Conservation of grassland birds in afforested landscapes requires understanding community responses to environmental conditions imposed by forestry practices along entire rotation and considering the most common commercial species planted. The ecology of avian communities has not been fully characterized in afforested landscapes across the RPG. Therefore, reliable information on which components of the avian community and to what extent, use the resources and conditions imposed by afforestation practices is needed for science-based conservation and management.

To better understand avian community response to afforestation, we assessed patterns of taxonomic bird alpha diversity and species composition (beta diversity) along environmental gradients in the northern Campos grasslands of Uruguay. For this, we included a chronosequence of age classes of both pine and eucalyptus plantations representative of the forestry rotation cycle. We sampled native environments (grasslands and forests) as reference conditions and assessed the link between the sampled environments and bird community responses through an evaluation of vegetation structure characteristics.

Based on the well-established link between vegetation characteristics and the structure of bird assemblages (Cody, 1985; Fuller, 2012; MacArthur et al., 1962; Morrison et al., 2012; Wiens, 1987a, 1987b), we predicted changes in vegetation composition and structure concomitant with stand development from grass-dominated, early succession plantations to mature, tree-dominated and closed-canopy conditions (Jones et al., 2012; Pairo et al., 2021; Six et al., 2014, 2013) would leave a measurable footprint on the avifauna. Further, given the greater plant diversity, and horizontal and vertical heterogeneity of seminatural grasslands and forests compared to tree monocultures (Fuhlendorf and Engle, 2001; Pozo and Säumel, 2018), we expected native environments would show greater bird diversity and within-compositional

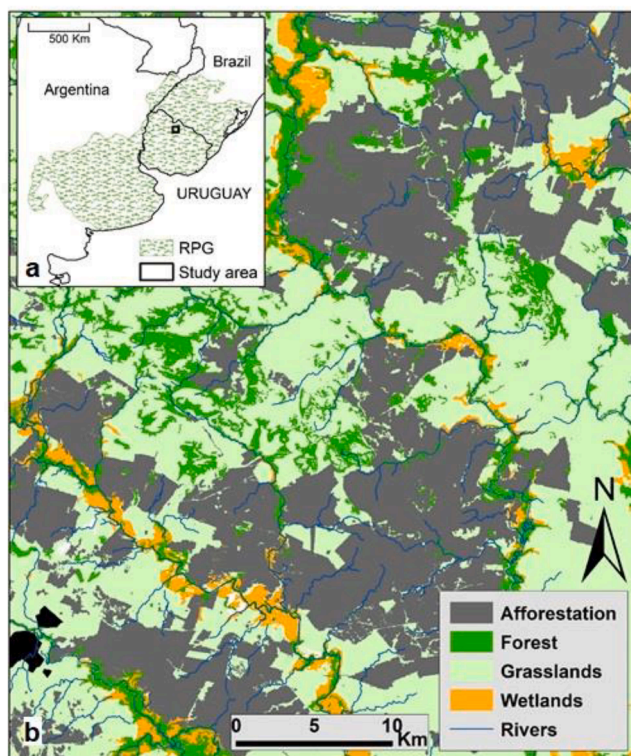


Fig. 1. Map of the study area in the Northern Campos of Uruguay, within the Río de la Plata Grasslands (RPG) in southeastern South America. The “Campos” sub-region of the RPG is primarily represented by subtropical grasslands in Uruguay and Southern Brazil; the Argentinean portion of the RPG is the temperate “Pampas” sub-region (a). The inset map details the study area in Tacuarembó and Rivera Departments in northern Uruguay sampled during the 2013–2014 austral bird breeding season, including native (grasslands and forests) and afforested environments (b). Limits of RPG according to Soriano et al., (1992).

heterogeneity (de Deus et al., 2020; Lorenzón et al., 2016; Mori et al., 2018; Stein et al., 2014; Tews et al., 2004). Lastly, we anticipated avian species would segregate along a habitat specialization gradient from grasslands to tree plantations to native forests (Devictor et al., 2010, 2008b; Julliard et al., 2006; Zurita and Bellocq, 2012), and the similarity in bird species composition would mirror the degree of habitat structural similarity among sampled vegetation types (Filloy et al., 2010; Zurita and Bellocq, 2012).

2. Methods

2.1. Study area

We conducted our study in the Northern Campos sub-region of the Río de la Plata Grasslands (Soriano et al., 1992) in Uruguay (Fig. 1a). The general climate pattern was humid subtropical with hot summers and mild winters. Annual and seasonal temperatures, precipitation patterns, and soil characteristics for the study area were summarized by Six et al. (2013, 2014). Topography was mostly undulatory with interspersed rocky outcrops and flat hills rarely exceeding 200 m elevation. Grasslands were dominant with drainage areas and swales forming low depressions scattered across the landscape; humid grasslands, shallow water wetlands, and marshes were found within these lowland areas. Upslope vegetation was characterized by upland grasslands with isolated native trees and small woodlots. Native forests were mostly confined to riparian areas along rivers and streams (gallery forests), with elevated hillsides and cliffs having xerophilic tree cover.

Our study area (Fig. 1b) was based primarily on lands owned and managed by Weyerhaeuser Company (16,500 ha) in the provinces of Tacuarembó and Rivera. Other properties included land owned by Cambium Forestal Uruguay Company (5,042 ha), interspersed within Weyerhaeuser's lands in Tacuarembó. Planted stands were composed of either flooded gum (*Eucalyptus grandis*, hereafter eucalyptus) native to Australia, or loblolly pine (*Pinus taeda*, hereafter pine) native to the southeastern United States. The rotation cycle in the region was typically 12–15 years for eucalyptus and 18–20 years for pine. Eucalyptus stands were planted upslope given their frost intolerance and poor growth in water-saturated soils. Pines were planted at lower elevations and closer to floodplains (Six et al., 2014). Approximate growth rates were $35 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ for eucalyptus, $\sim 30\%$ faster than pines (Geary, 2001).

2.2. Sampling design

We used a spatial database developed in ArcMap 10 (ESRI, Redlands, CA, USA) and a stratified sampling approach to select bird and vegetation sampling points in native and afforested environments. We located sampling points at a minimum distance of 200–250 m apart and 50 m from edges to accommodate a 50 m radius circular sampling point. Logistical considerations regarding terrain accessibility and temporal aspects determined sets of points as being closer to each other in space and time than to other such sets; we herein refer to these as clusters of points (see Section 2.3 below).

