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Juan Andrés Martínez Lanfranco

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Ecology and conservation of bird assemblages in native and afforested environments in
the Northern Campos Grasslands of Uruguay

By

Juan Andrés Martínez Lanfranco

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Wildlife, Fisheries and Aquaculture
in the Department of Wildlife, Fisheries and Aquaculture

Mississippi State, Mississippi

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2017

Ecology and conservation of bird assemblages in native and afforested environments in
the Northern Campos Grasslands of Uruguay

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Commercial forestry has expanded across the Rio de la Plata Grasslands (RPG) of South America in recent decades. I conducted a resource-use based study on bird communities during the 2013-2014 austral breeding season in northern Uruguay. I assessed relationships between habitat types and bird abundance as a function of vegetation structure. To compare avian responses to treatments, I included native environments, pine and eucalyptus plantations of different ages and thinning regimes. I detected differences in species richness and composition and species-specific responses in abundance along structural gradients sampled. Although poorer in species than native habitat types, tree plantations were extensively used by birds. Birds associated with plantations were primarily habitat generalists and forest dependent species, with low incidence of grassland specialists. Results of my study provide baseline information for stand-level management and future landscape design of timber plantations to benefit conservation of bird communities in afforested landscapes in the RPG.

DEDICATION

To my parents, Alejandro and Silvana, for their unconditional love and support, whose guidance always included freedom to pursue my own journeys, to whom I owe all opportunities I have had and that shaped who I am. They also gave me the best brothers and friends, Peque and Gugui, to whom I also dedicate this thesis.

"Without fundamental change in our behavior, we're doomed, as are all other life forms on this, our one and only spaceship, Planet Earth."

-- Pianka, E. R.

"The top environmental problems are selfishness, greed, and apathy. To deal with those, we need a spiritual and cultural transformation..."

-- Speth, G. J.

"Everyone thinks of changing the world, but no one thinks of changing himself."

-- Tolstoy, C. L. N.

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CHAPTER I

GENERAL INTRODUCTION

Land-use and land-cover change are two of the most pervasive components of human-induced global environmental change, with broad inter-related consequences on Earth's biogeochemical cycles, climate, ecosystem function and biodiversity (Vitousek 1994, Hooper et al. 2012). Land-use change reflects shifts in human use of natural resources, while land-cover change involves changes to physical and biotic properties of an area (e.g. conversion of native grasslands to tree plantations) and modifying conditions within a given vegetation cover type (e.g. selective logging in forests) (Meyer and Turner 1992). These processes may result in habitat loss, fragmentation, and degradation with concomitant negative effects on biological communities (Fischer and Lindenmayer 2007). Landscape alteration is recognized as primary driver of current and projected biodiversity loss at local, regional and global scales (Newbold et al. 2015).

Intensity and spread of human-induced change of the biosphere have prompted using terms such as "Anthropocene", implying that such impacts are comparable to those witnessed during distinct geologic periods (Corlett 2015). The sustained human alteration of natural ecosystems has led to the widespread emergence of novel ecosystems (sensu Hobbs et al. 2006, 2009) and the persistence of altered ecological conditions. In the face of current and projected global changes, conserving biodiversity beyond protected area networks will be required to conserve ecological and evolutionary processes that generate

and maintain biological diversity (Butchart et al. 2015). Thus, improved understanding of pattern and process in anthropogenic landscapes will improve managers' abilities to characterize habitat and species' conservation needs (Lindenmayer et al. 2008).

Global market forces of an expanding world economy, and sociopolitical and cultural constraints, play a key role in directing the nature and geography of land-use and land-cover change (Lambin et al. 2001). Much research has focused on biodiversity consequences of habitat loss, degradation and fragmentation in native forested ecosystems, especially in the tropics (Gardner et al. 2010). However, the worldwide conversion of native grasslands, savannas and other open-type vegetation environments to alternative uses, and the consequent effects on biodiversity and ecosystem function, have received considerably less attention (Hoekstra et al. 2005, Bond and Parr 2010, Parr et al. 2014, Veldman et al. 2015a). For example, temperate grasslands represent approximately 8% of earth's terrestrial surface and nearly 20% of all grassland biomes, and are considered the most modified and endangered (Henwood 2010). Nevertheless, they exhibit the lowest level of formal protection and representation within protected areas among all continental biomes (Hoekstra et al. 2005). Existing knowledge gaps on ecosystem dynamics of grassland biomes, market forces, and forest-centered views of conservation preclude effective management strategies of these imperiled ecosystems worldwide (Bond and Parr 2010, Putz and Redford 2010, Veldman et al. 2015a, b, c, Bond 2016).

Neotropical grasslands face similar conservation challenges and management needs (Carvalho and Batello 2009, Grau and Aide 2008, Grau et al. 2014, Overbeck et al. 2007, 2015). The Rio de la Plata grasslands (RPG) of South America (Fig. 1.1) represent

the most extensive grassland ecosystem in the Neotropics, encompassing nearly 700,000 km² in southern Brazil, Uruguay and eastern Argentina (Soriano et al. 1991, Paruelo et al. 2007). Two sub-regions are recognized within the RPG based on climate, geomorphology and soil characteristics; conditions that are mirrored by differences in vegetation floristics and physiognomy, and include the temperate 'Pampas' grasslands and the subtropical 'Campos' grasslands (Soriano et al. 1991, Bilenca and Miñarro 2004). Within these sub-regions, landscape change dynamics have varied as a consequence of different biophysical characteristics of the land and human dimensions such as policy, market trends, and technological advances (Baldi et al. 2006, Paruelo et al. 2006, Baldi and Paruelo 2008, Vega et al. 2009, Redo et al. 2012). Recent land cover data (2001-2013) has shown that most cropland expansion and intensification in Latin America, both within readily converted areas and as newly established crops on native grassland areas, occurred in the RPG (Graesser et al. 2015). Up to 55% of the RPG has been transformed to alternative land uses and what remains has been affected by livestock grazing and anthropogenic fire since early European settlement in the mid-16th century (Soriano et al. 1991, Azpiroz et al. 2012), and likely remains as an active agricultural frontier (Redo et al. 2012, Graesser et al. 2015).

Conversion of native grasslands to cultivated fields and grazing pastures has been the single most dominant form of landscape change in the RPG. In recent decades, however, there has been an expansion of large scale commercial forestry in areas originally devoted to cattle grazing in the Campos of Uruguay and southern Brazil, where the greater expanses of semi-natural grasslands remain (Overbeck et al. 2007, Vega et al. 2009, Azpiroz et al. 2012). The process of establishing tree plantations on native non-

forested ecosystems such as grasslands is termed afforestation (Veldman et al. 2015c). Planting small stands of non-indigenous trees has been a traditional practice in the past on the RPG, either for livestock shelter, firewood, or windbreaks. However, regional and global demand for forest products, high tree growth rates, high economic returns, and national land use policies have favored establishing and expanding of commercial tree plantations in recent years (Geary 2001, Overbeck et al. 2007, Morales-Olmo and Siry 2009, Redo et al. 2012). For example, in Uruguay, development and implementation of Forest Law in the 1990's established subsidies and tax incentives for investors and identified "soils of forest priority" (~20% of country area), which are designated as soil types of poor quality for conventional agriculture and suitable for tree planting (Mendell et al. 2007, Cespedes-Payret et al. 2009). At present, more than 1.5 million hectares have been afforested in the Campos grasslands of Uruguay and southern Brazil with pine (*Pinus* spp.) and eucalyptus (*Eucalyptus* spp.), with approximately one million hectares in Uruguay alone (Gautreau 2014).

Commercial afforestation represents the most notable form of land cover change in these grassland ecosystems (Paruelo et al. 2007, Paruelo 2012), and remains controversial due to its potential effects on ecosystem services and biodiversity (Geary 2001, Jobbágy et al. 2006, Cespedes-Payret et al. 2009, Paruelo 2012, Vassallo et al. 2013). Plantations established in native grasslands represent a "novel ecosystem" for plant and animal communities adapted to open environments that naturally present low tree cover (Overbeck et al. 2007, Six et al. 2014, Bernardi et al. 2016), as they represent a markedly different structural and functional vegetation cover type (Veldman et al. 2015b, c). Plantations may provide suitable habitat for some native forest taxa, especially where

plantations occur in forest-dominated ecosystems (Brockerhoff et al. 2008, Felton et al. 2010). However, where plantations replace native grassland ecosystems, afforestation may have negative consequences to grassland biodiversity (Veldman et al. 2015b, c, Bond 2016).

Large-scale conversion of native grasslands to alternative land uses due to recent intensification of agricultural practices and afforestation have been identified as major drivers of declining biodiversity over the RPG (Di Giacomo and Krapovickas 2005, Medan et al. 2011, Azpiroz et al. 2012). For example, populations of several breeding grassland birds have markedly declined in the region. Species such as the Pampas Meadowlark (*Sturnella defilippii*), Strange-tailed Tyrant (*Alectrurus risora*), Saffron-cowled Blackbird (*Xanthopsar flavus*) and Black-and-white Monjita (*Xolmis dominicanus*) have exhibited population declines and range contractions (Azpiroz et al. 2012). Also Nearctic long-distance migrant birds like the Bobolink (*Dolichonyx oryzivorus*) and the Swainson's Hawk (*Buteo swainsoni*) use RPG as wintering habitat (Di Giacomo and Krapovickas 2005). Populations of these species have declined in North America and evidence suggests that decreased survival on wintering areas could be contributing to documented declines (Vickery et al. 1999).

Most studies on avian responses to landscape and habitat changes over the RPG have been conducted in areas devoted to agriculture, pasture, and semi-natural grazed lands (Azpiroz et al. 2012 and references herein). However, despite the notable expansion of plantations during the past two decades over the RPG, especially in the Campos, research on afforested landscapes has been scarce. Recent studies focused on eucalyptus plantations only, were based on a narrow range of succession stages (i.e., a single age

class), have not included varying management practices, and have not assessed changes in habitat structure explicitly (Filloy et al. 2010, Dias et al. 2013, Phifer et al. 2016, Jacoboski et al. 2016). In summary, bird communities and patterns of species diversity have not been fully characterized in Campos grasslands under different land use practices and management regimes, and studies are particularly lacking within tree plantations. Information on bird ecology in afforested landscapes is needed to better understand and manage these novel ecosystems so that they can meet both production and conservation goals.

To better understand bird communities in afforested landscapes of the RPG, I developed a comparative bird-habitat approach to assess avian use of plantations in the Northern Campos grasslands of Uruguay. Working hypotheses and expectations for this research were based on the role of vegetation structure or physiognomy as a primary driver of bird community structure patterns (MacArthur 1964, Willson 1974, Roth 1976, Wiens and Rotenberry 1981, James and Wamer 1982), and on previous work on bird diversity in afforested landscapes (Allan et al. 1997, Lantschner et al. 2008, Filloy et al. 2010, Lipsey and Hockey 2010, Dias et al. 2013, Phifer et al. 2016, Jacoboski et al. 2016). I expected bird assemblages to respond to varying habitat characteristics in measurable attributes such as species richness, community composition, and abundance because vegetation structure varies markedly across native habitat types, versus plantations, and along the afforestation cycle from early succession stages through stand maturity (Souza et al. 2013, Six et al. 2014). Afforestation involves replacement of native open vegetation environments with a markedly different structural vegetation cover type,

thus expected to result in reduced incidence and abundance of grassland bird species while likely benefiting habitat generalists and forest species.

To evaluate the role of vegetation structure on bird diversity in the Campos, I first characterized bird diversity and composition in native environments and plantations, including representative forest management stages, and related bird community parameters (richness, evenness and composition) to habitat structure (Chapter II). Second, I developed bird-habitat models for selected avian species to describe plantation use and assessed importance of structural attributes influencing bird abundance patterns (Chapter III). Bird conservation in afforested grassland ecosystems requires understanding of how communities, and focal species within communities, respond to varying structural characteristics along the forestry cycle. As such, this study will generate information on relative value of plantations for native bird assemblages. This research was part of Weyerhaeuser's Global Timberlands Technology collaborative research program: "Quantifying the environmental effects of afforestation in Uruguay", designed to develop science-based management practices to minimize environmental and biodiversity effects of grassland afforestation in the country.

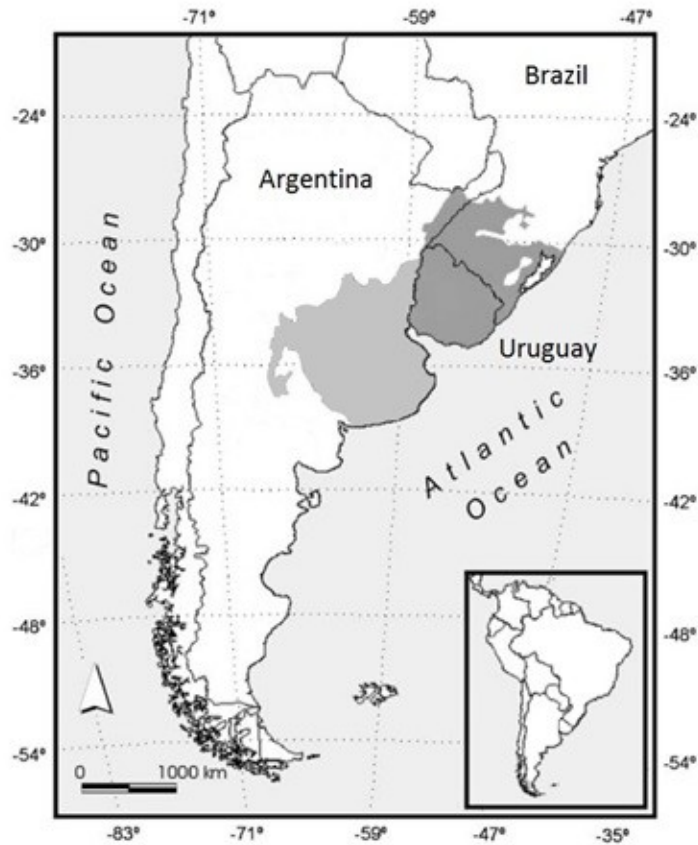


Figure 1.1 Map of the Río de la Plata Grasslands (RPG) in southeastern South America.

Within the RPG, two sub-regions are recognized: the Campos (dark gray) and the Pampas (light-gray). Figure modified from Baldi et al. (2006).

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CHAPTER II
AVIAN DIVERSITY AND COMPOSITION IN NATIVE ENVIRONMENTS AND
TREE PLANTATIONS IN THE NORTHERN CAMPOS GRASSLANDS
OF URUGUAY

Introduction

Expansion of commercial forestry represents a primary driver of landscape alterations in the Rio de la Plata grasslands (RPG) in recent years. Over 1.5 million hectares of the Campos sub-region of this prominent Neotropical grassland biome have been converted to intensively managed eucalyptus or pine plantations (Gautreau 2014). These plantations have become an integral component of the landscape in some areas of the Campos grasslands, especially in northern Uruguay (Geary 2001, Six et al. 2014). Establishing commercial tree plantations in grassland ecosystems involves replacing open, grass-dominated environments with stands of exotic, fast-growing trees (Phifer et al. 2016). Tree plantations represent a markedly different structural and functional vegetation cover type than the native grasslands where they are being established, which in turn has direct consequences to ecosystem processes and biodiversity (Veldman et al. 2015).

Despite concerns about environmental consequences of commercial forestry over the RPG, bird diversity research in this system has been minimal compared to bird work related to traditional land uses such as cattle grazing and agriculture (Azpiroz et al.

2012b). Grassland bird conservation in afforested landscapes requires understanding how bird assemblages respond to environmental conditions imposed by forestry practices along the entire rotation. The forestry cycle elicits changes in habitat structure concomitant with succession of tree development and management practices (e.g., thinning), from grass-dominated young plantation stages to older, closed tree-dominated vegetation (Jones et al. 2012, Six et al. 2013, 2014). These structural changes in the vegetation will be reflected on the structure of bird communities (Tews et al. 2004). Thus, I predicted that traits of bird assemblages such as species richness, evenness, and composition would differ across environmental gradients defined from native conditions to plantations, and along plantations of different species, age classes, and management regimes.

The main objective of this chapter was to quantify bird community patterns of diversity and species composition in native habitat types and plantations in the Northern Campos grasslands of Uruguay. Herein I focused on the following research questions: (1) how does bird species diversity and composition vary across native environments and tree plantations at different stages of succession and management practices? and (2) how does the physiognomy of vegetation along these environmental gradients affect bird community structure?

Methods

Study area

I conducted my study in the Provinces of Tacuarembó and Rivera (31° 29' S, 55° 40' W) in the Northern Campos grasslands of Uruguay (Fig. 2.1), located within the Campos sub-region of the Río de la Plata Grasslands (Soriano et al. 1991). The region is

found within the "North Quebradas and Grasslands" Important Bird Area (IBA; Devenish et al. 2009) of Uruguay. The general climate pattern was humid subtropical with hot summers and mild winters (Essenwanger 2001). Annual and seasonal temperatures, precipitation patterns, and soil characteristics for the study area were summarized by Six et al. (2013, 2014). Topography was undulating and dominated by grasslands with interspersed rocky outcrops and flat hills (or "mesas") rarely exceeding 200 m elevation. Drainages and swales formed low depressions scattered across the landscape and were dominated by moist grasslands and shallow water wetlands and marshes, with or without woody components. Grasslands located at higher elevations were referred as to hilltop or upland grasslands and some included isolated native trees. Native forest was mostly confined to riparian areas and along rivers and streams (gallery forests), though elevated hillsides and cliffs retained dryer native forest cover.

The study was based primarily on lands owned and managed by Weyerhaeuser Company Uruguay, and comprised over 16,500 hectares in Tacuarembó and Rivera Provinces. Other properties included lands from Cambium Forestal Uruguay Company (5,042 hectares) interspersed within Weyerhaeuser lands in Tacuarembó. In total, the study area included more than 100,000 hectares (Fig. 2.1). Commercial tree stands were planted in flooded gum (*Eucalyptus grandis*; hereafter, eucalyptus), native to Australia, and loblolly pine (*Pinus taeda*; hereafter, pine) native to the southeastern United States. Eucalyptus were planted upslope given their frost intolerance and poor growth in water saturated soils; pines were planted at lower elevations, closer to floodplains (Six et al. 2013, 2014).

Sampling design

I used a stratified sampling approach to select bird and vegetation sample points within native and afforested habitat types during the austral winter (August-September) of 2013 (Table 2.1). To select sampling points along transects (hereafter, clusters of points), I constructed a spatial database and determined proportion of each habitat type using ArcMap 10 (ESRI 2011) and GME 0.7.2.1 (Beyer 2012). I placed sampling points 200–250 m apart and minimum 50 m from edges to accommodate a 50 m radius circular point. Clusters contained 7–9 points as this was the maximum number a single observer could conduct in a morning sampling session (0600–0900). Whenever necessary, I adjusted point locations in the field and georeferenced them using portable GPS units. Sampled environments included native habitat types represented by upland (UG) and lowland (LG) grasslands, native forests (NF), and tree plantations of eucalyptus and pine (Fig. 2.2). The rotation cycle was 12–15 years for eucalyptus and 18–20 years for pine.

I further stratified plantations by age class and management regime across a gradient of plantation age with the following eucalyptus categories: newly planted (EA, planted 2012–2013, thus ~1 year old; excluded from cattle grazing), mid-rotation (EB, planted 2006–2007: ~7 year-old), an intermediate stage to EA and EB (EI, planted 2010: 3 years-old), and pre-harvest or mature plantations (EC, planted 2002: 11 years-old). Pine categories included mid-rotation (PB, planted 2004–2006: ~9 years-old) and mature stands (PC, planted 1997–1999: ~16 years-old). Within mature pine plantations, I included three thinning practices: systematic removal of the fifth row (PCrW), also called line or row thinning, and selective extraction of trees (PCrC), two commonly used thinning approaches (Toyoshima et al. 2013) that represented operational differences on

Weyerhaeuser and Cambium companies, respectively, and unthinned mature plantations (PCnr) present within Weyerhaeuser. Thus, the chronosequence of managed forest succession secured for sampling was representative of current dominant land use in northern Uruguay (Table 2.1, Fig. 2.2), with the exception of newly planted pine and post-harvest stands of both eucalyptus and pine as those were not available in the study area. I will further refer to these conditions or vegetation associations indistinctly as vegetation types or habitat types following Daubenmire (1968), acknowledging that there are long-standing disagreements on the proper use of habitat-related terms in the ornithological and wildlife management literature (Block and Brennan 1993, Hall et al. 1997, Jones 2001, Krausman and Morrison 2016).

Vegetation surveys

I quantified vegetation structure at all sample point locations. I included grassland-specific (Fisher and Davis 2010) and forest-specific (McElhinny et al. 2005) measures of vegetative structure. I used the point-intercept method (Floyd and Anderson 1987) to determine percent cover of life forms (i.e. herbaceous and non-herbaceous vegetation classes), coarse woody debris, and other dead plant material, by randomly placing four 20-m long ropes in each cardinal direction, centered at point location, with markings every meter totaling 80. I determined cover class in vertical projections at every mark and recorded height in centimeters. I estimated the vertical profile at sample locations as the percent of a 1.8-m by 20-cm board, divided into six 30-cm sections, that was visually obstructed by vegetation (dead or alive). I placed the board at point center of each plot and quantified the area covered by vegetation at 20% increments for all six

intervals in eight cardinal directions standing 20 m away from and viewing it from a height of ~1m above ground level (Nudds 1977).

Additionally, at points within plantations and native forests, I used a spherical densiometer (Forestry Suppliers, Jackson, MS; Convex Model A) to estimate canopy closure at each cardinal direction 10 m from point center. I obtained tree height (m) using a clinometer from eight trees, the two closest at 10 and 20 m from point center along the rope in each cardinal direction. Further, I measured diameter at breast height (DBH) of the same trees (in centimeters), and counted number of trees in each semicircular quadrant to estimate stand basal area (McElhinny et al. 2005). I averaged measurements for each variable within points. For habitat types other than native forests, I also counted number of native trees taller than 2 m and/or DBH greater than 5 cm but were not included on basal area estimates.

Bird surveys

During October 2013 to April 2014, encompassing a full breeding season (Azpiroz 2003), I used standard methods for surveying land bird communities (Ralph et al. 1993). Within circular 50 m fixed-radius plots, I recorded all birds heard or seen within 10 minute point count periods. Two trained observers performed all surveys from sunrise until three hours after sunrise. I noted birds flying overhead during counts but these were not included in analyses unless they were directly using (e.g., feeding, searching) the habitat type being surveyed. I did not conduct surveys during heavy precipitation, fog, or when winds exceeded 20 km/h. I visited each point up to 3 times during the survey season. To reduce bias in bird detection related to the order of visiting

sites, I randomly selected order of points to be surveyed within clusters and rotated observers conducting subsequent visits to the same clusters.

Statistical analysis

I used raw bird point count data for bird diversity and community composition analyses. Detection-uncorrected counts and derived relative abundance indices are widely used in bird community-level studies and monitoring programs (Johnson 2008, Nichols et al. 2009), especially in situations where study objectives rely on relative community-level variability rather than on absolute abundance estimates (Banks-Leite et al. 2014). Unless otherwise noted, I performed all data analysis using functions from the *vegan* package (Oksanen et al. 2015) in program R (R Core Team 2015). I considered statistical tests significant at $\alpha = 0.05$.

I aggregated point level vegetation information by taking the mean values for each variable across sampling points in the same cluster. I performed Principal Component Analysis (PCA) in software PAST v.3.06 (Hammer et al. 2001) on the standardized variables and selected the correlation matrix option (Legendre and Legendre 1998). To select number of components to be retained for interpretation, I used the broken-stick random model approach (Peres-Neto et al. 2003) as a null against which compare my empirical data. I visualized ordination as distance bi-plots and projected the original axes (i.e., vegetation variables) in a scatter graph representation. Projection of a point at right angles from a vector variable approximates its position within the gradient defined by that variable, and the length of the vector signals contribution of that variable to the multivariate environmental space. I used minimum convex polygons to delineate the different habitat types on the ordination axes.

For bird diversity and multivariate analysis, I calculated maximum abundance value for each bird species recorded across all visits per point (Toms et al. 2006). I calculated observed richness as the maximum number of species registered by pooling all sample points from the same habitat types. I used accumulation curves constructed from abundance-based data using an asymptotic non-parametric first-order jackknife estimator to calculate expected number of species per habitat type, which is also a way to standardize for sample size (Colwell and Coddington 1994). Jackknife species richness estimators were developed within population capture-recapture models to estimate population size as a community-level analog for the total number of species in the sample (Burnham and Overton 1979, Boulinier et al. 1998), which provides good performance regarding bias, precision and accuracy (Walther and Moore 2005). I evaluated completeness of the bird species inventory by habitat type as a percentage of observed versus expected species richness. Traditional composite diversity indices such as Shannon and Simpson indices confound species richness (number of species in the community) and evenness (abundance distribution among species) into a single, unit-less quantity (Hurlbert 1971, Purvis and Hector 2000), and are sensitive to sample size (Gotelli and Colwell 2001). Thus, I performed comparisons of species richness and evenness separately across habitat types and used individual-based rarefaction to control for differences in overall abundance (James and Rathbun 1981, Gotelli and Colwell 2001).

Non-parametric extrapolators of richness estimate the asymptote of the species accumulation curve. In contrast, rarefied estimates are always within the range of the data, as it is an interpolation method, and give estimates lower than observed richness

values. Numerous indices have been derived for assessment of evenness or equitability of ecological communities (Tuomisto 2012). I calculated Hurlbert's probability of inter-specific encounter (PIE; Hurlbert 1971), which yields the probability that two randomly sampled individuals represent two different species. Using PIE overcomes some of the limitations of traditional diversity indices as the outcome from this analysis is not influenced by sample size and is mathematically linked to abundance-based rarefaction as it represents the initial slope of the curve (Olszewski 2004). More equitable assemblages are represented by communities with higher PIE values. I used re-sampling algorithms implemented in EcoSim 7.72 (Gotelli and Entsminger 2012) with 9,999 Monte Carlo iterations, to calculate point rarefied estimates of species richness and PIE. I rarefied point estimates to 176 individuals as this was the smallest number of birds counted for any habitat type (PCnr, unthinned mature pine). I used non-overlapping 95% confidence intervals (CI) of point estimates as conservative criterion of statistical difference (see Colwell et al. 2012).

I assessed variation in bird species composition among and within habitat types with variance partitioning methods, and along continuous environmental gradients with ordination techniques, using multivariate measures of pair-wise ecological distances (Anderson et al. 2011). I used Bray-Curtis distance as a measure of dissimilarity given its supported suitability for multivariate abundance data, particularly for stressing changes in composition and relative abundance while ignoring joint absences (Faith et al. 1987, Clarke et al. 2006). I aggregated point level bird data across clusters summing abundance of each species and converted it to relative frequency by dividing by the number of points per cluster. I only included species recorded in $\geq 5\%$ of points for at least one habitat type

(70 out of 110 species, Table A.1) and square root transformed relative abundance data to minimize importance of very rare and overly abundant species respectively (Legendre and Legendre 1998).

To assess differences in species composition among habitat types, I used the *adonis* function to perform non-parametric multivariate analysis of variance (PERMANOVA) with 9,999 permutations (Anderson 2001, McArdle and Anderson 2001). This approach is a distance-based, distribution-free analog to the classic multivariate analysis of variance (MANOVA) (Warton et al. 2012, Anderson and Walsh 2013). I used software PAST v.3.06 to generate pair-wise tabulated comparisons and applied Holm's sequential Bonferroni correction procedure to avoid inflation of Type I error rate given multiple testing (Roback and Askins 2005, Aho 2014). I conducted PERMANOVA analysis on both squared-rooted relative abundance and incidence data (presence/absence) to disentangle influence of compositional and/or and relative abundance shifts on uncovered differences (Anderson et al. 2006, 2011).

I used the *betadisper* function to perform analysis of multivariate homogeneity of group dispersions or variances (PERMDISP), a nonparametric analog to test for homoscedasticity (Anderson 2006), to examine within-group variation (within each habitat type) of bird species composition (Anderson et al. 2006). This routine calculates Euclidean distance from site clusters to group centroid in multivariate space. I thus assessed pair-wise differences of multivariate dispersions using parametric Tukey-Kramer honest significance difference test (HSD) to control family-wise Type I error (function *pairw.anova* in *asbio* package, Aho 2015). To visualize these analyses beyond the dichotomy of hypothesis testing, I calculated mean between and within group

dissimilarity values with function *meandist* and constructed a dendrogram of the resultant matrix using a hierarchical clustering algorithm with function *hclust*. The branching pattern of the dendrogram reflects mean dissimilarity between groups and the vertical position of terminal nodes reflects mean within-group dissimilarities (Legendre and Legendre 1998).

To explore bird species composition patterns along habitat types and environmental gradients, I used function *metaMDS* to perform non-metric multidimensional scaling ordination (NMDS, Kruskal 1964a), an indirect gradient (unconstrained) analysis technique. This ordination approach uses iterative algorithms to maximize rank-order correlation between the dissimilarity matrix and Euclidean distances in multivariate ordination space. Because NMDS can use any resemblance measure and is based only on ranks, it can handle non-linear species' responses to underlying environmental gradients and it is more robust than other ordination methods that rely on linearity assumptions (Minchin 1987, Legendre and Legendre 1998). I relied on Shepard diagrams and stress statistic of goodness-of-fit to determine the most appropriate number of dimensions (d) leading to reliable representations of site/cluster scores in multidimensional space. Stress values ranging 10–20% are considered a fair representation of the data (Kruskal 1964b). However, caution is urged on values at the higher end of that range (Clarke 1993). Whenever possible, I balanced choice of best solution in two or three dimensions by keeping stress below 15%. When retaining three-dimensional solutions, I only presented a bi-plot with the first two axes. Verification of other combinations yielded consistent results. I performed separate bird ordinations to

focus on different relationships whenever strong clustered situations required closer examination.

I used the *ordiellipse* function to create 95% dispersion ellipses to map cluster scores by habitat type. Degree of overlap between ellipses is indicative of between-group similarity in species composition, while its relative sizes are indicative of within-group variation (Anderson 2001, Anderson et al. 2006). I also assessed the linkage between bird species composition and vegetation structure attributes within the unconstrained framework of NMDS (Clarke 1993). Sites with similar habitat structure are expected to possess similar bird species composition, so that the match of site ordination (conveying bird compositional information) and vegetation structure attributes could be evaluated via correlation analysis (Clarke 1993). I tested significance of correlations using the *envfit* function with 9,999 permutations for each habitat variable regressed on the ordination axes. This function scales the vector length to its individual correlation coefficient to visually identify the most important gradients in the NMDS plot. I also used *ordisurf* function to plot selected habitat attributes (e.g., herbaceous cover) onto ordination space as smoothed surfaces.