We sampled native environments including grasslands (nG) and forests (nF). Grassland sites represented adjoining grazing areas and unplanted grassland sites within the forestry properties (all of which were suitable for afforestation), and collectively ranged 0.5–10 ha. Native forests were found along with riparian and hillside areas, forming local assemblages of up to 30–50 woody species out of a regional pool of over 100 species (Haretche et al., 2012; Traversa-Tejero and Reyes Alejano-Monge, 2013). The overstory of native forests was dominated by species in the families Myrtaceae, Fabaceae, Euphorbiaceae, and Lauraceae. In turn, managed forest stands included a chronosequence of planted pine and eucalyptus with age classes representing most phases of the forestry rotation (Fig. 2; Table 1). Age classes included young eucalyptus (yE) planted during 2012–2013, older eucalyptus (oE)

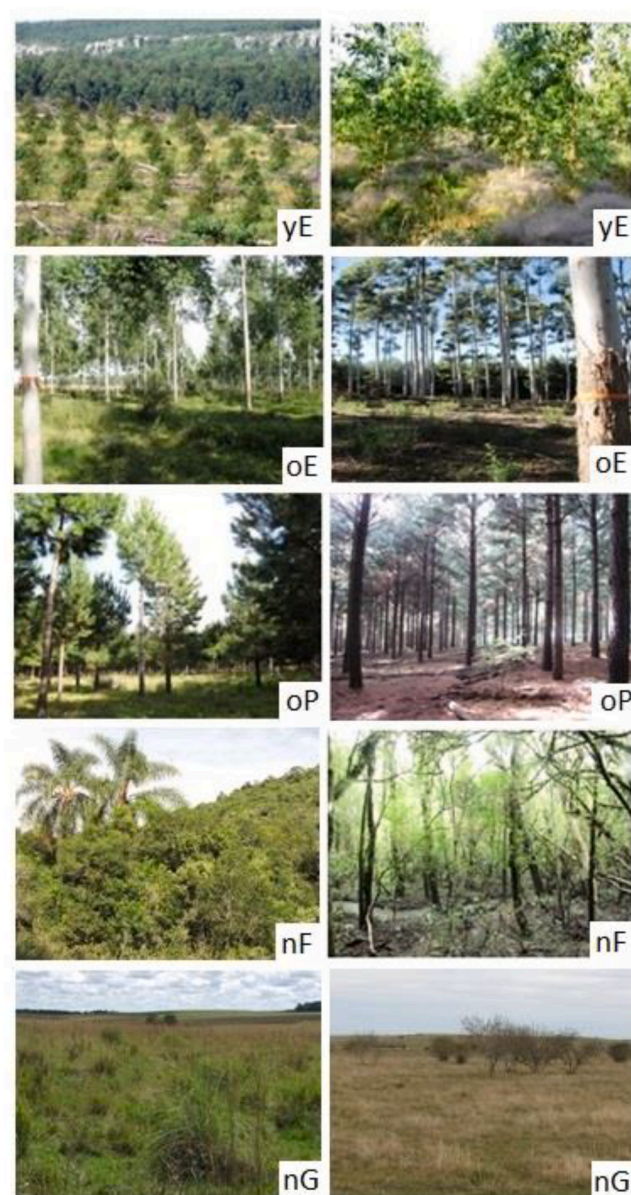


Fig. 2. Vegetation types sampled during the 2013–2014 bird breeding season in the Northern Campos Grasslands of Uruguay. Acronyms as follows: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG).

Table 1

Allocation of sampling effort per vegetation type for bird communities surveyed during the 2013–2014 breeding season in the Northern Campos Grasslands of Uruguay. Sampling included 1,513 10-minute bird counts (Visits) on 570 different sampling units of 50-meter radii (Points), arranged along 104 transects of points (Clusters).

Veg. type	Description	Age	Visits	Points	Clusters
yE	young Eucalyptus	1 year old	183	61	9
oE	older Eucalyptus	3–11 years old	477	159	22
oP	older Pine	9–16 years old	723	241	34
nF	native Forest		45	45	16
nG	native Grassland		85	64	23
			1,513	570	104

planted in 2010, in 2006–2007, and 2002, while older pine (oP) included stands planted in 2004–2006 and 1997–1999. The rationale behind these categories was to reflect within plantations those that structurally resemble open (yE) versus closed canopy (oE and oP) environments. Newly planted pine and post-harvest stands were not available within our study region. Herein, we refer to sampled conditions as vegetation types in terms of their distinctive structure and composition (Daubenmire, 1968; Fuller, 2012).

2.3. Bird and vegetation surveys

From October 2013 to April 2014, encompassing a full austral breeding season (Azpiroz, 2003), we used standard methods for surveying land bird communities (Bibby et al., 2000; Ralph et al., 1993). Within circular 50 m fixed-radius points, we recorded all birds heard or seen during a 10-minute sampling window. Two observers performed all surveys from sunrise until four hours after sunrise. We visited each point 3 times during the survey season for planted stands, 1–2 times for native grasslands, and once for native forests. Clusters contained 7–9 points for planted stands and 2–4 points for native environments. We randomly selected the order of points to be surveyed within clusters and rotated observers conducting subsequent visits to the same clusters to reduce bias. We did not include birds flying overhead during counts unless they were directly using (e.g., feeding, searching, or subsequently perched) the vegetation type being surveyed. We avoided conducting surveys during rain, fog, or when winds exceeded 20 km/h.

We assessed local habitat structure by measuring grassland (Fisher and Davis, 2010) and forest-specific (McElhinny et al., 2005) vegetation characteristics. We used the point-intercept method (Floyd and Anderson, 1987) to determine the percent of herbaceous cover at all sampling points, and the percent cover of coarse woody debris for tree plantations and native forests. Additionally, for plantations and native forests, we used a spherical densiometer to estimate canopy openness, measuring tape for diameter at breast height (DBH; cm), and tree height (m) using a clinometer. We counted all trees in four quadrants in all points to obtain a measure of tree density (trees/hectare). We averaged measurements for each variable within points and subsequently per cluster of points within each vegetation type.

2.4. Data analyses

We processed raw bird counts by retaining the maximum recorded for each species across repeated visits at the same points for all analyses (Toms et al., 2006) and used detection data to assess relative community-level variability in species diversity and composition across vegetation types and environmental gradients (Banks-Leite et al., 2014; Johnson, 2008). For the species diversity assessment, we used the information at the point level ($n = 570$). Alternatively, for compositional analyses, we aggregated point-level data across clusters of points ($n = 104$) by summing counts for each species and converting these to relative frequency by dividing by the number of points per cluster. We performed all statistical analyses in program R (R Core Team, 2020) and evaluated significance at $\alpha = 0.05$.

2.4.1. Bird species diversity

We estimated bird diversity using Hill Numbers (qD), or the effective number of species of order q , which tailors the metric's sensitivity to the relative abundance distribution across species (Chao et al., 2014). For example, when $q = 0$, diversity is measured by species richness (0D), with all species having equal weight. Conversely, 1D represents the exponential of Shannon diversity index, with species weighted by relative abundance, whereas 2D represents the reciprocal Simpson diversity index, i.e., the effective numbers of dominant species. Moreover, 2D is equivalent to Hurlbert's probability of interspecific encounter (PIE), where greater values reflect on higher assemblage evenness (Chao et al., 2014; Hurlbert, 1971). To compare qD diversities across vegetation

types, we used standardization based on sample completeness (as measured by sample coverage) (Chao and Jost, 2012), rarefying and extrapolating to lesser and greater coverage respectively, using sample-based incidence data with package iNEXT (Hsieh et al., 2016). We used non-overlapping 95% confidence intervals of diversity curves and point estimates as a conservative criterion of statistical difference (Colwell et al., 2012).