To assess bird use of plantations, I classified all detected species according to their degree of habitat specialization with respect to open areas and forests (Zurita et al. 2006, Kennedy et al. 2017). I used published information (Azpiroz 2003, Azpiroz 2012, Azpiroz et al. 2012b) and my own field experience to classify birds into three general categories: a) non-forest species (e.g., grasslands and shallow wetland species, including obligate and facultative grassland birds), b) habitat generalists using a wide array of habitats types and conditions, including open woodland, savanna and edge forest species,

and c) forest dependent species. I assigned species that could not be defined as specialists of either grasslands or forests to the "generalist" category. Further, I mapped species scores onto the site ordination specifying expected habitat affiliation. In this framework, species pairs with shorter inter-point distances were more similar in their habitat preferences than those located more apart in the graph, and sites closer to a given species score exhibited the greater relative abundance for that species.

Results

I assessed vegetation structure characteristics on 613 different sample points across native environments and tree plantations (Table 2.1). The PCA ordination reflected strong vegetation structure gradients along the chronosequence of tree plantations and management regimes and structural differences of plantations compared to native forests. Based on 8 habitat structure variables (herbaceous and non-herbaceous cover, leafy and woody debris, visual obstruction, tree height, basal area and canopy cover), the first three axes from the PCA ordination of plantation types and native forests attained clear separation between groups and accounted cumulatively for ~90.2% of total variation in the data (Fig. 2.3a, Table 2.2). The first PCA axis explained 62% of the variation and separated two main sets of conditions along positive scores of the axis. One included unthinned mature pine (PCnr), selectively thinned mature pine (PCrC) and mid rotation eucalyptus (EB), where variable loadings were higher for leafy litter cover, basal area and tree height. The other set scored lower for those variables and represented mature eucalyptus (EC), mid-rotation pine (PB) and systematically thinned mature pine (PCrW). Despite being composed of plantations of different species, age class and thinning condition, there was structural convergence within both sets, as the former

exhibited more closed canopies, very low herbaceous cover percent, and lower visual obstruction readings while the latter had more opened canopies, hence higher coverage of life forms. Along negative scores of the first axis, dominated by visual obstruction and cover of life forms, newly planted eucalyptus (EA) emerged at the negative end of the axis, and a cluster composed of intermediate eucalyptus (EI) and native forest towards the origin. The second (18% of explained variability) and third axes (10% of explained variability) were dominated by herbaceous cover, woody debris and canopy closure, tree height, woody debris and non-herbaceous cover, respectively. Both axes (Fig. 2.3b) separated habitat types within the sets recognized along the first component. Native forests differentiated clearly from all plantation types and were characterized by highly structured understory, higher non-herbaceous cover, and more closed canopies. Newly planted eucalyptus (EA), despite regularly spaced growing trees, remained structurally more similar to native grasslands as being open-type vegetation dominated conditions, with higher cover of herbaceous vegetation and lower cover of leaf and wood debris in older plantations (Fig. 2.2). Within native grasslands, lowland grasslands (LG) presented higher herbaceous height (66.2 ± 7.7 cm vs. 27.6 ± 4.4 cm; mean \pm SE) and higher number of native trees (inter-quartile range: 5–18 vs. 0–3 trees) than upland grasslands (UG).

During 2013-2014 breeding season, observers completed 1,573 bird counts (i.e., 10-min visits) on 613 different sample points along 109 different clusters (Table 2.1). During these systematic surveys, observers recorded 4,184 individuals representing 110 bird species in 32 families and 15 orders, of which 90 were resident species and 20 were summer breeding migrants. Of these, 26 species were classified as grassland species, 47

as habitat generalists, savanna or edge species, and 37 as forest species. The aggregation of species counts across visits at same points (i.e., maximum abundance per species) resulted in 3,446 individual bird records (Table A.1). The Rufous-collared Sparrow (*Zonotrichia capensis*) was the most common species overall, present across all habitat types sampled and representing ~30% of all individual records. Within plantations, Rufous-collared Sparrow displayed the highest relative abundance in all types except mid-rotation eucalyptus (EB), where it was ranked second. Within native habitat types this species had the highest abundance in lowland grasslands (LG) and was second in abundance in upland grasslands (UG) and native forests (NF). The House Wren (*Troglodytes aedon*) was the second most frequently recorded species overall with ~10% of total records. Within plantations, the House Wren had the second highest relative abundance in all but in mid-rotation eucalyptus (EB) and unthinned mature pine plantations (PCnr). No other species accounted for more than 4% of all individual counts. Two grassland specialist species, the Straight-billed Reedhaunter (*Limnortyx rectirostris*) and the Grass Wren (*Cistothorus platensis*), considered threatened ("Vulnerable") in Uruguay under IUCN criteria (Azpiroz et al. 2012a), were recorded at lowland and upland grasslands sites respectively, and two others classified as "Near Threatened", the Burrowing Owl (*Athene cunicularia*) and Wedge-tailed Grass-Finch (*Emberizoides herbicola*), were recorded in upland grasslands. No species of conservation concern were registered in plantations.

Observed number of species (Table 2.3) was greater in native habitat types (range 42–69 species) than plantations (range 21–32 species). Extrapolated point estimates of species richness (Jack-1, Fig. 2.4a) indicated that native habitat types had greater number

of species (range 61–87 species) than plantations (range 28–44 species). Further, inventory completeness was greater for plantations (range 73–83%) than for native environments (range 69–79%) as number of unseen species, given by the difference between estimated and observed richness, was greater for native habitat types (Table 2.3). In addition, the steepest increase of rarefied species accumulation curves for native conditions as compared to plantations (Fig. 2.4c) indicated that, had sampling continued, new species would accumulate in native habitat types at higher rates and numbers than in plantations. Comparisons at equal levels of abundance confirmed that native habitat types were richer in species than plantations, shown by higher asymptotes (Fig. 2.4b and 2.4c). On the other hand, evenness did not show a dichotomy between native conditions versus plantations (Fig. 2.5, Table 2.3). Estimates of Hulbert's PIE showed that evenness was significantly higher in native communities and in two particular plantation types (range 0.91–0.95), mid-rotation eucalyptus (EB) and not thinned mature pine (PCnr), than in the other plantation treatments (range 0.75–0.88). The fraction of the assemblage represented by the most abundant species ranged 13–24% for the former, more even group, contrasting with 41–46% for the latter, less equitable group.

After retaining only those species recorded on at least 5% of bird survey points, the resulting data matrix for species composition analysis consisted of 70 species in 109 clusters of points. Of these species, 14 (20%) were classified as open-habitat or grassland species, 28 (40%) as closed-habitat or forest species, and 28 (40%) as habitat generalists (Table A.1). Native habitat types and plantation types all differed in bird species composition (PERMANOVA, Bray-Curtis distance: $F_{10, 108}=8.9$, $P<0.01$); all pair-wise combinations were significant after correcting for multiple comparisons. However, when

I employed the incidence matrix I found that mid-rotation eucalyptus (EB) was not different from mature eucalyptus (EC) plantations, nor did I find differences across pine plantations. Further, native habitat types showed greater multivariate dispersions overall, hence higher within-group variation in bird species composition than plantations, which were more homogeneous (Fig. 2.6). In plantations, newly planted and mid rotation eucalyptus (EA and EB) showed higher within-group dispersions than other types. On the other hand, native forests (NF) and lowland grasslands (LG) showed similar dispersions and were lower than in upland grasslands (UG).

Mean between and within dissimilarity values calculated across habitat types provided an initial representation of relationships among groups in terms of species composition beyond the uncovered statistical differences across all conditions (Fig. 2.7). Pine plantations clustered together (38–44% dissimilarity), with pines and older eucalyptus forming a more inclusive cluster (38–58% dissimilar), which in turn clustered with newly planted eucalyptus (38–71% dissimilar). Plantations clustered with lowland grasslands, hence more similar in bird composition, than to upland grasslands or native forests. Greatest dissimilarity was documented between upland grasslands (UG) and native forests (NF) (93% dissimilar), while the most similar habitat types were mid-rotation pine (PB) and systematically thinned mature pine (PCrW) (38% dissimilar).

The NMDS ordination of the full environmental gradient yielded an optimal solution in three dimensions with stress value 0.12 (Fig. 2.8). There was a clear separation between native grasslands and native forests along the first axis, and native habitat types and plantations along the second axis. Ordination was strongly correlated with vegetation structure variables (Table 2.4), where the first axis was dominated by

herbaceous cover, sharply decreasing from left to right towards forested habitat types. Visual obstruction and non-herbaceous vegetation cover on the second axis increased along negative scores towards native conditions, while afforestation characteristics such as leafy and coarse woody debris cover were higher along positive scores. Tight clustering of site scores by plantation types required further exploration and the new matrix excluding native habitat types was composed of 46 species in 65 clusters. NMDS ordination of plantations converged on three dimensions with stress 0.14 (Fig. 2.9) and exhibited a marked environmental gradient (Table 2.5). The first axis displayed separation within the chronosequence of eucalyptus plantation types along the first axis, with some overlap between the two youngest age classes (EA and EI). Mid-rotation eucalyptus (EB) appeared at the end of positive scores and mature eucalyptus (EC), the oldest eucalyptus age class, presented between younger conditions. The second axis separated overall eucalyptus from pine plantations. Mid-rotation pine (PB) and both systematically and selectively thinned mature pine (PCrW and PCrC) overlapped and were placed closer to intermediate eucalyptus (EI) and unthinned mature pine (PCnr) separated well along negative scores. Considering the overlapping pine plantations, having excluded unthinned mature pine (PCnr), the data matrix included 33 bird species in 34 clusters. First two ordination axes ($d=3$, $stress=0.172$) displayed some degree of overlap between mid-rotation pine (PB) and intensively thinned pine (PCrW), which separated from selectively thinned mature pine (PCrC) along both positive scores of the axes (Fig. 2.10, Table 2.6).

Within the full environmental gradient ordination (Fig. 2.8), avian species associated with forest environments clustered along positive scores of the first axis,

particularly around native forests, and to a lesser extent with positive values along the second axis towards plantations. An opposite pattern characterized grassland species, with negative scoring along the first axis around native grasslands. Habitat generalist bird species scores were scattered along the ordination gradient, though appeared more centered in the graph and included native grasslands, mostly lowland grasslands (LG), and plantations. Only three of 14 grassland species included in the ordination dataset were present in the plantation ordination (Fig. 2.9), the Grassland Sparrow (*Ammodramus humeralis*), Blue-black Grassquit (*Volatinia jacarina*) and Red-winged Tinamou (*Rhynchotus rufescens*). These species scored along the negative end of the first axis and were present only within newly planted eucalyptus (EA) conditions, where herbaceous cover is the highest along plantations.

Discussion

Results of my study highlighted strong bird community responses to contrasting structural habitat conditions within native environments and plantations as illustrated by measures of species richness, evenness and composition. I found higher bird species richness in native forests than in pine or eucalyptus plantations regardless of age or management regime. Jacoboski et al. (2016) found a similar pattern comparing native forests and eucalyptus plantations in afforested grasslands in the Campos of southern Brazil. Harboring more avian species in native forests than plantations represents a general pattern across temperate and tropical forest-dominated ecosystems (Zurita et al. 2006, Calviño-Cancela 2013). Results of my study suggest this pattern could be extended to grassland-dominated ecosystems. Native forests are structurally more heterogeneous compared to plantations regardless of which is the dominant vegetation cover type.

Furthermore, I found higher bird species numbers in native upland and lowland grasslands than in plantations, similar to what was found across grazing lands, Espinal savannas and plantations in the Argentinean pampas of the RPG (Phifer et al. 2016). Lantschner et al. (2008) also reported a similar pattern where plantations replaced native steppe in Patagonia, where steppe exhibited higher richness.

In general, bird diversity within plantations is higher than in open pasture and agricultural land in forest-dominated ecosystems (Felton et al. 2010). Despite grasslands being characterized by simpler vertical structure compared to planted forests (Zurita and Belloq 2012), the structural homogeneity within plantations may elicit lower species richness than native open environments in the Campos (Dias et al. 2013). Previous bird work in the Campos grasslands showed higher bird diversity in native grasslands than agricultural land (Azpiroz and Blake 2009; da Silva et al. 2015). Comparative studies on plantations, agricultural lands and pasture are needed to better characterize diversity patterns across these contrasting land use types in the Campos.

Considering native environments, lowland grasslands presented the highest species richness. These sites were a mixture of grasslands and shallow-water wetlands, with high incidence of isolated native trees and woodlots of various sizes. Bird assemblages within these grasslands were composed of a mix of grassland, savanna and forest dependent species, holding higher cumulative richness compared to other native and planted conditions, likely as a reflection of this increased habitat heterogeneity (Hsu et al. 2010). Isolated trees have been identified as an important driver of farmland bird diversity (Fischer et al. 2010, Ambarli and Bilgin 2014) and can shape the diversity and

composition of bird assemblages in native grasslands such as in the Campos (Dias et al. 2014).

Estimates of species richness remained comparable across plantation types regardless of age class and thinning procedure. Jacoboski et al. (2016) also did not find differences in bird richness across eucalyptus age classes. Plantations exhibiting multiple vegetation strata, dense understory and multispecies canopy cover, are expected to have greater bird species richness than structurally homogenous, simpler plantations (Nájera and Simonetti 2009). However, fast growing, even-aged, regularly spaced plantations in the Campos have not been shown to promote differentiation of multiple forest strata, have undeveloped understories, and homogeneous forest canopies (Phifer et al. 2016, Jacoboski et al. 2016). Thus, even though plantation types in my study had varying structural characteristics linked to plantation age and thinning operations, the overall lack of structural complexity (sensu Nájera and Simonetti 2009) might explain the low species diversity and invariable species estimates across plantation types. Furthermore, tree species planted (eucalyptus or pine) had no effect on species richness. Pine plantations have shown to hold more species than eucalyptus where pines are native, while the opposite is true where eucalyptus are. The rationale for explaining these differences has been that the native versus exotic nature of plantations and the degree of "ecological integration" within native flora (Calviño-Cancela 2013). Because both pine and eucalyptus are exotic and functionally dissimilar to native forests in the RPG, neither seemed to provide any additional resources to birds sufficient to elicit a measurable response in species richness.

Despite richness not changing across plantation types, I found marked differences in measures of evenness. Anthropogenic disturbance on habitat conditions may elicit differences in abundance distribution across species along environmental gradients (e.g. across plantation types) while richness could remain insensitive to such changes (Hillebrand et al. 2008, 2017). Mid-rotation eucalyptus (EB) and unthinned mature pine (PCnr) exhibited similar greater values of evenness than other plantation types and were comparable to those of native habitat types. Both EB and PCnr exhibited relatively similar structure as stands were characterized by closed canopies and lack of woody debris. Both plantation types showed reduced numerical dominance of Rufous-collared Sparrow, leading to more equitable communities. Relative abundance patterns of the House Wren across plantations mimicked that of the Rufous-collared Sparrow. The Rufous-collared Sparrow nest predominantly on the ground and the House Wren uses mostly lower forest strata, so that the lack of cover and woody debris at EB and PCnr could be linked to diminished abundance of these species at those plantation types compared to the remainder of conditions that had more structured lower forest layers (see Chapter III). Phifer (2016) also found lower abundance of Rufous-collared Sparrow in mature eucalyptus plantations with closed canopies that similarly lacked understory structure. It is worth noting that, as most woody debris is a byproduct of thinning, older plantations with completely closed canopies and substantial woody debris were not available for sampling. As such, there could be some confounding at determining whether birds are responding to the lack of woody debris and understory development per se, and/or to other conditions linked to thinning and canopy openings (Lindenmayer and Hobbs 2004).