2.4.2. Bird community composition and species-habitat relationships

We assessed bird use of vegetation types by classifying the regional species pool according to their degree of habitat specialization using published information (Azpiroz, 2012, 2003; Azpiroz et al., 2012b) and field experience. Habitat categories included: a) grassland specialists, b) forest-dependent species, and c) habitat generalist species that used a wide array of vegetation types, including treed grasslands, shrublands, open woodlands, savannas, and forest edges. Further, we used package *indicspecies* to quantify the strength of association to vegetation types for each species with correlation indices and 9,999 permutations (Cáceres and Legendre, 2009). Within this framework, we assessed the vegetation type combination that maximized the phi index of association (ϕ) including a correction for unequal sample size (De Cáceres et al., 2010; Tichy and Chytrý, 2006). Lastly, to assess trophic structure across vegetation types, we classified species into granivores, insectivores, omnivores, carnivores, frugivores, and nectarivores following Azpiroz (2003). We ultimately mapped the frequency of occurrence of species across vegetation types for both habitat and trophic guilds. We only considered the optimal vegetation type (combination) for assessing frequencies and only for species showing the overall strength of habitat association $\phi > 25\%$ (i.e., "representative species"), regardless of the species was also detected in other vegetation types.

We used package *vegan* (Oksanen et al., 2019) for variance partitioning and ordination routines to assess variation in bird species composition (i.e. beta-diversity; Whittaker 1972) between and within vegetation types, and along environmental gradients, using multivariate measures of pair-wise ecological dissimilarities with Bray-Curtis distance on the squared-rooted relative frequency data (Anderson et al., 2011; Clarke, 1993; Faith et al., 1987). Furthermore, to disentangle the effect of species richness on compositional analysis, we used the *betapart* package on the incidence matrix (Sørensen distance) to partition the multiple-site total dissimilarity (β_{sor}) into nestedness (richness differences, β_{nes}) and turnover (species replacement, β_{sim}) components (Baselga, 2010; Baselga and Orme, 2012). Finally, we obtained the mean and standard deviation for each component by resampling 10 sites randomly 100 times.

To assess avian community composition, we first calculated the mean between and within-vegetation type dissimilarity and constructed a dendrogram of the resultant matrix using a hierarchical clustering algorithm (Legendre and Legendre, 2012). To test for differences across vegetation types, we conducted a permutational multivariate analysis of variance (PERMANOVA, McArdle and Anderson 2001; Anderson 2001) with 9,999 permutations and assessed the explained dissimilarity as the proportion of the factor's sum of squares relative to the total sum of squares. To assess within-group variation, we used multivariate homogeneity of group dispersion analysis (PERMDISP, Anderson et al. 2006; Anderson 2006). For this routine, we combined all plantation types (yE, oE, and oP) into a single group (Affor). We used the Bonferroni correction procedure to avoid inflation of the Type I error rate given multiple comparisons (Roback and Askins, 2005) in PERMANOVA and PERMDISP analyses.

To visualize species composition patterns along environmental gradients, we conducted a non-metric multidimensional scaling ordination (NMDS) (Clarke and Ainsworth, 1993; Minchin, 1987) and relied on a goodness-of-fit stress statistic to determine the most appropriate number of dimensions (k). Stress values ranging from 10 to 20% were considered adequate (Clarke, 1993). We mapped cluster scores by vegetation type with 95% dispersion ellipses, where the degree of overlap is indicative of

between-group variation and the relative size indexes within-group variation in species composition. We mapped the vegetation structure information onto the ordination biplots as fitted vectors and evaluated the statistical significance of the correlations with 9,999 permutations. We performed two separate ordinations, one with the full environmental gradient (104 clusters by 103 species), and a second one for tree plantations and native forests (82 clusters by 77 species) so that forest-specific vegetation structure could be incorporated in the assessments.

3. Results

3.1. Bird assemblage description

We completed 1,513 counts at 570 different sample points in 104 clusters of points (Table 1). We recorded 3,760 individual birds representing 103 species in 32 families and 15 orders. Counts across repeated visits at the same points (i.e., maximum count per species) yielded 3,168 counts for subsequent analyses (Table 2). Detected species represented 47 generalists, 36 forest specialists, and 20 grassland specialists (Supplementary Material, Appendix I). Furthermore, guilds of the sampled species pool were represented by 53 insectivores, 17 granivores, 13 omnivores, 11 carnivores, 6 frugivores, and 3 nectarivore species. The Rufous-collared Sparrow (*Zonotrichia capensis*) was the most common species representing ~ 30% of all individuals recorded. This species exhibited the greatest relative abundance in all forest types except native forests. The House Wren (*Troglodytes aedon*) was the second most frequently recorded species with ~ 10% of total records. No other species accounted for >4% of species counts. Three grassland specialist birds recorded in native grasslands represented species of conservation concern according to IUCN criteria at the national level (Azpiroz et al., 2012a): Grass Wren (*Cistothorus platensis*; Vulnerable), Burrowing Owl (*Athene cunicularia*; Near Threatened), and Wedge-tailed Grass-Finch (*Emberizoides herbicola*; Near Threatened). No species of conservation concern were documented in planted stands or native forests. Three grassland facultative species, Red-winged Tinamou (*Rhynchotus rufescens*), Blue-black Grassquits (*Volatinia jacarina*), and Grassland Sparrows (*Ammodramus humeralis*) occurred solely in yE among plantation types albeit with low incidence and relative abundance (Supplementary Material, Appendix I).

3.2. Bird species diversity

The observed species richness was greater in native vegetation types (49 in nF and 60 in nG) than plantations (range 32–40) despite the latter being sampled more intensively. Plantations included nearly 4-fold more points and were visited 10-fold more times than native environments (Table 1). Sample coverage (completeness) across vegetation types ranged from 90% in nG to 99% in oP (Table 2; Fig. 3a). Interpolation and extrapolation of species diversity at the coverage boundaries, respectively, showed consistently greater bird diversity in native vegetation types than in plantations (Table 2; Fig. 3b), albeit the difference

was broader considering the abundance-weighted diversities 1D and 2D than for species richness (0D). For example, at 90% coverage, the effective number of dominant species in nF was 2.7, 2.4, and 2 times greater than in yE, oP, and oE, respectively. Overall, the proportional abundance of the most common species (i.e., Rufous-collared Sparrow) was ~ 3-fold greater in plantations than in native environments (Supplementary Material, Appendix I).

3.3. Bird community composition and species-habitat relationships

Species-habitat correlation analysis resulted in 72 species (70%) with an association index of $\phi > 25\%$, 59 of which were significantly correlated with single vegetation or vegetation type combination (Supplementary Material, Appendix I). For forest-dependent species, 11 (31%) included oE and/or oP in the optimal arrangement. For example, White-spotted Woodpeckers (*Veniliornis spilogaster*) were most strongly associated with oP, Gilded Hummingbirds (*Hylocharis chrysura*) with oE, and Roadside Hawks (*Rupornis magnirostris*) and Hepatic Tanagers (*Piranga flava*) with both oP and oE. Other forest species, such as Mottled-cheeked Tyrannulets (*Phylloscartes ventralis*) and Red-eyed Vireos (*Vireo olivaceus*), were associated with planted forest stands but also included nF in the optimal vegetation type combination.

Considering the most representative species per vegetation type (i.e., $\phi > 25\%$), grassland specialists composed 42% of species in nG and 18% in young eucalyptus. No grassland bird species occurred in older planted or native forests (Fig. 4a). The relative frequency of generalist birds peaked in yE (82%) and had the lowest incidence in nF (8%). In turn, forest-dependent species exhibited greater relative incidence in nF (92%) and represented nearly half of the species found in oP and oE combined. No forest species occurred regularly in nG or yE.

Regarding trophic guilds (Fig. 4b), we found yE and nG were characterized by the same dietary groups, albeit with shifted proportions. Namely, while granivores and carnivores remained comparable, nG showed a greater incidence of insectivores and lesser incidence of omnivore species than yE (69% versus 47%, 4% versus 18%, respectively). Carnivores (primarily raptors) were over 2.5 times more frequent in oP and oE than other vegetation types. In contrast, nectarivores attained the highest incidence among oE, over 3-fold greater than in nF, and were not represented in oP.

The partition of dissimilarity showed 94% of total assemblage dissimilarity was driven by species turnover ($\beta_{sor} = 0.84 \pm 0.02$; $\beta_{nes} = 0.05 \pm 0.02$; $\beta_{sim} = 0.79 \pm 0.04$). Further, PERMANOVA indicated all vegetation types differed in bird species composition ($F_{4,103} = 13.8$, $P < 0.001$; 36% explained dissimilarity) with all pair-wise comparisons being statistically significant (Bonferroni correction). Including herbaceous cover and tree density in the model explained an additional 3% of total dissimilarity ($F_{6,103} = 14.2$, $P < 0.001$), while the model with only the two covariates explained 13% of dissimilarity ($F_{2,103} = 15.8$, $P < 0.001$). Beyond these dichotomous differences, nG and nF were the most dissimilar assemblages (0.91 mean dissimilarity). Conversely, tree plantations had the most similar avian communities (mean dissimilarity

Table 2

Summary of bird counts, observed species richness, and diversity estimates of Hill numbers (qD) [95% CI] per vegetation type for bird communities sampled during 2013–2014 in northern Uruguay. Estimates of qD were obtained by interpolating and extrapolating to the minimum (90% for nG) and maximum (99% for oP) sample coverage: species richness (0D), Shannon (1D), and Simpson diversity (2D). Vegetation types: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG).

Veg. Type	Bird Counts	Observed Richness	Sample Coverage	qD (interpolated to 90% coverage)			qD (extrapolated to 99% coverage)		
				(q = 0) Richness	(q = 1) Shannon	(q = 2) Simpson	(q = 0) Richness	(q = 1) Shannon	(q = 2) Simpson
yE	337	32	94%	26 [22–31]	13 [11–15]	8 [6–9]	44 [29–58]	15 [13–18]	8 [7–9]
oE	647	40	98%	23 [21–24]	15 [14–16]	11 [10–12]	45 [38–52]	18 [17–20]	12 [11–13]
oP	1461	39	99%	18 [17–19]	12 [12–13]	9 [9–10]	38 [33–43]	15 [14–16]	10 [9–11]
nF	379	49	96%	39 [36–42]	28 [26–31]	22 [20–24]	57 [48–65]	33 [30–37]	24 [21–27]
nG	344	60	90%	56 [49–63]	38 [33–42]	27 [23–32]	77 [58–97]	45 [39–50]	30 [25–34]
	3,168	103							

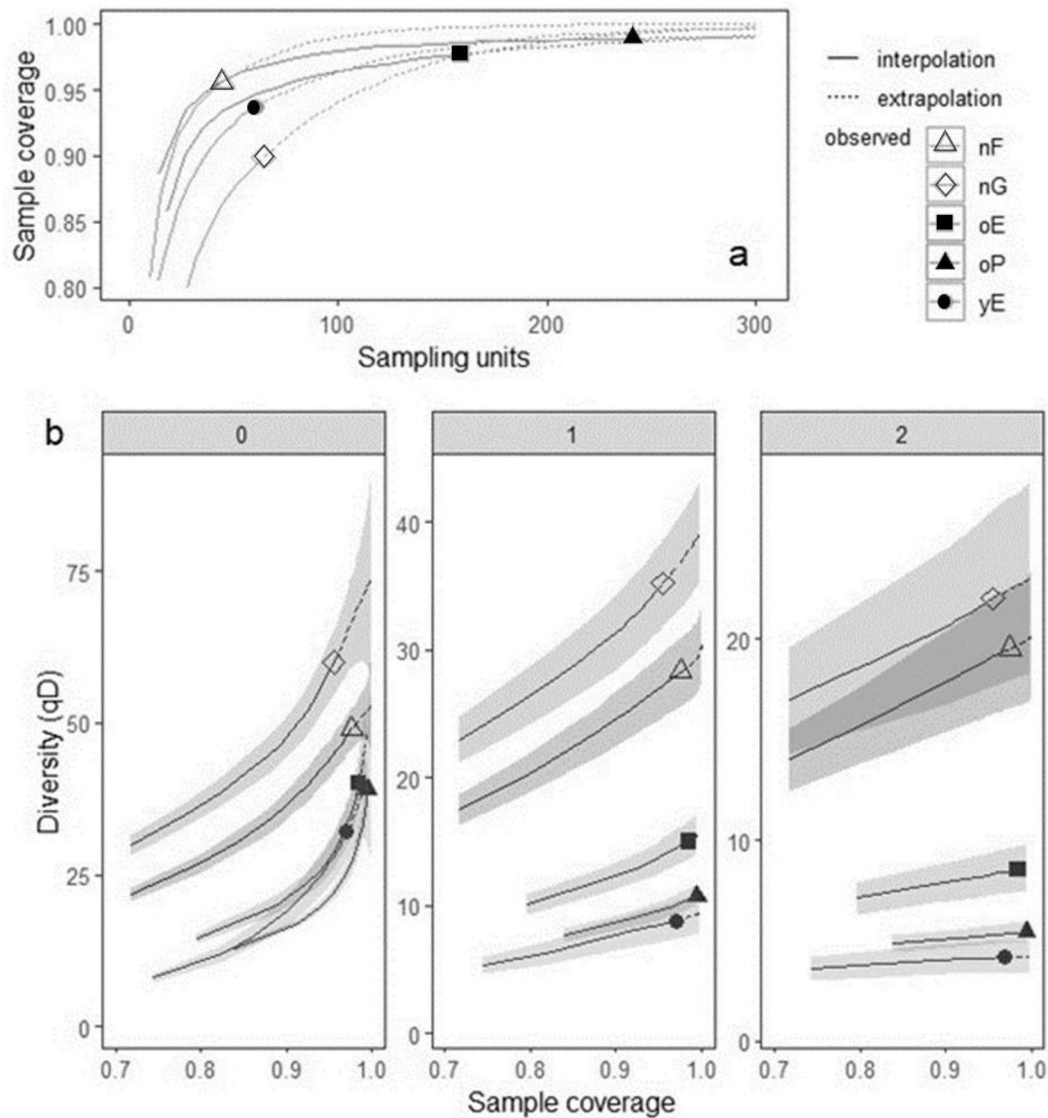


Fig. 3. Among-vegetation type sample coverage (completeness) (a), and interpolation and extrapolation curves of Hill number diversities of order q (qD) with 95% CI (b) for bird communities sampled during 2013–2014 austral breeding season in northern Uruguay. The qD estimates are species richness (0D), Shannon (1D), and Simpson diversity (2D). Vegetation types: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG).

ranged 0.55–0.67), with oE and oP being the most similar (0.55 mean dissimilarity) among vegetation type pairs (Fig. 5a). Tree plantations were nearly as dissimilar to nG as to nF (mean dissimilarity of ~ 0.83 with each). Among plantations, yE was most similar to nG (0.79 mean diss.), while oE and oP were more similar to nF (0.81 mean diss.). Furthermore, PERMDISP indicated native vegetation types and plantations (yE, oE, and oP combined) showed different multivariate dispersions, with nG and nF having 1.6 and 1.2 times greater within-group variation in species composition than tree plantations combined, respectively (Fig. 5b).