Species richness, a univariate measure of diversity, is used extensively in biodiversity studies. However, it may not be the best target measure to assess wildlife in managed landscapes and for setting conservation priorities because it does not consider species identities nor abundance shifts across species (Fleishman et al. 2006, Hillebrand et al. 2017). For example, high species richness could be the result of improved conditions for exotic, generalist, or non-target species. Furthermore, same levels of diversity could be attained within communities that present similar species but different numerical dominance across them, or between communities with completely different species assemblages (Sax et al. 2002).

Thus, multivariate measures that incorporate species composition (i.e. track the identities of the species composing the assemblage) and relative abundance may provide a better, complementary approach to inform conservation in human dominated landscapes (Fleishman et al. 2006, Filippi-Codaccioni et al. 2010). I found differences in bird species composition (species identities and/or relative abundance) across all native habitat and plantation types, reflecting characterized differences in vegetation structure across conditions and in agreement with similar studies (Lipsev and Hockey 2010, Hsu et al. 2010, Graham et al. 2015, Phifer et al. 2016). Not surprisingly, the most dissimilar bird assemblages were found between native grasslands and native forests, as these represented the most contrasting vegetation characteristics. However, bird assemblages were more similar within plantation types than to native environments. Among plantations, some differences were determined by shifts in abundance distribution across species only, rather than by changes in species composition itself. For example, there were no differences in the identities of bird species present across pine plantation types

regardless of plantation age or thinning practice. However, there were marked differences in relative abundance of species across pine plantations, as evidenced also by estimates of evenness, which were likely driving the uncovered differences found with compositional analysis. A similar pattern was found in mid-rotation and mature eucalyptus (EB and EC), having the same species but in different proportions. Hence, differences in bird community structure across older managed stands of pine and eucalyptus may have been mediated by alterations in relative abundance of species as a function of contrasting vegetation characteristics (Cramer and Willing 2005, Filloy and Belloq 2013). Overall then, bird community similarities reflected habitat structure similarities, as previously reported for birds in managed forests (Zurita et al. 2006, Filloy et al. 2010, Zurita and Belloq 2012).

I expected that species found in plantations would be a subset of the available native forest species pool (Jacoboski et al. 2016), but it turned out to be mostly generalist species that naturally occur in savanna-type environments and treed grasslands and wetlands with minor contribution of truly forest interior species. Most native forest species were only associated with native forest conditions. However, various species seem to be benefited by plantations as revealed higher incidence and relative abundance across plantation types compared to native environments. For example, White-spotted Woodpecker (*Veniliornis spilogaster*) occurred on pine plantation types only, while Glittering-bellied Emerald Hummingbird (*Chlorostilbon lucidus*) and Gilded Hummingbird (*Hylocharis chrysura*) occurred mostly in eucalyptus plantations. Other species were present mostly on plantations but were independent of tree species planted, such as the Roadside Hawk (*Rupornis magnirostris*). Interestingly, bird communities in

eucalyptus compared to pine were composed of different species assemblages, which cannot be explained by vegetation structure alone, at least not from the habitat structure measures included in this study. For example, mid-rotation eucalyptus (EB) and unthinned mature pine (PCnr) showed vegetation structural convergence yet, despite having similar bird species richness and evenness, exhibited different bird species assemblages. Differences in bird composition between eucalyptus and pine plantations have been reported in the literature and attributed partly to differences in flower production and bark texture, which may in turn affected incidence of bird guilds that rely on nectar and insects for feeding, respectively (Hsu et al. 2010, Calviño-Cancela 2013). Results of my study agreed with this observation as illustrated by, for example, greater relative abundance of hummingbirds (nectar feeders) and woodpeckers (bark-insect feeders) in eucalyptus versus pine plantations. Other species showed similar use of plantations and native forests, such as Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*) and Red-eyed Vireo (*Vireo olivaceus*). Overall, responses of native bird species to ecological conditions imposed by the forestry cycle is likely to be species-specific and related to degree of habitat and trophic specialization (Devictor et al. 2008, Ehlers-Smith et al. 2015), which was reflected in the structure of bird communities across habitat types with different structural (and functional) vegetation components.

Native habitat types showed greater within-group variation in bird species composition than plantation types. This simplification of bird assemblages, not only from native conditions to plantations but also within plantation types, was expected given the structural homogeneity characterizing plantations as opposed to the natural heterogeneity of native environments (Filloy et al. 2010, Jeliaskov et al. 2016). This argument also

applies to greater bird richness found in native environments versus plantations. At a regional scale, grassland afforestation has resulted in homogenization of bird communities across very different biomes with contrasting native vegetation communities such as the Atlantic Forest and RPG of South America (Fillooy et al. 2010). Basically, plantations promoted similarity of environmental conditions at distant sites, thus reducing beta diversity (i.e., species turnover) between otherwise dissimilar bird assemblages (Karp et al. 2012, Vázquez-Reyes et al. 2017). At a local scale, I found a similar pattern across my study sites, with simplified and less variable communities (reduced beta diversity) across plantations compared to native environments. Graham et al. (2015) found decreased beta diversity of birds in intensively managed conifer plantations versus open environments under lower levels of management intensity. The suite of structurally contrasting plantation types included in my study, which were homogeneous within, matched the uncovered bird community differentiation pattern, as bird assemblages differentiated across plantation types while exhibiting low within-group variation. Thus, despite simplification of communities with respect to native conditions, stand structural heterogeneity across the landscape promoted varying structure in bird communities (Lindenmayer and Hobbs 2004).

Interestingly, despite plantations having consistently less within-group variation than native habitat types, newly planted and mid rotation eucalyptus (EA and EB) were more variable than other plantation types, possibly owing to how these plantation types were defined. For example, newly planted eucalyptus included stands planted in 2012 and 2013, which in turn exhibited different tree heights. This structural variability within otherwise homogeneous plantation types may have influenced within-group variation in

bird composition present at EA and EB plantation types. Similarly, upland grasslands showed higher within-group variation in bird community composition relative to lowland grasslands or native forests. This may be a result of the lower incidence of isolated trees across upland versus lowland grasslands, hence the former having contrasting sets of treeless versus treed sites. Given the disproportionate effect of isolated trees on grassland bird communities (Fischer et al. 2010), this could account for the increased variation found within upland grasslands. These results highlighted the influence that vegetation characteristics could have at eliciting measurable responses on bird community structure.

While plantations were more similar to each other in bird species composition, assemblages in newly planted eucalyptus (EA) were more similar to grassland communities than any other plantation type. Early stages of tree succession are typically structurally similar to open environments (Six et al. 2014). Furthermore, newly planted stands were excluded from cattle that would otherwise eat the growing trees, which allows grasses and other herbaceous vegetation to grow higher than in adjoining native grazed sites. Therefore, newly planted stands are available to some species of grassland and savanna birds (Dias et al. 2013, Phifer et al. 2016), which may explain the similarities between grasslands and early succession plantations. However, I only detected three grassland species in young eucalyptus plantations and occurrence was low. Furthermore, suitability of habitat conditions for grassland birds will quickly diminish given the rapid tree growth and transition to older age classes, which are dominated by generalists and species associated with native forest environments. As a matter of fact, distinct vegetation structural differences between newly planted eucalyptus and more mature stand classes (e.g. EI) were attained in less than three years after planting, and no

grassland birds were recorded in older eucalyptus or pine stands. Interestingly, one of the mid-rotation pine stands in my study was surveyed for birds when newly planted (0–3 years) and several species of grassland specialist birds were recorded (Blumetto, unpubl. data). Pine rotations are longer in this system as growth rate is slower than for eucalyptus (Geary 2001), hence available conditions for grassland birds could extend for longer periods in pine than in eucalyptus plantations at early stages. Unfortunately, there were no newly planted pine stands available during my study to evaluate this. It is worth noting also that bird assemblages in newly planted eucalyptus were more similar to those from lowlands than to those from upland grasslands (Fig. 2.8). As a consequence, early plantation stages may not represent surrogate conditions for birds whose typical habitat is directly replaced by tree planting, i.e. upland grassland bird communities.

In sum, I found differences in community structure of bird assemblages across native environments versus plantations, and within different native and planted habitat types. These differences were a reflection of structural variation across habitat types, highlighting the role of vegetation physiognomy as a primary correlate of bird diversity and species composition patterns. Native environments were richer in number of species and more variable than plantations, likely a consequence of structural heterogeneity of native habitat types versus structural simplification and homogeneity found within plantations. Despite no change in richness across plantations, I detected shifts in the relative abundance of species and composition linked to differences in stand structural attributes that characterized age classes and thinning regimes, and functional differences between pine and eucalyptus. Bird assemblages of plantations were composed of habitat generalists, edge and forest species. Among plantations, open canopy stands were the

most similar to grasslands. Hence, as plantation structure can be manipulated with predictable bird community responses, this information will assist stand management practices designed to benefit a subset of the native bird community. Lastly, given a negligible incidence of grassland birds across plantations, best conservation opportunities for grassland specialist birds within afforested landscapes may rely on management of unplanted grassland areas at the landscape level, rather than on standard forestry practices at the stand level.

Table 2.1 Sample point allocation per habitat type for bird and vegetation sampling during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Sp. Planted	Year	Age	Habitat type	Site	Visit	Point	Cluster
Eucalyptus	2012-13	~1	EA	PB	39	13	2
				MO	42	14	2
				GA	45	15	2
				SS1	21	7	1
				NA	48	16	2
Eucalyptus	2010	3	EI	SS4a	30	10	1
				MO	24	8	1
				PE	27	9	1
				CA	18	6	1
				SS1a	18	6	1
Eucalyptus	2006-07	~7	EB	LCWa	66	22	3
				SS4b	75	25	3
				PE	21	7	1
				HO	42	14	2
Eucalyptus	2002	11	EC	AR	84	28	4
				CA	84	28	4
Pine	2004-06	~9	PB	MO	48	16	2
				LCWb	108	36	5
Pine	1998	16	PCnr	LCWc	84	28	4
				SS1b	42	14	2
Pine	1997-99	~16	PCrC	LCC	147	49	7
				LT1	45	16	2
				LT2	42	14	2
Pine	1997-99	~16	PCrW	LCWd	84	28	4
				LP1	35	14	2
				LP2	84	28	4
				NF	45	45	16
				LG	67	48	15
				UG	58	49	13
Totals					1,573	613	109

Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG). Note the nested structure of bird point counts (each visited up to three times) within clusters of points at different replicate sites.

Table 2.2 Variable loadings for first three axes of principal component analysis (PCA) of vegetative structure variables for plantation types and native forests sampled 2013-2014 in the Northern Campos Grasslands of Uruguay.

	PC 1	PC 2	PC 3
Gcov	-0.317	-0.550	-0.093
Zcov	-0.322	0.410	0.449
Hcov	0.414	0.121	-0.313
Rcov	0.280	-0.415	0.592
Vobs	-0.390	0.333	0.089
Treeh	0.359	-0.029	0.517
Canopy	0.316	0.480	0.086
Barea	0.408	0.028	-0.244

Vegetation variables: Gcov - herbaceous cover percent; Zcov - non-herbaceous cover percent; Hcov - pine/eucalyptus leaf debris cover percent ; Rcov - pine/eucalyptus woody cover percent; Vobs - visual obstruction; Treeh - tree height; Canopy - canopy closure percent; Barea - basal area.

Table 2.3 Diversity statistics per habitat type for bird communities sampled during 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Habitat type	Ind.	Obs. S	Extrap. S (CI)	IC(%)	Raref. S (CI)	PIE (CI)
EA	337	32	44 (37-51)	73	25 (21-29)	0.76 (0.72-0.80)
EI	178	21	28 (22-34)	75	21 (20-21)	0.75 (0.75-0.76)
EB	203	26	32 (27-37)	81	25 (24-26)	0.92 (0.91-0.93)
EC	266	27	35 (29-40)	77	24 (21-26)	0.88 (0.86-0.89)
PB	380	32	43 (35-51)	75	25 (21-29)	0.8 (0.76-0.84)
PCnr	176	23	28 (24-32)	83	23 (NA)	0.91 (NA)
PCrC	307	23	29 (24-34)	80	20 (16-22)	0.78 (0.74-0.81)
PCrW	598	26	33 (27-39)	79	20 (17-23)	0.79 (0.74-0.83)
NF	379	49	62 (54-70)	79	40 (36-44)	0.95 (0.94-0.96)
LG	409	64	87 (74-99)	74	48 (42-53)	0.94 (0.92-0.95)
UG	213	42	61 (50-71)	69	40 (37-42)	0.95 (0.94-0.95)

References: Ind. - total number of individuals; Obs. S - observed species richness; Extrap. S - estimated total number of species (Jack-1); IC - inventory completeness; Raref. S - individual-based rarefied species richness; PIE - individual-based point rarefied estimate of probability of specific encounter. 95% CI are in parenthesis; not appropriate for the reference sample (i.e. 176 individuals in PCnr). Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

Table 2.4 Correlation (r^2) of vegetation structure variables with full environmental gradient ordination axes from non-metric multidimensional scaling (NMDS, Bray-Curtis distance; $d=3$, stress=0.124) analysis of species composition for bird communities sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

	NMDS1	NMDS2	r2	P-value
Gcov	-0.919	-0.395	0.656	***
Hcov	0.597	0.802	0.484	***
Rcov	0.358	0.934	0.440	***
Vobs	0.139	-0.990	0.352	***
Zcov	-0.072	-0.997	0.209	***

Vegetation variables: Gcov - herbaceous cover percent; Hcov - leafy debris cover percent; Rcov - woody debris cover percent; Vobs - visual obstruction; Zcov - non-herbaceous cover percent. P-value codes: *** $P < 0.001$.

Table 2.5 Correlation (r^2) of vegetation structure variables with plantation ordination axes from non-metric multidimensional scaling (NMDS, Bray-Curtis distance; $d=3$, stress=0.138) analysis of species composition for bird communities sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

	NMDS1	NMDS2	r2	P-value
Hcov	0.735	0.678	0.648	***
Barea	0.492	0.871	0.612	***
Vobs	-0.665	-0.747	0.595	***
Canopy	0.805	-0.593	0.584	***
Treeh	0.980	-0.198	0.529	***
Gcov	-0.920	-0.392	0.517	***
Zcov	-0.417	-0.909	0.449	***
Rcov	0.922	-0.386	0.107	*

Vegetation variables: Hcov - pine/eucalyptus leaf debris cover percent; Barea - basal area; Vobs - visual obstruction; Canopy - canopy closure percent; Treeh - tree height; Gcov - herbaceous cover percent; Zcov - non-herbaceous cover percent; Rcov - pine/eucalyptus dead branches cover percent. P-value codes: *** $P < 0.001$, * $P \leq 0.05$.

Table 2.6 Correlation (r^2) of vegetation structure variables with pine plantations ordination axes from non-metric multidimensional scaling (NMDS, Bray-Curtis distance; $d=3$, stress=0.172) analysis of bird communities sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

	NMDS1	NMDS2	r2	P-value
Barea	0.484	0.875	0.505	***
Hcov	0.507	0.862	0.464	***
Treeh	0.094	0.996	0.446	***
Canopy	0.620	0.785	0.445	***
Gcov	-0.344	-0.939	0.411	**
Vobs	-0.704	-0.711	0.358	**
Rcov	-0.737	-0.676	0.271	*
Zcov	-0.575	-0.818	0.170	.