Ordination of the full environmental gradient yielded an optimal solution in two dimensions (i.e., $k = 2$) with a stress value of 0.15 (Fig. 6a). The relative position and size of the ellipses mirrored the uncovered patterns of between and within-group variation in species composition. The ordination was correlated with vegetation type as factor variable ($r^2 = 0.42$, $p < 0.001$) and more strongly so with herbaceous percent cover ($r^2 = 0.68$, $p < 0.001$). Herbaceous cover decreased from negative to positive scores on the first axis, across nG sites (mean % 73 ± 20 SD) to yE (mean % 54 ± 10 SD), and towards older plantations and nF (combined mean % 16 ± 13 SD). Tree density

followed an opposite pattern along the first axis ($r^2 = 0.55$, $p < 0.001$). Forest bird species clustered along with the positive scores of the first axis, particularly around nF, and, to a lesser extent, within positive values along the second axis towards plantations. Grassland bird species exhibited an opposite pattern, with negative scoring along the first axis around nG. In turn, habitat generalists scored predominantly within the afforested environmental space. Lastly, the subset NMDS ordination for plantations and native forests ($k = 2$, stress = 1.8) complemented the assessment of forest-specific structural gradients (Fig. 6b), with significant correlations ($p < 0.001$) for vegetation type ($r^2 = 0.64$), tree density ($r^2 = 0.48$), tree height ($r^2 = 0.47$), woody debris cover ($r^2 = 0.39$), canopy openness ($r^2 = 0.27$), and DBH ($r^2 = 0.21$).

4. Discussion

Our study represented a comprehensive evaluation of bird taxonomic (alpha) diversity and species composition (beta diversity) response to afforestation in the Campos in terms of sampling intensity, analytical methods, and the breadth of environmental conditions assessed. We found marked shifts in bird community structure to contrasting

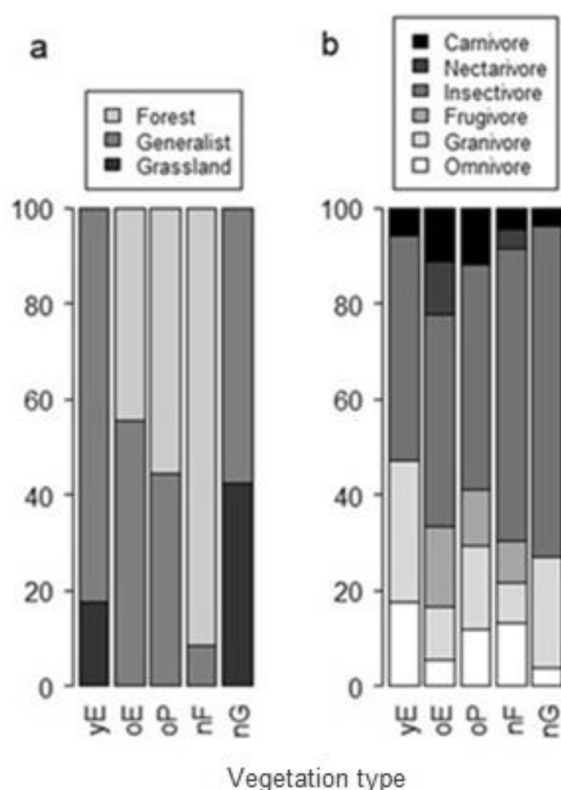


Fig. 4. Frequency composition of species across vegetation types grouped according to expected habitat affiliation (a), and trophic guilds (b) for bird communities sampled during the 2013–2014 austral breeding season in northern Uruguay. Vegetation type and trophic group frequencies were constructed by only considering the optimal vegetation type combination for species with an estimated strength of habitat association of $\phi > 25\%$. Vegetation types: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG).

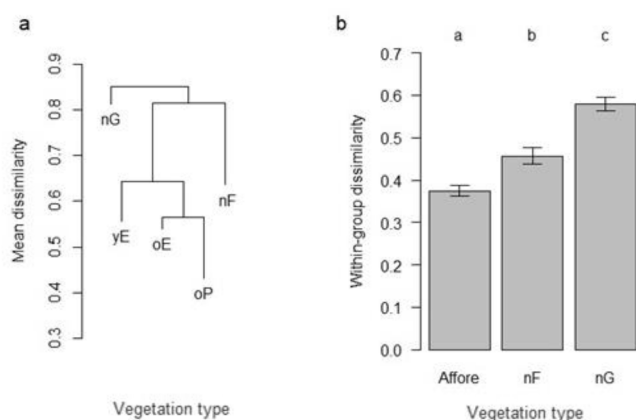


Fig. 5. Branching arrangement of vegetation types based on mean dissimilarity of bird species composition (a), and estimates of within-group variation of community composition (b) for bird communities sampled during the 2013–2014 austral breeding season in northern Uruguay. Different letter codes above the bars indicate statistical significance after Bonferroni correction (error bars represent standard errors). Vegetation types: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG); all tree plantation types combined (yE, oE, and oP = Affore).

structural conditions between native environments and tree plantations, and among plantation types. Overall, native environments showed greater species diversity and compositional heterogeneity than

plantations. Tree plantations were extensively used by generalists species, to a lesser extent by a subset of forest-dependent species, and plantations were largely void of grassland specialist birds.

4.1. Bird species diversity

We found bird species richness was greater in native grasslands and forests than in tree plantations. These responses were a baseline expectation based on species-habitat relationships and aligned with other published reports in the RPG where native environments showed greater taxa species richness than eucalyptus plantations including birds (Brazeiro et al., 2018; Dias et al., 2013; Jacoboski et al., 2019, 2016b; Phifer et al., 2017; Vaccaro et al., 2019), mammals (Cravino and Brazeiro, 2021), amphibians and reptiles (Saccol et al., 2017), and plants (Pairo et al., 2021). A similar pattern was reported in Patagonia, where the open steppe showed greater bird species richness than pine plantations (Lantschner et al., 2008). The Campos is characterized by a mixture of grasslands under different grazing regimes and varying incidence of isolated native trees and woodlots. For example, bird assemblages within our grassland sites included a mixture of grassland, savannah, and some forest species. This level of diversity is likely maintained in the landscape as a reflection of these horizontally heterogeneous grassland mosaics (Devictor and Jiguet, 2007; Fuhlendorf and Engle, 2001; Hovick et al., 2015; Hsu et al., 2010). Further, isolated trees have been identified as keystone structural attributes contributing to bird diversity in agroecosystems (Ambarli and Bilgin, 2014; Fischer et al., 2010), and may represent important components structuring bird assemblages in native grasslands of the RPG (Dias et al., 2013; Phifer et al., 2017).