Vegetation variables: Barea - basal area; Hcov - pine/eucalyptus leaf debris cover percent; Treeh - tree height; Canopy - canopy closure percent; Gcov - grass cover percent; Vobs - visual obstruction; Rcov - pine/eucalyptus dead branches cover percent; Zcov - other green vegetation cover percent. P-value codes: *** $P < 0.001$, ** $P < 0.01$, * $P \leq 0.05$, . $P > 0.05$.

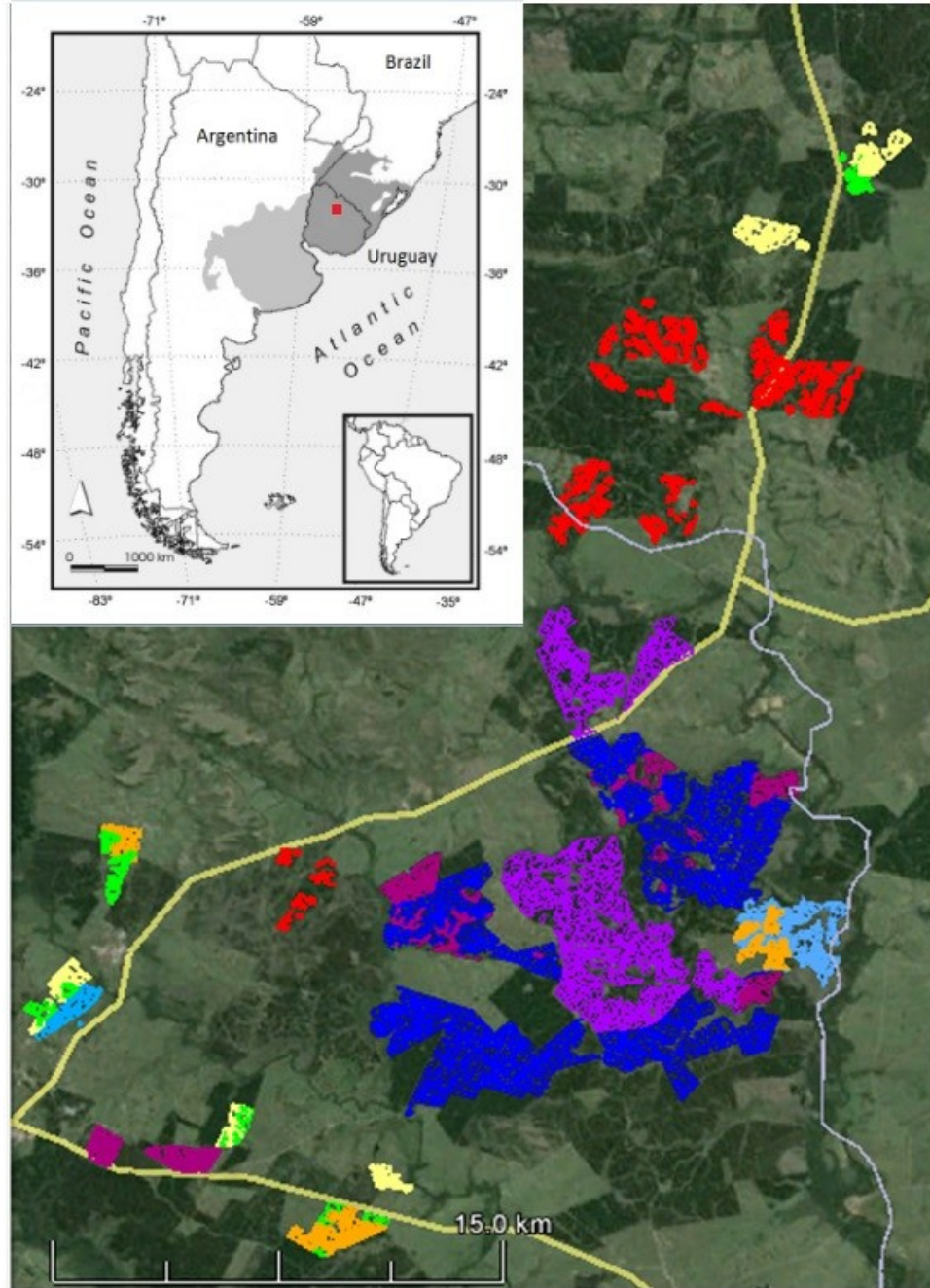


Figure 2.1 Map of study region in the Northern Campos Grasslands of Uruguay.

The RPG are depicted in gray in the regional map: Pampas grasslands (light gray) and Campos Grasslands (dark gray). Forested habitat types: newly planted eucalyptus (EA, yellow), intermediate eucalyptus (EI, neon green), mid-rotation eucalyptus (EB, orange), mature eucalyptus (EC, red), mid-rotation pine (PB, light blue), unthinned mature pine (PCnr, violet), selectively thinned mature pine (PCrC, lilac), systematically thinned mature pine (PCrW, blue). Yellow lines are major highways. Gray line represents Tacuarembó River.



Figure 2.2 Habitat types sampled during the 2013-2014 bird breeding season at study site in the Northern Campos Grasslands of Uruguay.

Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

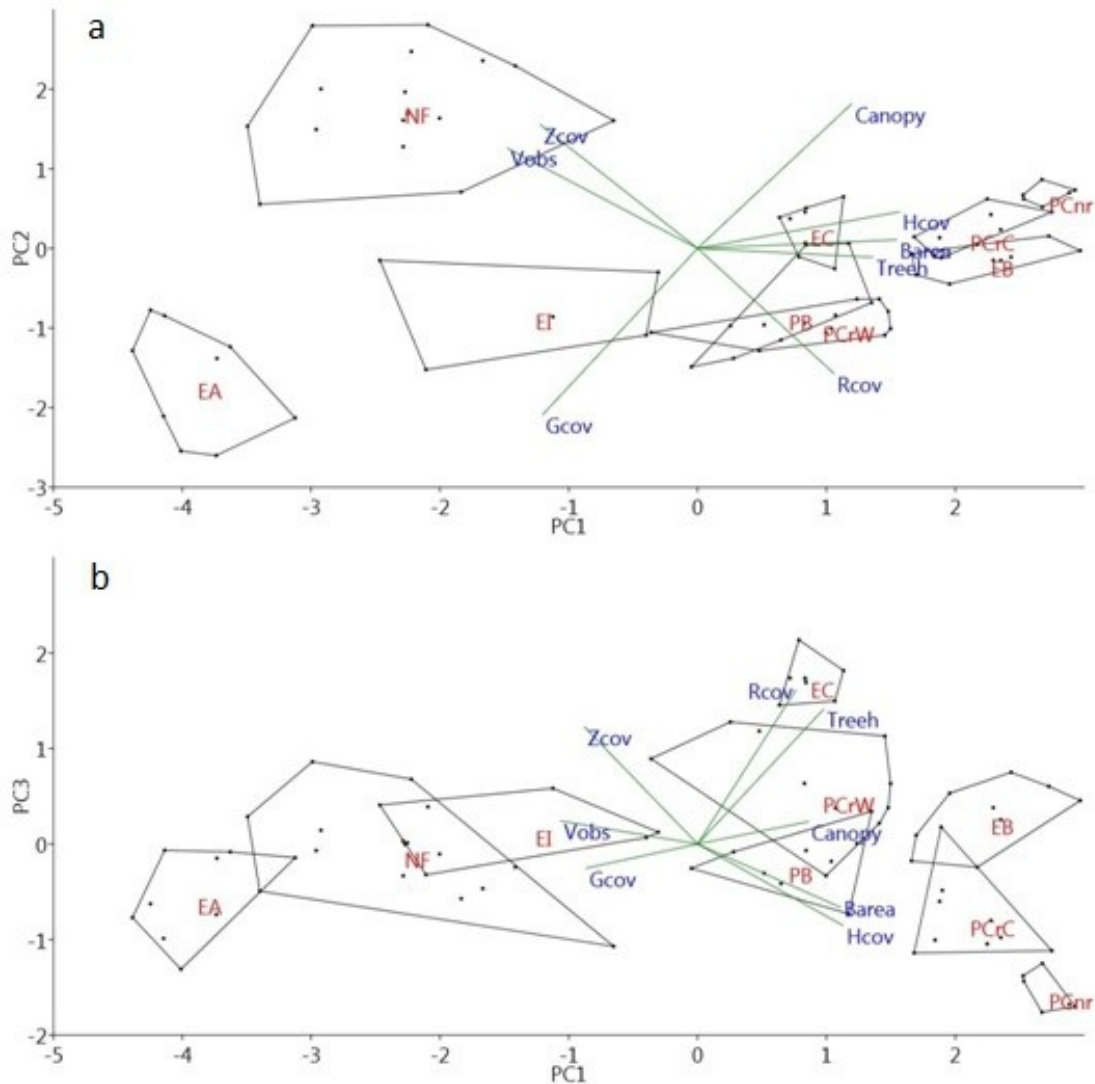


Figure 2.3 Ordination plots from principal component analysis (a: PC1 vs. PC2, b: PC1 vs. PC3) of vegetation characteristics for plantation types and native forests sampled 2013-2014 in the Northern Campos Grasslands of Uruguay.

Polygons depict habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG). Vectors represent vegetation variables: Barea - basal area; Hcov - pine/eucalyptus leafy debris cover; Treeh - tree height; Canopy - canopy closure; Gcov - herbaceous cover; Vobs - visual obstruction; Rcov - pine/eucalyptus woody debris cover; Zcov - non-herbaceous cover.

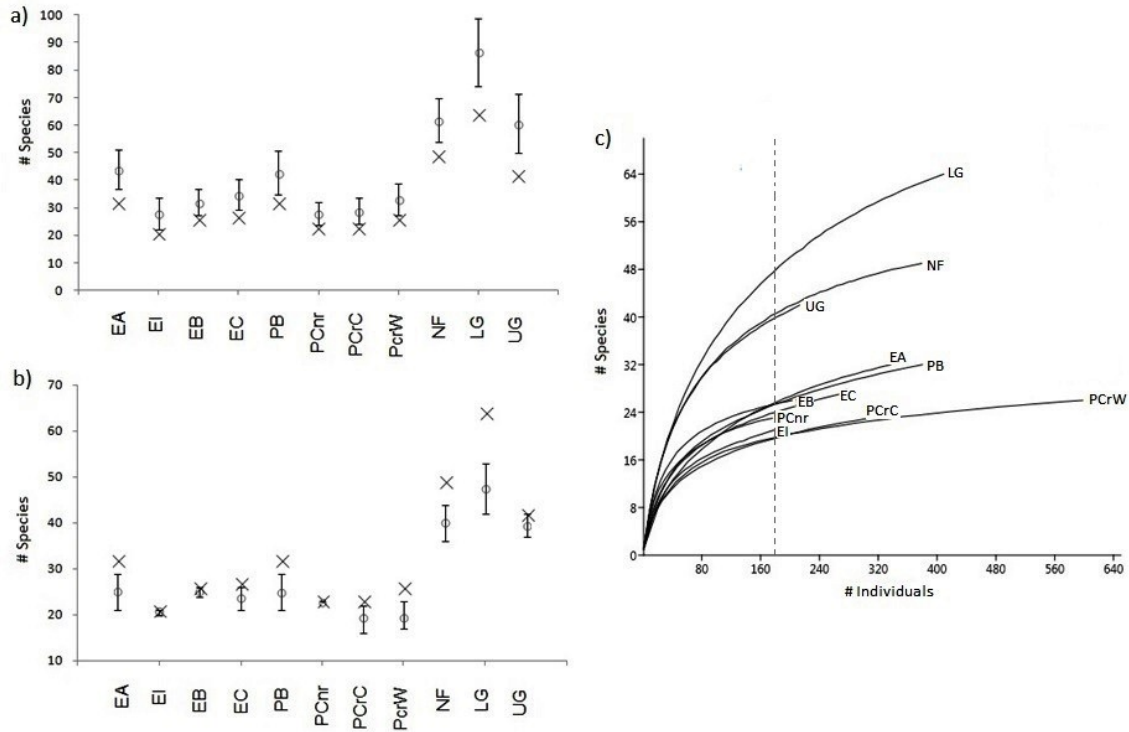


Figure 2.4 Extrapolated (a) and rarefied (b) point estimates (○) of bird species richness per habitat type, and species accumulation curves (rarefaction method) for habitat types sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

'x' in a) and b) indicates the observed number of species in each habitat type. Error bars are 95% CI. "Dashed line" in c) represent the number of individuals (176) in the reference sample (PCnr) to which species richness estimates are rarefied to. Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

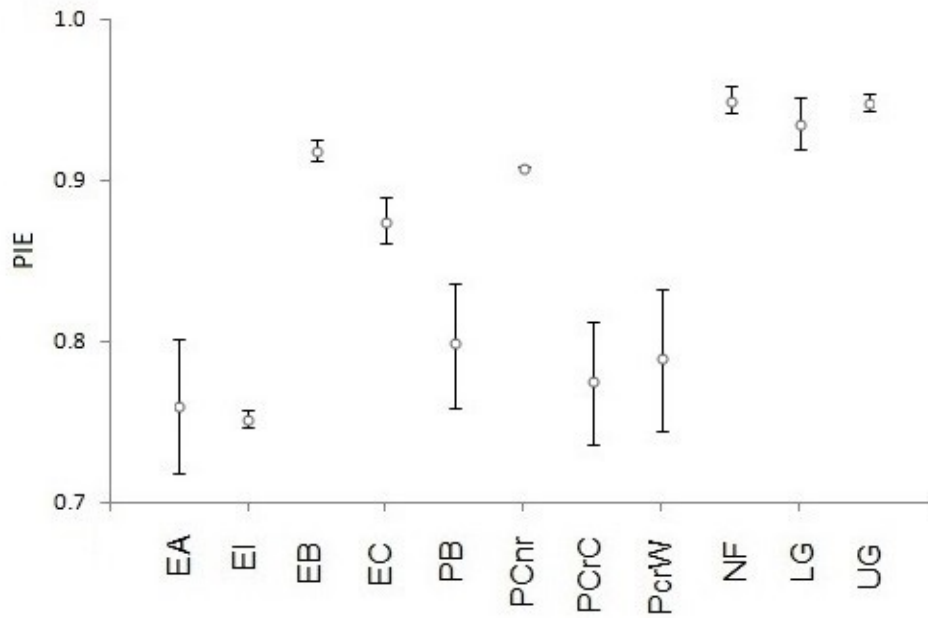


Figure 2.5 Individual-based rarefied point estimates (○) of Hulbert's probability of interspecific encounter (PIE) with 95% CI for bird communities sampled across habitat types during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Error bars are 95% CI. PCnr represents the reference sample with the minimum number of individuals detected. Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