Conversely, bird diversity within plantations in forest-dominated ecosystems reforested with native and/or commercial tree species is usually greater than open pasture and agricultural lands that replaced native forest cover (Felton et al., 2010). This highlights the importance of which original vegetation type is replaced by plantations and the native versus. exotic nature of planted tree species (Castaño-Villa et al., 2019). Lastly, native forests in the Campos are compositionally and structurally more complex and diverse than plantations (Pozo and Säumel, 2018) manifested by greater bird diversity of native forests in our study. Notably, previous studies in the RPG reported decreased bird functional diversity in eucalyptus plantations compared to native forests in the Campos (Jacoboski et al., 2016a) and forests and grasslands in the Pampas (Vaccaro et al., 2019). However, a later similar study in the Campos revealed no differences in functional diversity between eucalyptus and native environments, including grasslands (Jacoboski and Hartz, 2020). The disparity in results on the overall functional diversity facet concerning afforestation among these studies awaits further investigation. Notwithstanding, the filtering out of grassland species and concomitant loss of trait-mediated ecosystem function from those species constitutes a straightforward consequence of grassland afforestation (Vaccaro et al., 2019).

Species diversity among native and afforested environments in our study was not driven by species richness alone but also by shifts in relative abundance distributions across species, highlighted by species that were conspicuous across several vegetation types, yet exhibited markedly different relative abundances. For example, the most widespread species in our study, Rufous-collared Sparrow, was over twice as abundant in plantations compared to native vegetation types. From the diversity metrics used, the “unevenness” footprint was captured by those stressing the influence of relative abundance (Shannon and Simpson diversities). Native environments had a greater diversity of common and dominant species than plantations, reflecting not only a richer bird community but also a more equitable distribution of abundance across species. It has been hypothesized that evenness might play similar importance as species richness modulating species coexistence and community structure, and on species’ trait-mediated ecosystem function (Barros et al., 2019; Hillebrand et al., 2008; Tilman et al., 2014). For

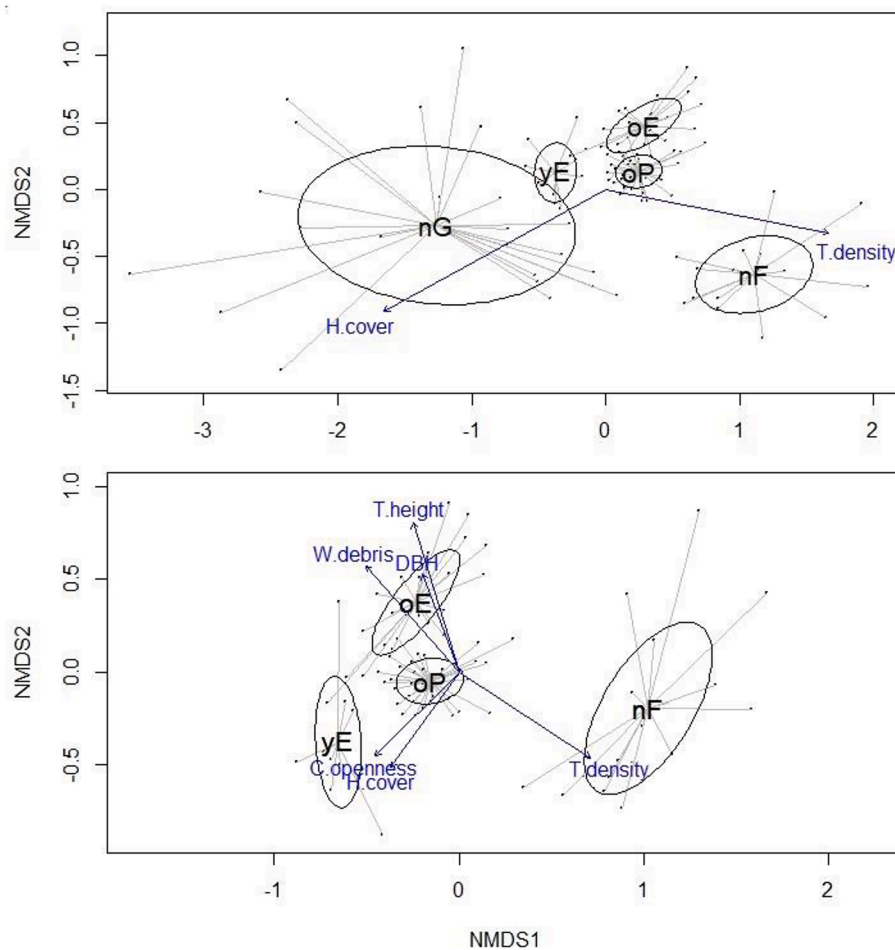


Fig. 6. NMDS ordination biplots for bird species composition (Bray-Curtis distance) sampled during the 2013–2014 austral breeding season in northern Uruguay. Full ordination (104 clusters by 103 species; $k = 2$, stress = 0.15) (a), and afforestation-nF subset ordination (82 clusters by 77 species; $k = 2$, stress = 0.18) (b). Distance from cluster scores to multivariate centroids are depicted as black points and gray lines. Fitted vectors represent herbaceous cover (H.cover), tree density (T.density), canopy openness (C.openness), woody debris cover (W.debris), tree diameter (DBH), and tree height (T.height). Vegetation types are mapped as 95% confidence ellipses: young eucalyptus (yE), older eucalyptus (oE), older pine (oP), native forest (nF), and native grasslands (nG).

instance, shifts in bird density along land-use intensity gradients in the Pampas were shown to relate to ecosystem functioning (Gavier-Pizarro et al., 2012). Thus, identifying the niche position of species driving dominance shifts in afforestation systems grants a more nuanced investigation due to both theoretical and management underpinnings (Crowder et al., 2012; Hillebrand et al., 2008; Rohr et al., 2016; Symonds and Johnson, 2008).

4.2. Bird-vegetation associations and assemblage composition

We found differences in bird species composition across native and planted vegetation types, a pattern also mimicked by shifts in trophic guild composition of sampled bird assemblages. These shifts reflected differences in structure across vegetation type conditions and agreed with previous studies (Graham et al., 2017; Hsu et al., 2010; Lipsey and Hockey, 2010; Phifer et al., 2017; Vaccaro et al., 2019). Thus, bird community structure and composition tracked the composition and structure of vegetation types (Filloy et al., 2010; Zurita et al., 2006; Zurita and Bellocq, 2012). The greatest dissimilarity in our study was attained between bird communities in native grasslands and native forests. We expected this effect given that native grasslands and forests represented the endpoints of the structural vegetation gradients in our study region. Interestingly, bird communities in older eucalyptus compared to pine included different species assemblages despite having a similar structure. This suggests other factors besides vegetation structure may partially drive the composition of avian assemblages (Hewson et al., 2011) across these plantation types. Dissimilar avian communities in sympatric pine and eucalyptus plantations previously reported have been attributed partly to differences in flower production

and bark texture, which in turn affected the incidence of bird guilds using nectar and insect resources (Calviño-Cancela, 2013; Hsu et al., 2010; Willis, 2002). Our results agreed with this observation. For example, the relative abundance of hummingbirds (nectar feeders) was greater in eucalyptus than pine, whereas the opposite pattern occurred for woodpeckers (bark-insect feeders).

Even though all plantation types were more similar in bird composition, assemblages in young eucalyptus were most like native grasslands. This could be because vegetation structure at the earliest stages of the forestry rotation resembles open environments (Six et al., 2014; Souza et al., 2013; Zurita and Bellocq, 2012). Further, cattle are routinely excluded from newly planted stands, allowing grasses and other herbaceous vegetation to develop more than adjoining grazed grassland sites. Therefore, newly planted stands were potentially available to some bird species that primarily use grasslands but are considered less sensitive to disturbance than grassland-dependent specialists (Azpiroz et al., 2012b), or species that use treed grasslands or savannahs (Dias et al., 2013; Phifer et al., 2017). We detected only three facultative grassland species in young eucalyptus plantations albeit at low relative occurrence and abundance, the Red-winged Tinamou, Blue-black Grassquits, and Grassland Sparrows. These species use grasslands extensively but are also found along with row crop environments within agroecosystems (Azpiroz et al., 2012b). Furthermore, the relative suitability of newly planted eucalyptus stands for grassland birds likely diminishes quickly given their rapid growth rate. For example, young eucalyptus stands in our study would shift to the older age class in less than two years. Even though pine rotations are longer eucalyptus given slower growth rates (Geary, 2001), surrogate conditions for grassland birds may extend for longer periods in pine than

eucalyptus during the early stages of a stand rotation. Unfortunately, there were no young pine stands available during our study to evaluate this point and grants future investigation.

Tree plantations represented unique assemblages in terms of community structure compared to native conditions. New species combinations (species types and relative abundances) that do not naturally occur within native environments are among the key defining features of “novel ecosystems” (Hobbs et al., 2009, 2006; Lindenmayer et al., 2008). The RPG has been considered a novel ecosystem because of the sustained forces of cattle grazing and agriculture since early European settlement (Six et al., 2014). In this regard, the onset of afforestation in the Campos brings further novelty shaping the composition and structure of native vegetation and animal communities in unique ways (Buisson et al., 2019; Lindenmayer et al., 2019; Six et al., 2014). Novel ecosystems are characterized by a decrease in ecological specialization, where narrowly ranged specialists (“losers”) are systematically replaced by widespread generalist species (“winners”) along sustained anthropogenic gradients (Newbold et al., 2018; Viol et al., 2012). This was reflected in the structure of bird communities in our study where habitat specialization endpoints were represented by grassland and forests. Tree plantations were occupied mostly by generalist species, with few becoming overabundant. Many generalist species and some forest species exhibited greater use of plantations than native environments (i.e., winner species). Most conspicuously, the Rufous-collared Sparrow was twice as abundant in plantations. This result mimics that of similar studies in the region (Dias et al., 2013; Filloy et al., 2010; Phifer et al., 2017), highlighting a species that is a “winner” of grassland afforestation in the RPG.

From a theoretical perspective, environmental degradation can be conceptualized as a directional, non-random bottleneck process, filtering out from the community species that depend on structural and functional abiotic and biotic attributes of the natural ecosystem (Clavel et al., 2011; Jeliakzov et al., 2016). The direction and magnitude of species’ response to changes in land use may depend on species’ ecological niche breadth characterized by the degree of trophic and habitat specialization (Devictor et al. 2008; Newbold et al. 2020), and ultimately on functional traits as mediators of environmental responses (Weiss and Ray, 2019). As such, the systematic replacement of specialists by widespread generalists is expected to drive biotic homogenization of communities over space and time as a consequence of land-use intensification (Devictor et al., 2008b, 2008a; Gossner et al., 2016; Jeliakzov et al., 2016; Karp et al., 2012; Newbold et al., 2019, 2018; Vázquez-Reyes et al., 2017). We detected such a footprint of biotic homogenization in our study, where native vegetation types had greater within-group heterogeneity in bird species composition than plantations compared to native environments. This simplification of bird assemblages was expected given the structural homogeneity typical of non-native, planted forest stands (Filloy et al., 2010; Jeliakzov et al., 2016). A similar reduction in avian community dissimilarity has been reported for tree plantations substituting open environments in the Pampas (Filloy et al., 2010) and Ireland (Graham et al., 2017). This pattern may have implications for community structure at larger spatial scales, as plantations may promote similar environmental conditions at distant sites, with a consequent reduction in beta diversity among otherwise dissimilar bird assemblages. For instance, afforestation using non-native tree species has been shown to trigger biotic homogenization across biomes with contrasting native vegetation and taxa, such as the Atlantic Forest and the RPG for birds (Filloy et al., 2010), mammals (Iezzi et al., 2021), and ant communities (Santoandré et al., 2019). The results of our study, albeit at a smaller scale, are consistent with these findings and suggest afforestation could be acting as a homogenization driver of bird communities at the national scale.

4.3. Conservation implications and research prospects

The decline in grassland specialist bird species has been proposed as

an early indicator of landscape-scale transition from grassland to planted forests (Bond and Parr, 2010). Our results revealed a minimal representation of grassland species across the tree plantation age classes studied. Only three species were recorded on young eucalyptus stands, albeit with low incidence and relative abundance, whereas grassland-dependent specialist birds were completely absent from plantations. Grassland bird communities are endangered across the region, and most bird species of conservation concern in the RPG are grassland specialists (Azpiroz et al., 2012b). Thus, grassland communities and obligate grassland birds need increased conservation efforts in afforested landscapes rather than overall bird diversity. Given the range of conditions representative of a forestry rotation included in our study, our findings suggested conservation of grassland birds may not be attainable from a traditional stand-management perspective of single, isolated afforested landscapes and ownerships. Thus, a larger scale, multiple-landscape perspective ought to be explored as an improved alternative. This would entail maintaining large, contiguous, and functionally connected grassland patches within and among afforested landscapes while intensifying wood production via stand management practices. This “land-sparing” approach, as opposed to “land-sharing” (Balmford et al., 2005), might be a better strategy to optimize wood production while promoting appropriate conditions for grassland birds (Dotta et al., 2016; Phifer et al., 2017).

Grassland biodiversity conservation in the RPG within the novel conditions imposed by afforestation offers multiple theoretical and practical challenges for effective management (Hobbs et al., 2009, 2006; Lindenmayer et al., 2008; Seastedt et al., 2008). For example, implementing a multiple-landscape, land-sparing approach would require knowledge on the minimum size, shape, and spatial arrangement of functionally connected grassland patches needed to maintain viable populations of grassland-dependent species (Herrera et al., 2017; Lipsey and Hockey, 2010; Pretelli et al., 2018, 2015; Ribic et al., 2009). Developing reliable information to address these knowledge gaps would require studies at the interplay of organismal to landscape-levels of ecological organization. Considering focal species, autecological studies that assess more direct measures of fitness (e.g., vital rates) remain an important avenue of research. These studies would be particularly relevant for afforestation systems as the mismatch between the intensity of habitat use and the perceived habitat quality (i.e. “ecological traps”) may occur more frequently in systems subjected to intense and novel anthropogenic disturbances (Bock and Jones, 2004; Van Horne, 1983). Population studies considering the consequences of establishing plantations in open environments, including edge effects (Phifer et al., 2017; Reino et al., 2009), trees as barriers to dispersal for grassland (Renfrew et al., 2005; Thompson et al., 2014), and forest species (Mortelliti et al., 2014; Tomasevic and Estades, 2008), nest predation (Ellison et al., 2013; Reino et al., 2010) and brood parasitism (Pietz et al., 2009; Pretelli et al., 2015) would benefit avian biodiversity conservation in the RPG. These processes could differentially affect grassland bird species survivorship and/or reproductive outcome beyond area sensitivity considerations (Okada et al., 2017; Pretelli et al., 2015; Ribic et al., 2009).