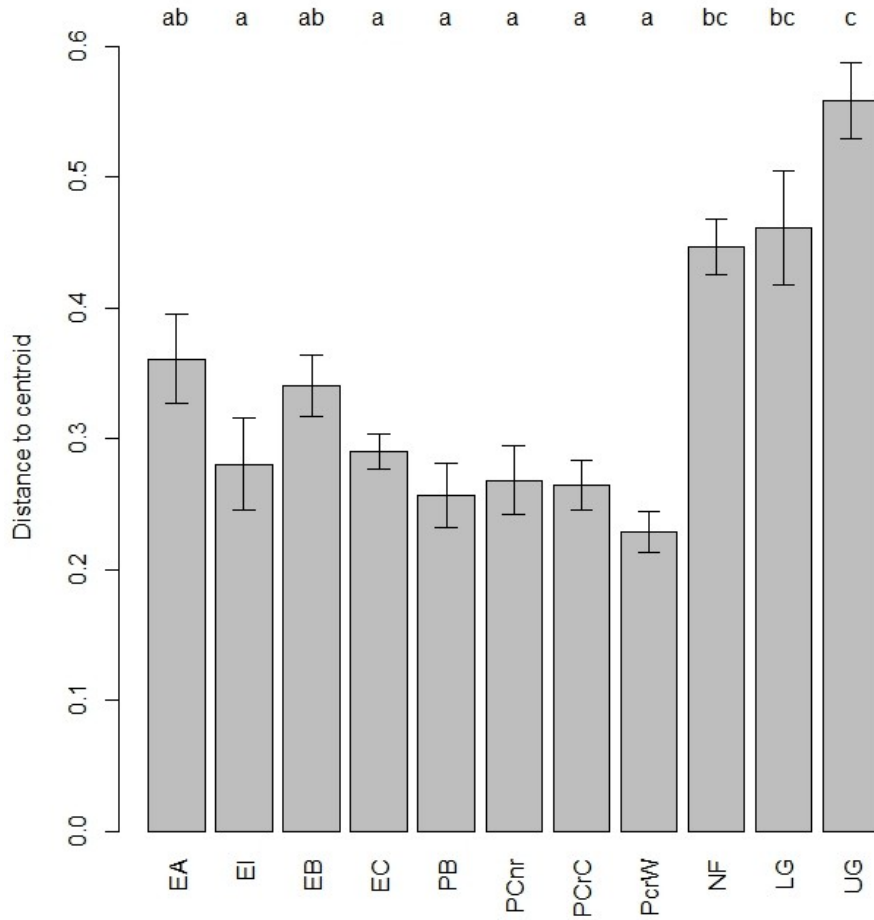


Figure 2.6 Mean distance to centroid in multivariate analysis of within-group variance based on bird species composition (Bray-Curtis distance) per habitat type sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Error bars are standard errors. Group mean with different letter code are significantly different under Tukey-Kramer HSD method. Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

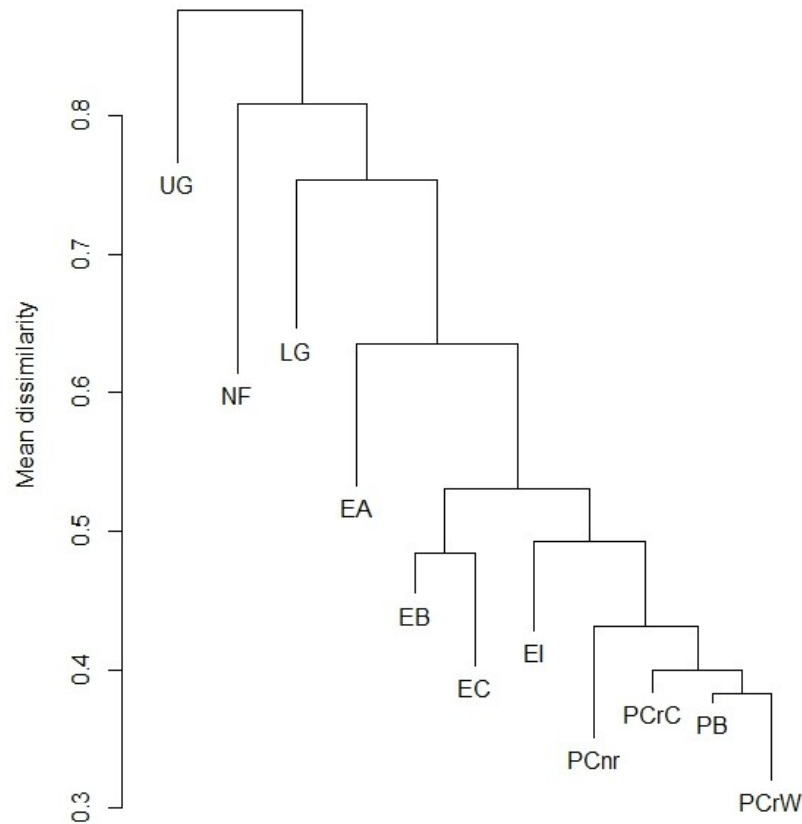


Figure 2.7 Dendrogram of bird community relationships based on mean between and within-group dissimilarity (Bray-Curtis distance) across habitat types sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).

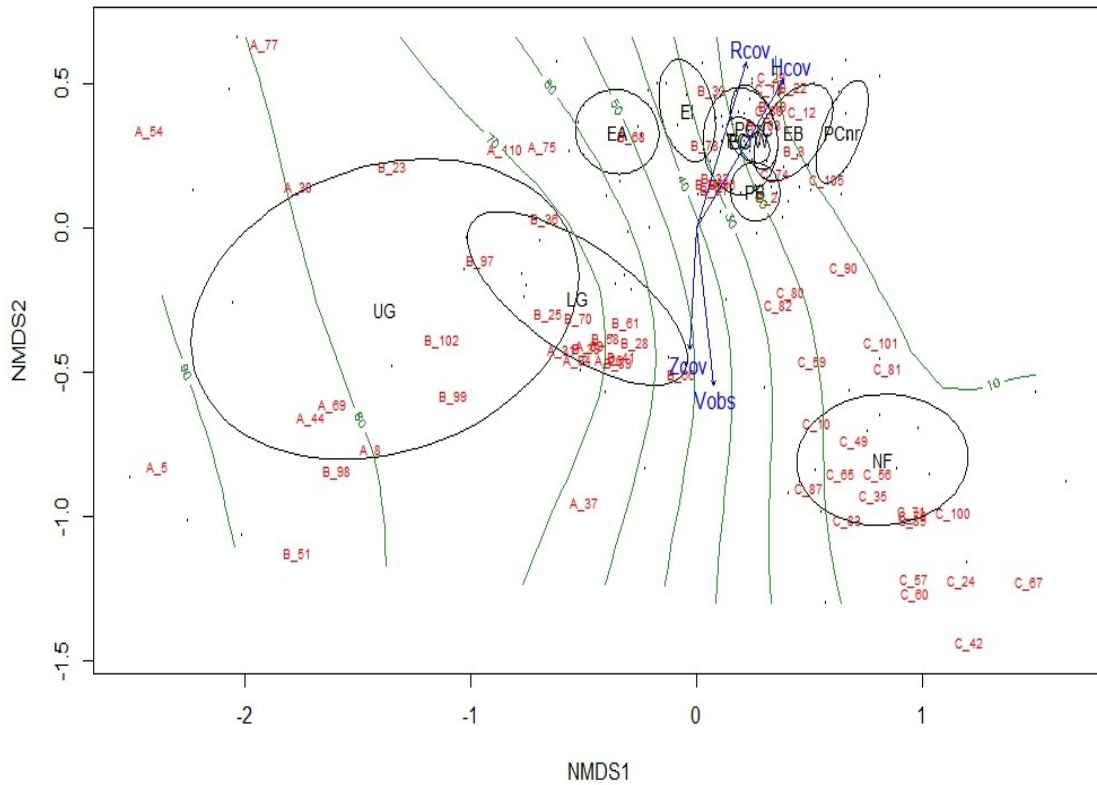


Figure 2.8 Ordination plot for non-metric multidimensional scaling (NMDS) for bird species composition (Bray-Curtis distance) across the full environmental gradient ($d=3$, stress=0.124) sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Habitat types are depicted with 95% CI ellipses: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG). Black dots and alpha-code in red represent site/cluster and bird species scores along ordination axes, respectively. Species codes concatenates habitat preference code and species identification number separated by "_". Environmental gradients are represented with fitted surface for herbaceous cover percent and as vectors for other vegetation structure variables: Rcov - woody debris cover; Hcov - leafy debris cover; Vobs - visual obstruction; Zcov - non-herbaceous cover.

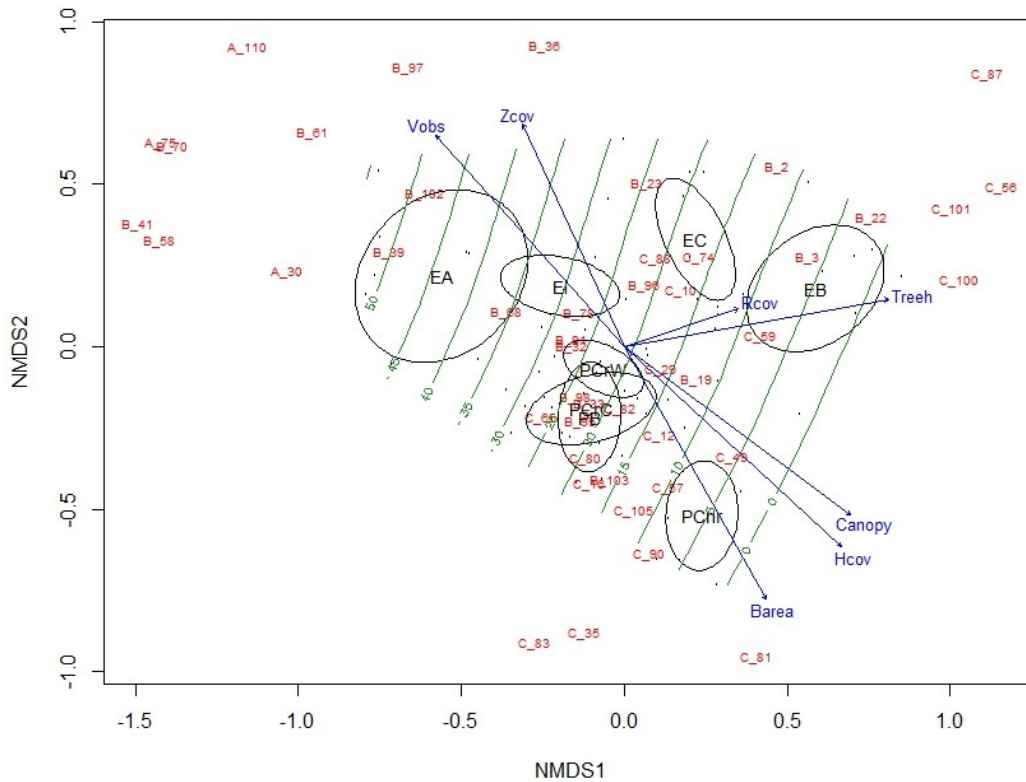


Figure 2.9 Ordination plot for non-metric multidimensional scaling (NMDS) for bird species composition (Bray-Curtis distance) for tree plantations (pine and eucalyptus) ($d=3$, stress=0.138) sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Habitat types are depicted with 95% CI ellipses: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW). Black dots and alpha-code in red represent site/cluster and bird species scores along ordination axes, respectively. Species codes concatenates habitat preference code and species identification number separated by "_". Environmental gradients are represented with fitted surface for herbaceous cover percent and as vectors for other vegetation structure variables: Vobs - visual obstruction; Zcov - non-herbaceous cover; Rcov - pine/eucalyptus woody debris cover; Treeh - tree height; Canopy - canopy closure; Hcov - pine/eucalyptus leafy debris cover; Barea - basal area.

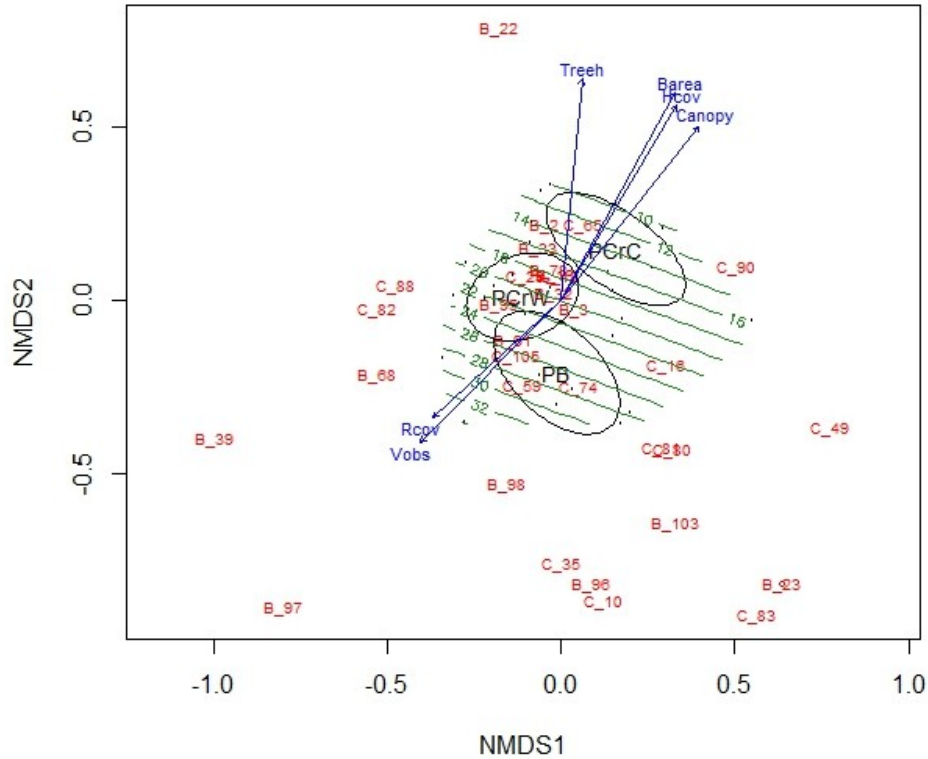


Figure 2.10 Ordination plot for non-metric multidimensional scaling (NMDS) for bird species composition (Bray-Curtis distance) for pine plantations (excluding PCnr, unthinned mature pine) ($d=3$, stress=0.1724) sampled during the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Habitat types are depicted with 95% CI ellipses: mid-rotation pine (PB), (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW). Black dots and alpha-code in red represent site/cluster and bird species scores along ordination axes, respectively. Species codes concatenates habitat preference code and species identification number separated by "_". Environmental gradients are represented with fitted surface for herbaceous cover percent and as vectors for other vegetation structure variables: Treeh - tree height; Barea - basal area; Hcov - pine/eucalyptus leafy debris cover; Canopy - canopy closure; Vobs - visual obstruction; Rcov - pine/eucalyptus woody debris cove

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CHAPTER III
BIRD-VEGETATION ASSOCIATIONS FOR SELECTED PASSERINES IN PINE
AND EUCALYPTUS PLANTATIONS IN THE NORTHERN CAMPOS
GRASSLANDS OF URUGUAY

Introduction

Increasing demand for forest products, especially cellulose for the paper industry, has resulted in expansion of commercial forestry in the Campos sub-region of the Rio de la Plata Grasslands (RPG). More than one million hectares of eucalyptus and pine were planted in Uruguay during the last 20 years (Gautreau 2014). As tree plantations replace native grasslands, this structurally and functionally different vegetation cover type may affect native plant and animal communities (Veldman et al. 2015, Bond 2016). Thus, characterizing wildlife use of plantations will inform forest management and conservation strategies in the rapidly changing landscapes of the Campos grasslands.

In the previous chapter, I reported on bird responses to plantations at the community level and found differences in community structure across pine and eucalyptus plantations of different ages and thinning procedures (e.g. unthinned stands, and selective and systematic thinning). Shifts observed in bird assemblages reflected differences in species composition and changes in species relative abundance across these structural gradients. In this chapter, I used a species-level approach to model relative abundance of selected bird species directly as a function of fine scale vegetation

structure. Identifying vegetation characteristics of plantations influencing abundance is important to understand bird use of these plantations and species-specific habitat requirements to inform management. Stand-level vegetation structure characteristics are important predictors of bird abundance in plantations (Nájera and Simonetti 2009, Verschuyt et al. 2011). Hence, I hypothesized differential responses in bird abundance to vegetation structural attributes characterized by forest succession and stand thinning. Further, I predicted that direction of responses in bird abundance would reflect the degree of habitat specialization of individual species (Devictor et al. 2008).

Thus, my main objective was to assess stand-level vegetation characteristics associated with abundance of selected bird species across pine and eucalyptus plantations of different age classes and varying thinning regimes in the northern Campos grasslands of Uruguay. I approached this objective by posing the following questions: (1) what is the direction and magnitude of bird abundance responses to vegetation structure?, and (2) “which forest structural attributes most mediate abundance shifts along these structural gradients?”

Methods

Study area and sampling design

See Chapter II for details on study area and sampling design. For this chapter, I was interested in elucidating abundance responses of birds to forest structure attributes that could be linked to age class and forestry management practices (i.e. thinning). Therefore, I restricted species-habitat models to plantations. In addition, because early succession stages of plantations resemble open environments from a structural

standpoint, I based my analyses on birds and habitat characteristics sampled across 406 points in older (i.e. >3 years) eucalyptus and pine plantations (Fig. 3.1, Table 3.1).

Bird and vegetation surveys

I used standard methods to sample birds and assess habitat vegetative structure at each point count location. See Chapter II for details on of bird and vegetation data collection. From the sampled bird community (Table A.1), I selected seven songbird species to develop habitat models using stand-level vegetation information. Passerines have been used extensively as indicators of bird responses to forest habitat conditions (Sallabanks et al. 2000, Piratelli et al. 2008). I based my selection on species that 1) exhibit different habitat preferences and life history characteristics, and 2) for which I had enough detections to generate robust abundance estimates. Species I selected included habitat generalists [Rufus-collared Sparrow (*Zonotrichia capensis*, Emberizidae), House Wren (*Troglodytes aedon*, Troglodytidae) and White-crested Tyrannulet (*Serpophaga subcristata*, Tyrannidae)], and forest dependent species [Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*, Tyrannidae), Tropical Parula (*Parula pitiayumi*, Parulidae), Sayaca Tanager (*Thraupis sayaca*, Thraupidae) and Hepatic Tanager (*Piranga flava*, Cardinalidae)].

Statistical analysis

I used the greatest number of individual birds recorded at a point count locations out of all repeated visits at each point (Bibby et al. 2000, Toms et al. 2006) for each species to generate estimates of bird relative abundance across vegetation structure gradients. For this, I used generalized linear mixed-effect models (GLMMs) with Poisson

(P) or negative binomial (NB) error distribution and a log-link function to incorporate covariate effects (Zuur et al. 2009). This approach is well established and commonly used to model count data in ecological field studies to generate estimates of relative abundance (Dénes et al. 2015). I performed all data analysis in program R (R Core Team 2015). I fitted GLM using the base *stats* package and GLMMs with function *glmer* from *lme4* package (Bates et al. 2015). For the overall statistical modeling process, I followed the step-by-step approach recommended by Zuur et al. (2010) and Zuur and Ieno (2016). The workflow included data exploration, identification of data dependency structures, model description, model fit, selection and validation, and model interpretation from tabular and graphical outputs. I assessed statistical significance of model coefficients at $\alpha = 0.05$.

During the data exploration phase, I made special emphasis to diagnose outliers and zero-inflation of the response variable, common sources of overdispersion in count data (Zuur et al. 2010). To assess zero-inflation, I performed Chi-squared goodness-of-fit (GOF) tests on the observed versus expected frequency of counts using the parametric distributions selected (P and NB) with function *goodfit* from package *vcd* (Warton 2005, Meyer et al. 2016). Based on these results, I discarded the need for zero inflated models and selected a Poisson error structure as the best initial approach for my data. Multi-collinearity among explanatory variables represents a common cause of estimation bias in GLM(M)s (Zuur et al. 2010, Dorman et al. 2013). Therefore, I used a restrictive threshold and avoided including predictors in the model with Pearson correlation coefficient $|r| > 0.5$ (Dorman et al. 2013). As a post model-fit check for collinearity, I used *vif* function from *car* package (Fox and Weisberg 2011) to estimate variance inflation factors (VIFs)

for covariates used, where $VIF > 3$ are considered unsuitable for inclusion in the final model (Zuur et al. 2010).

In addition, correlations among predictor variables can be particularly problematic in observational field studies where there is less influence over confounding factors than in controlled experimental settings (Mac Nally 2000, Graham 2003). Thus, to minimize spurious associations and aiming for model generality, I included two descriptors of forest structure as predictors: mean diameter at breast height (DBH) and percent canopy openness (CO; 0% indicated completely closed canopy) ($|r| = 0.34$). I used DBH mainly as a measure of succession stage to account for plantation age class (McElhinny et al. 2005) and focused primarily on influence of canopy on selected species counts. I also used tree species planted (TS) as a factor variable with two levels [eucalyptus (E) or pine (P)]. I used the *scale* function to standardize continuous covariates before fitting models (Schielezeth 2010).

I constructed four different structural (fixed-effects) models for each bird species reflecting competing predicted responses: 1) null model, 2) model containing only factor TS, 3) model containing covariates DBH and CO, and 4) full model containing all predictors. The intercept only model (1) predicted a mean response in abundance across all sampled conditions regardless of species planted and stand structure. The ANOVA-type model (2) predicted bird abundance response to species planted independent of structure. The regression-type model (3) predicted bird abundance responses as a function of plantation structure independent of species planted. Lastly, the ANCOVA-type model (4) predicted bird abundance response to plantation structure with different abundance baselines (i.e. intercepts) for each species planted. Because I sampled bird point counts

along transects ("clusters" of points) located on different sites (Table 3.1), I constructed four more models (totaling eight per species) retaining the fixed-effect variants (1-4) but allowing random variation in intercept among sites (S) and among clusters (C) within sites. I incorporated the random effects structure to account for sources of variation and dependency structures given my field design rather than for variance estimation itself, treating them as nuisance parameters and were not reported (O'Hara 2009). Given that sites had varying number of clusters/points across sampled conditions, the random intercept could also have accounted for sample size differences (Gillies et al. 2006).

I used the Akaike Information Criterion corrected for small sample size (AICc) employing the package *MuMIn* (Barton 2016) to identify the best models given data for each bird species (Burnham and Anderson 2003). I considered models within two $\Delta AICc$ units from the top model as competitive and presented them assessing significance of the fixed-effects. For competitive fixed effect models, I calculated explained deviance (an analog of R^2 from standard lineal models, also referred as pseudo- R^2 in GLM) using function *Dsquared* from package *modEvA* (Barbosa et al. 2016). I did not model average parameter estimates from the best supported models (Cade 2015). I reported the effects of predictors for fixed effect-only models in the text as beta coefficients in the log scale \pm standard errors. Graphical representation of model predictions are on the response scale with 95% confidence intervals (CI).

Standard model validation procedures for Poisson GLMMs requires assessment of overdispersion (Zuur et al. 2009, 2010), the condition by which data appear more dispersed than expected under a reference model (i.e. variance greater than the mean for a Poisson distribution, which assumes their equality). The choice of Poisson error structure

assumes randomness in the distribution of counts and that departure from randomness is a consequence of ecological heterogeneity that is effectively modeled by covariate effects (Dénes et al. 2015). Thus, overdispersion may indicate clustering and dependence of observations, and incorrectly assumed mean-variance relationship, but also error in specifying the systematic part of the model (e.g. missing covariates, interactions or non-linear effects).

I graphed the empirical fit of the variance to mean relationship for the Poisson regression models and equivalent Quasi-Poisson (QP) and Negative Binomial error distribution models, which are standard variants to deal with extra-Poisson variation in count data (Ver Hoef and Boveng 2007). The graphs revealed that Poisson models had the best fit for the observed mean-variance relationship better. Further, I estimated overdispersion parameter (\hat{c}) from top models as the ratio of sum of residual deviance to residual degrees of freedom using function *overdisp.glmer* from package *RVAideMemoire* for GLMM objects (Hervé 2015) and I conducted a Chi-squared GOF test to assess significance (i.e. $P < 0.05$ will indicate overdispersion) (Zuur et al. 2009). I did not find traces of overdispersion among top ranked models and proceeded with interpretation of numerical and graphic outputs from best models for each species (Zuur et al. 2016).

I did not consider higher order terms in the set of eight original models constructed for each species. However, because responses to habitat characteristics could be non-linear (Meents et al. 1983), I explored thresholds in abundance for each species relative to canopy openness. I used function *lowess* from the base package (Cleveland 1979) to perform a (univariate) locally-weighted polynomial regression (a type of

generalized additive model, GAM; Zuur et al. 2009) and plotted results on top of prediction graphs from top Poisson GL(M)M models. After visual inspection, I refitted models adding a second order polynomial term for canopy openness for Rufous-collared Sparrow and House Wren, given that for these species smoothed plots revealed possible curvilinear response pattern of abundance along canopy openness. I assessed the significance of higher order terms and used AICc to evaluate overall performance in relation to original model sets.

Lastly, I explored for possible interactions between predictors by including a multiplicative term between canopy openness and DBH in the ANCOVA-type (full) model for each species, and by changing the order of predictors in the full model. I did not find evidence for interactions being important for model performance and did not consider them any further.

Results

I summarized 1,394 counts across repeated visits on 406 sampled points (retaining the maximum count across three visits) for the seven passerine species selected for analysis [749 Rufous-collared Sparrow, 253 House Wren, 118 Hepatic Tanager, 93 White-crested Tyrannulet, 78 Sayaca Tanager, 60 Mottle-cheeked Tyrannulet and 44 Tropical Parula (Table A.1)].

Four species (Rufous-collared Sparrow, House Wren, Mottle-cheeked Tyrannulet and White-crested Tyrannulet) displayed substantial variation in abundance across sampled conditions as evidenced by significant effects of covariates included in best ranked models (Table 3.2). For the Rufous-collared Sparrow, the full model with and without random effects were the two best models, with nearly identical estimates for the

fixed effects. Relative abundance of Rufous-collared Sparrow was influenced by species planted, with estimates for pine almost three times higher than for eucalyptus ($P < 0.01$; Fig. 3.2a), and relative abundance positively associated with canopy openness (0.37 ± 0.04 , $P < 0.01$; Fig. 3.2b). Local polynomial regression evidenced a possible curvilinear abundance relationship with canopy openness for this species, showing an asymptote at mean canopy values and lower than predicted abundance with increasing canopy opening (Fig. 3.2b). Addition of a second order polynomial to the top model showed a significant negative squared relationship with canopy openness (-0.08 ± 0.03 , $P < 0.05$; Fig. 3.2c), while improving model performance by 4.8 $\Delta AICc$ units ($AICc = 1273.40$, $k=5$, 31% explained deviance). This suggests that the relative abundance of Rufous-collared Sparrow was greatest around canopy openness of 35–45%, after which it reaches a plateau. This relationship was most noticeable for pine plantations and less so for eucalyptus.

There were four competitive models for House Wren; forest structure only and the full model, with and without random effects (Table 3.2). Forest structure models ranked first and, for the full models, species planted had no effect. House Wren relative abundance was positively related to canopy openness (0.36 ± 0.09 , $P < 0.01$) (Fig. 3.3a) and DBH (0.36 ± 0.10 , $P < 0.01$). Local polynomial regression analysis showed House Wren had a curvilinear hump-shaped pattern of abundance along the canopy openness gradient (Fig. 3.3a). Effect of quadratic term added to top model was negative and significant (-0.19 ± 0.06 , $P < 0.01$, Fig. 3.3b) and improved model ranking by 7.7 $\Delta AICc$ units ($AICc = 758.2$, $k=6$, 20% explained deviance). Maximum House Wren counts were found at sites

with approximately 25–30% canopy opening, with decreasing relative abundance and precision of predictions with increasing canopy openness.

For the Mottle-cheeked Tyrannulet, there was only one best model represented by the full model without random effects (25% explained deviance). Mottle-cheeked Tyrannulet counts were predicted to be up to 15 times higher in pine versus eucalyptus plantations ($P < 0.01$) and negatively influenced by canopy openness (-0.63 ± 0.20 , $P < 0.01$) (Fig. 3.4). For the White-crested Tyrannulet, three models were competitive; the random effects model with species planted followed by the full model with and without random effects. Counts of White-crested Tyrannulet were nearly three times higher in pine versus eucalyptus plantations ($P < 0.01$) (Fig. 3.5). The third ranked model, the full model without random effects (10% explained deviance), indicated a negative effect of DBH (-0.28 ± 0.12 , $P < 0.05$). The top model however, did not include forest structure covariates and the random effect version of the full model showed no significant effect of covariates.

For the remaining three focal species, a mean response in abundance across sampled conditions appeared to be the best representation for observed counts as top models contained only, or also included, the null models (Table 3.2). For Tropical Parula, Hepatic Tanager and Sayaca Tanager, the null model with random effects was the best ranked model. However, the composition of competitive models differed among species. The second competitive model for Tropical Parula was the random effects model which included species planted. For the Hepatic Tanager, three other models were competitive; the null model without random effects and the model with species planted with and without random effects. For the Sayaca Tanager, the four models with random effects

were found to be competitive and the global model, ranked third, showed a positive effect of DBH (0.59 ± 0.28 , $P < 0.05$); no other fixed effect had any influence on counts. Models containing species planted for Tropical Parula and Sayaca Tanager showed consistently negative coefficients (i.e. higher relative abundance in eucalyptus compared to pine) but this effect was not significant for all of the best supported models.

It is worth noting that the inclusion of random effects had different implications in model performance across species (Table 3.2). For example, for Rufous-collared Sparrow, House Wren, Mottle-cheeked Tyrannulet, White-crested Tyrannulet and Hepatic Tanager, equivalent models with and without random effects yielded very similar results. However, for Tropical Parula and Sayaca Tanager, models with random effects outperformed fixed-effect only models.

Discussion

The selected bird species exhibited variable responses to stand-level forest structure characteristics. Relative abundance of Rufous-collared Sparrow and Mottle-cheeked Tyrannulet showed strong, yet opposite responses to canopy cover (positive and negative, respectively), with numerical difference relative to whether plantations were pine or eucalyptus. House Wren counts also exhibited a strong positive effect to canopy openness, though not to species planted, while White-crested Tyrannulet responded to species planted but not to canopy cover. These results coincide with previous studies documenting bird abundance shifts linked to structural changes in plantations through the silviculture cycle (Guenette and Villard 2005, Venier and Pearce 2005, Ellis and Betts 2011, Verschuyt et al. 2011).