From the community-level standpoint, more nuanced assessments incorporating other facets of diversity, such as measures of alpha and beta functional and phylogenetic diversity, would provide a complementary view to bird community responses to afforestation (Boesing et al., 2018; Jacoboski and Hartz, 2020; Luck et al., 2013; Meynard et al., 2011). Furthermore, functional trait-based approaches would favor a more direct assessment of species’ functional roles onto the potential effects of afforestation on ecosystem processes and services provided by birds (Barros et al., 2019; Gavier-Pizarro et al., 2012; Gorosábel et al., 2020; Jacoboski and Hartz, 2020; Luck et al., 2013; Michel et al., 2020; Newbold et al., 2013). From a landscape perspective, information on landscape-level thresholds above which grassland bird diversity or species’ abundance may decline, leading to local or regional extinctions is needed (Boesing et al., 2018; Huggett, 2005; Melo et al., 2018; Toms and Villard, 2015). Previous studies have shown species

richness thresholds ranging from 20 to 40% of remaining native vegetation types for a wide range of taxa, including small and large-bodied mammals, forest birds, and vascular plants (see Boesing et al. 2018 and references therein). Research in the prairies of North America reported grassland birds exhibited greater sensitivity to fragmentation than woodland species and that several grassland-dependent species only occurred where 70–90% of grasslands remained (Cunningham and Johnson, 2019). In the Campos, Brazeiro et al. (2018) showed a reduction of ~38% in species richness of grassland specialist birds in a landscape where 13% of the area was afforested versus a landscape afforested up to 40% with eucalyptus. Work in the Pampas showed richness and abundance of grassland specialist birds were negatively affected in a matrix dominated by tree plantations compared to pasture and agricultural land (Pretelli et al., 2018; Vaccaro et al., 2019). It is yet unknown whether persistence thresholds have already been exceeded for some grassland obligate bird species within afforested landscapes within our study region, an important future research topic. In any case, the potential use of extinction thresholds in landscape-level management and conservation needs to be approached with caution as time-lagged species' responses to landscape transformation are rather frequent in modified landscapes (Kuussaari et al., 2009; Lindenmayer and Luck, 2005; Semper-Pascual et al., 2018). This implies that a given community could be beyond tipping points not readily detected, or underestimated, by contemporary studies (Essi et al., 2015).

More generally, both synthesis research and new field studies across replicate landscapes with varying afforestation extents and successional stages along a longitudinal gradient through time (Lindenmayer et al. 2001; Law et al. 2014, 2017) are needed to better assess the spatial-temporal “scale of effect” of afforestation on grassland bird communities and on grassland dependent species in particular (Chandler and Hepinstall-Cymerman, 2016; Crouzeilles and Curran, 2016; Jackson and Fahrig, 2015). Furthermore, studies incorporating agricultural practices while accounting for surrounding matrix type and land-use history (Graham et al., 2017; Lindenmayer et al., 2019), would place afforestation effects in the context of alternative land uses and assess production-biodiversity tradeoffs (Dotta et al., 2016; Vaccaro et al., 2019). For instance, with direct comparisons, Vaccaro et al. (2019) showed that among traditional land uses in the Pampas, pasture and agriculture retained a greater proportion of taxonomic and functional bird diversity typical of native and protected grasslands in the region compared to tree plantations. Such studies will need to account for cattle grazing intensity as grazing-mediated changes in vegetation structure can be pervasive in the system (Etchebarne and Brazeiro, 2016; Six et al., 2016, 2014) with expected influence on the avifauna (Donald et al., 1998), particularly for grassland specialist birds (Azpiroz et al., 2012b; Azpiroz and Blake, 2016; Dias et al., 2017). Lastly, despite the overall lack of use of tree plantations by grassland-dependent birds in afforested landscapes, our results indicated that generalist birds and a selection of forest species benefitted from plantations, many of which were the same species displaying increased dominance across plantations in similar studies (Brazeiro et al., 2018; Dias et al., 2013; Jacoboski and Hartz, 2020; Phifer et al., 2017). Thus, evaluating alternative measures to further enhance plantation use by a broader suite of forest species considering practices within both stand and landscape-level perspectives (Greene et al., 2016; McFadden and Dirzo, 2018; Nájera and Simonetti, 2010) merit future investigation.

4.4. Conclusion

The value of commercial forestry to biodiversity has often been reduced to dichotomic arguments with analogies such as “green deserts” (Bremer and Farley, 2010), or conservation “oxymoron” (Brockhoff et al., 2008). As knowledge accumulates regarding the functional roles of managed forests and ecological responses of the organisms using these systems, these overly simplistic terms may start to be discarded (Brockhoff et al., 2013; Horák et al., 2019). Nevertheless, our study

reinforces the value of plantations to local biodiversity is contingent on the nature of the original ecosystem, particularly on the ecological requirements of the taxa whose habitat is being transformed. In the Campos, grassland bird specialist assemblages are regionally declining due to a combination of factors that diminish and fragment grassland landscapes (e.g., crop agriculture and afforestation), and further degrade the remaining natural and seminatural grassland patches (i.e., overgrazing) (Azpiroz et al., 2012b; Medan et al., 2011). Thus, specialist birds dependent on grasslands would be suitable targets of conservation and management in production systems. As such, given the infrequent use of managed plantations by grassland birds, our results suggest that best conservation opportunities for grassland bird species in afforested systems might depend on larger and multiple landscape-level approaches rather than stand-level management of tree plantations in single landscapes and land ownerships. An integrative research agenda and science-based management at the population, community, and landscape levels would ensure the long-term persistence of grassland bird assemblages in the face of current and possible further expansion of afforestation in Uruguay and in the Campos.

CRedit authorship contribution statement

Juan Andrés Martínez-Lanfranco: Conceptualization, Methodology, Investigation, Formal analysis, Project administration, Funding acquisition, Writing – original draft. **Francisco J. Vilella:** Conceptualization, Methodology, Resources, Project administration, Funding acquisition, Supervision, Writing – review & editing. **Darren A. Miller:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are particularly indebted to M. J. Rodríguez-Cajaville and A. E. Rhördanz-Rosa for invaluable help during bird and vegetation sampling. Sonia and Kike's hospitality and friendship made the field experience even more memorable. We thank S. Rush, C. Brooks, and R. Iglay for their feedback on earlier versions of this work. We are grateful to R. (Bob) Bilby from Weyerhaeuser Company for his integral support of this project. Personnel from Weyerhaeuser Co. Uruguay J. P. Posse, L. Ingaramo, J. Castro-Baroffio, J. Martínez, and F. Irureta helped on all aspects of the field logistics, same as personnel from CAMBIUM Forestal Uruguay Juan Elhordoy. We thank the financial support received for this project from Weyerhaeuser Company, The Rufford Foundation, Cleveland Metroparks Zoo and Cleveland Zoological Society, and the Department of Wildlife, Fisheries, and Aquaculture at Mississippi State University, USA. Lastly, two anonymous reviewers provided valuable comments that improved the clarity of the manuscript.

Funding

This work received financial support from Weyerhaeuser Company, The Rufford Foundation (Grant No. 12961-1), Cleveland Metroparks Zoo and Cleveland Zoological Society, and the Department of Wildlife, Fisheries, and Aquaculture at Mississippi State University, USA. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.119765>.

org/10.1016/j.foreco.2021.119765.

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