Further, the selected species differ in habitat preferences and life history traits, therefore, I expected species-specific responses along these vegetation gradients (Devictor et al. 2008, Hewson et al. 2011). For example, Rufous-collared Sparrow showed a positive response to canopy openings, a habitat generalist species that primarily feeds and nests on the ground (Phifer et al. 2016). On the other hand, reduced canopy cover negatively affected Mottle-cheeked Tyrannulet, a forest interior species (Rosa et al. 2013). Conversely, Tropical Parula, Hepatic Tanager and Sayaca Tanager exhibited no response either to species planted nor stand structure. For edge and forest generalist species such as Hepatic Tanager and Sayaca Tanager, which have been reported across a variety of wooded habitat types and disturbed areas over the RPG (Vizentin-Bugoni and Jacobs 2011, Phifer et al. 2016), an indiscriminate use of plantations was not unexpected. However, it was unexpected for a species found to be sensitive to canopy and foliage architecture such as Tropical Parula (Cueto and Lopez de Casenave 2002).

Stand-scale canopy cover is an important correlate for bird distribution and abundance in forests (Doyon et al. 2005, Guenette and Villard 2005). The observed positive effect of canopy openness on relative abundance of Rufous-collared Sparrow and House Wren could have been mediated by understory conditions such as increased herbaceous or shrub cover due to higher light availability (Verschuyl et al. 2011) and/or accumulation of woody debris through thinning. Retained downed coarse woody debris (CBD) has been shown to be important for bird diversity and abundance in intensively managed temperate forests (Riffell et al. 2011). Increased structural complexity of the understory through CBD could provide cover, foraging, and nesting opportunities for these habitat generalist and ground foraging birds (Lohr et al. 2002, Doyon et al. 2005,

Hanberry et al. 2012). On the other hand, open canopy conditions may discourage use of plantations by aerial foragers like the Mottle-cheeked Tyrannulet, either by reducing insect abundance and foraging efficiency (Ellis and Betts 2011) or increased nest predation in open canopy plantations (Bourque and Villard 2001). Interestingly, this pattern could not be extended to a related flycatcher species as the White-crested Tyrannulet was insensitive to canopy openness, while exhibiting increased relative abundance in pine than in eucalyptus.

Similar responses to species planted was observed for the Rufous-collared Sparrow and Mottle-cheeked Tyrannulet, but not for House Wren, a pattern not readily explainable purely based on structural attributes measured and known life histories. Functional features of eucalyptus' foliage had been linked to depauperate insect communities within exotic plantations (Calviño-Cancela 2013), which may negatively affect leaf-gleaners and aerial-foraging insectivorous birds such as Mottle-cheeked Tyrannulet, but not ground-feeding insectivores like the House Wren. Thus, pine and eucalyptus plantations may have differing functional significance for distinctive bird species beyond standard measures of vegetative structure, which highlights importance of both vegetation structure and floristics for a more complete understanding of species-specific bird-habitat relationships (Hewson et al. 2011, Seavy and Alexander 2011, Calviño-Cancela 2013).

Besides stand-scale vegetation structure, landscape-level factors are also known to be important for predicting forest bird distribution and abundance (Mitchell et al. 2001, Lichstein 2002, Betts et al. 2007, Deconchat et al. 2009). Further, even if stand-level factors show greater effects than landscape-scale factors when modeled separately,

accounting for landscape effects could improve variance explained by stand-level variables on bird abundance in plantations (Lichstein et al. 2002). Although I did not include landscape-level effects directly in my models, I specified dependency structures in the models as random effects to account for the differing landscape context of sampling points along clusters and sites placed at different locations. Thus, higher performance of random effects models over fixed effects for Sayaca Tanager and Tropical Parula may hint at missing spatial information about arrangement and composition of important resources in the landscape (Christman 2008). It is also known that the ability to detect species-habitat relationships vary depending on the scale at which important features are incorporated into predictive models (Wiens 1989). Furthermore, a mean response in abundance for some species illustrated either a homogeneous use of plantation stand conditions or that I failed to recognize important predictors. Therefore, it is important to incorporate landscape level features as predictors at different spatial scales to further refine uncovered bird-habitat relationships in my study. This is also true for the four species that were responsive to forest structure, as explained deviances suggested considerable variation is still not accounted for by best models (range 69–90% of unexplained deviance).

As a post-hoc approach to dissect relationships between bird abundance and vegetation structure, I used local and polynomial regressions to identify non-linearity in bird responses. Rufous-collared Sparrow and House Wren showed strong evidence for non-linear responses to canopy openness, suggesting an ecological threshold may exist between canopy cover and abundance for these species (Huggett 2005). Rufous-collared Sparrow abundance evidenced an asymptotic response to canopy openness, suggesting a

saturation point at approximately 35–45%, beyond which abundance remained at a maximum and insensitive to further increase in canopy gaps. On the other hand, abundance of House Wren exhibited a hump-shaped response, suggesting a maximum at intermediate levels of canopy openness (~25–30%). Overall, thresholds in bird occupancy/abundance are important because these might indicate an underlying environmental gradient represents a critical resource. Thus, identification of these thresholds is key as quantitative targets for conservation management (Guenette and Villard 2005, Hugget 2005). Characterizing thresholds however, particularly accurately delimiting their location within the gradient, require more sophisticated statistical procedures than the ones I used (Toms and Villard 2015) and merits further investigation.

Using abundance as an indicator for ecological responses along environmental gradients in the light of correlative studies (Hiddink and Kaiser 2005), even if abundance truly reflects habitat quality (see Van Horne 1983), could be misleading. For example, at a given time, the factor limiting abundance at a site could be different across sites, especially in heterogeneous landscapes subject to human disturbance (Hiddink and Kaiser 2005). Identifying confounding factors is thus fundamental to tailor this potential issue. In my study, canopy openness was related to plantation age class and thinning intensity (i.e., canopies close as plantations age, and tree removal generates canopy gaps). On the other hand, I sampled across different thinning conditions within mature pine (selectively and systematically thinned, and un-thinned stands) but mature eucalyptus plantations were all thinned. Further, pine and eucalyptus plantations have very different growth rates and attain canopy closure at different ages. Thus, equivalent age classes of pine and eucalyptus had very different canopy openness (Fig. 3.1). As a consequence, the effects

on bird species abundance by vegetation structure characteristics associated to plantation age, thinning, and to other structural (and functional) characteristics associated to pine versus eucalyptus were confounded. I tried to account for these issues statistically by including DBH as a correlate of stand age and by setting a different intercept for pine and eucalyptus when assessing canopy openness effects on abundance.

To assess effects of thinning treatments on bird abundance without confounding effects of age and species planted, future research should examine patterns of bird abundance in mature pine plantations only (Verschuyl et al. 2011, Greene et al. 2016). Also, because there were not unthinned conditions with woody debris in the understory, an interesting experiment would be translocation of different levels of woody debris (low, medium, high) from thinned to un-thinned stands, and assessing bird abundance responses along all these combinations (i.e. minimally four treatments, thinned and unthinned mature stands with and without coarse woody debris). This would allow a more direct assessment of abundance shifts as consequence of accumulation of woody debris and/or to other conditions related to thinning, such as canopy openings. Yet another uncontrolled, potential confounding factor across my study was cattle grazing. Cattle grazing intensity has been shown to have a strong effect on structure and composition of understory vegetation in tree plantations and native forests in Uruguay (Six et al. 2014, Etchebarne and Brazeiro 2016). Thus, cattle-mediated effects on vegetation structure is expected to influence bird use of plantations under different grazing regimes (Donald et al. 1998). So, rather than simply excluding treatments from cattle, which could be logistically unfeasible, if cattle density is at least known across treatments it could be introduced as a covariate in the models. Lastly, special

consideration should be taken on temporal aspects of such a manipulative study (Wiens et al. 1986), as lagged responses and decoupling between proximate cues and ultimate resources has been hypothesized for birds in planted forests after disturbance events such as thinning (Yegorova et al. 2013).

There are at least two other important caveats to consider when interpreting the results of species-habitat relationships in this study. One is methodological and pertain to the selected detection-naïve modeling approach for abundance estimation, for which I provide justification and comments on the alternatives (Dénés et al. 2015). The second is more theoretical and refers to using abundance as indicative of habitat quality (Van Horne 1983, Bock and Jones 2004). I present these ideas in light of the assumptions made along with cautionary notes, and finally connect both issues by proposing an approach to consider them simultaneously without collecting new data. Imperfect detection is a pervasive concept in current ecological applications, which is reflected in the continuous development of methods to correct occupancy and abundance estimates for false-negative error rates and bias induced by imperfect observation process (Dénés et al. 2015, Guillera-Arroita 2017). The most common of these methods require either a covariate linked to detectability such as distance (Thomas et al. 2010) or temporal replication of sampling units across space (Royle and Nichols 2003, Royle 2004). Methods that do not adjust for imperfect detection rely on counts representing a constant fraction of true abundance. This assumption of proportionality is attained under perfect detection conditioned on availability given presence (i.e. an individual is present at a sampling location and made itself noticeable by sight or sound), else that detection probability remains constant across space and time, conditions that are hardly ever met for most taxa

and field sampling schemes (Thomson 2002). However, detection-adjusted methods also rely on strong assumptions (Rota et al. 2009, Hutto 2016) and high controversy remains on its universal application over index methods (Johnson 2008, Banks-Leite et al. 2014, Guillera-Arroita et al. 2014, Hutto 2016, Guillera-Arroita 2017).

In my study, I did not use detection-adjusted methods for density/abundance for the following four reasons: 1) distance sampling is data hungry and I had only enough detections for robust density estimation for one, potentially two species (Rufous-collared Sparrow and House Wren); 2) most importantly, traditional distance sampling applications do not allow direct modeling of density as a function of covariates but only detectability; 3) it has been shown that the assumption of population closure is frequently violated even within a single breeding season, which is usually the single statement provided to justify the repeated-visit approach (Rota et al. 2009, Dail and Madsen 2011); and 4) repeated-visit methods assume that during a single visit all birds have equal probability of being detected, which basically ignores theory behind distance sampling. Thus, instead of adopting species-specific modeling approaches trying to accommodate for these pitfalls, I opted for a general approach for the selected species using detection-uncorrected counts. Provided that factors used to model relative abundance do not also strongly influence detectability, unadjusted counts methods are appropriate for inference on species-habitat relationships (Johnson 2008, Dénes et al. 2015). I believe this is the case in my study for two reasons. First, I accounted for potential bias introduced by observer skill, varying bird conspicuousness during a single day and across season, and other survey-level sources of bias by design (Banks-Leite et al. 2014); and second, I selected common and abundant species and plantations types that were relatively simple

from a structural standpoint. Therefore, I could assume that failing to detect a bird that was present at a survey location occurred in a random fashion across plantation types, conditions for which the assumption of proportionality holds true (Johnson 2008).

Another implicit assumption made for reliable application of bird-habitat models based on abundance to conservation management is that greater abundance (or density) is indicative of greater habitat quality (Van Horne 1983, Bock and Jones 2004). However, abundance and habitat quality could be decoupled if, for example, dominant birds became established in higher quality sites therefore causing other individuals to spill over into adjacent sites and attain greater abundance in what may actually be lower quality sites (Van Horne 1983, Johnson 2007). This decoupling is predicted to have higher incidence on modified landscapes such as plantations where fair cues for high quality conditions in native habitat types could become ecological traps in disturbed areas (Bock and Jones 2004, Robertson et al. 2007). This issue could be disentangled by assessing bird fitness (e.g. nesting success, juvenile and adult survival) along vegetation structure gradients and plantation types (Johnson 2007).

Given that direct measures of fitness were not an objective of my study, I envision two alternative, complementary approaches to expand on this issue for future research, without the need of extra field data collection. One avenue relies on 'isodar' theory and analysis (Morris 2003), which only requires that abundance is measured at multiple replicate sites of at least two different habitat types (Johnson 2007, but see Shochat et al. 2005). For the second approach, I propose implementing open population N-mixture models to generate site-specific estimates of bird abundance and 'apparent' recruitment and survival (Dail and Madsen 2011, Chandler and King 2011). Empirically derived

population parameters could be used as a measure of fitness across sites, and the shape of its relationship with abundance could give an indirect assessment of potential "sink" conditions and "ecological traps", places where abundance does not match reproductive success (Bock and Jones 2004). Using methods based on unmarked individuals to estimate demographic parameters instead of using more labor-intensive techniques such as capture-mark-recapture is appealing (Johnson 2007) and subject of continuous development (Zipkin et al. 2017). My system and study design could bring the opportunity to test some of these applications empirically. At the same time, these open population models that account for imperfect detection by relaxing the assumption of population closure that constrained the original model (Royle 2004) would allow revisiting abundance estimates and covariate relationships that I generated with detection-naïve approaches as a further test of their adequacy.

In sum, I found stand-level vegetation characteristics across pine and eucalyptus plantations of different age classes and canopy cover gradients were associated with abundance shifts for some of the selected species. As expected, habitat generalists and savanna bird species benefited from open canopy conditions while forest interior birds responded negatively to canopy gaps. However, forest generalist and edge species showed homogeneous use of plantations. Thus, given the opportunities to manipulate vegetation structure at the stand level as part of standard forestry practices, my results may serve as guidelines for habitat-based management of selected species. However, the species-specific nature of uncovered responses underlined that no single management strategy would provide suitable conditions for all species. Consequently, management decisions should be based on clear objectives as to which species or guilds are to be

avored. Stand-level management practices that enhance incidence and abundance of species typical of open habitat conditions will contribute to conservation of bird communities as similar as possible to the ones replaced by tree planting. Along this line, identification of community-level thresholds based on composite-community metrics (i.e. species composition, see Chapter II), or by overlapping species' optimal ranges, as I estimated individually for Rufous-collared Sparrow and House Wren, would be an interesting avenue to set and assess conservation management objectives while still meeting production goals.

Table 3.1 Sample point allocation within plantation types included in bird-vegetation models for selected passerines sampled in the 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Sp. Planted	Year	Age	Habitat type	Site	Cluster	Points
Eucalyptus	2010	3	EI	SS4a	1	10
				MO	1	8
				PE	1	9
				CA	1	6
				SS1a	1	6
Eucalyptus	2006-07	~7	EB	LCWa	3	22
				SS4b	3	25
				PE	1	7
				HO	2	14
Eucalyptus	2002	11	EC	AR	4	28
				CA	4	28
Pine	2004-06	~9	PB	MO	2	16
				LCWb	5	36
Pine	1998	16	PCnr	LCWc	4	28
				SS1b	2	14
Pine	1997-99	~16	PCrC	LCC	7	49
				LT1	2	16
Pine	1997-99	~16	PCrW	LCWd	4	28
				LT2	2	14
				LP1	2	14
				LP2	4	28
Totals				21	56	406

Habitat types: intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW). Bird point counts were nested within clusters at sites replicated within habitat types.

Table 3.2 Model selection results for generalized linear (mixed) models (GLMM) used to estimate relative abundance for selected passerine species across tree plantations sampled during 2013-2014 breeding season in the Northern Campos Grasslands of Uruguay.

Rufous-collared Sparrow

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	wi
mod4	-0.18	1.08*	0.37*	-0.08	4	-635.06	1278.20	0.00	0.60
mod4mix	-0.2	1.09*	0.37*	-0.08	6	-633.40	1279.00	0.78	0.40
mod3mix	0.42		0.24*	-0.03	5	-648.01	1306.20	27.94	0.00
mod2mix	0.09	0.59*			4	-653.72	1315.50	37.32	0.00
mod1mix	0.43				3	-656.34	1318.70	40.50	0.00
mod2	0.09	0.77*			2	-688.37	1380.80	102.54	0.00
mod3	0.57		0.28*	0.10*	3	-704.67	1415.40	137.18	0.00
mod1	0.61				1	-733.18	1468.40	190.15	0.00

House Wren

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	wi
mod3mix	-0.69		0.36*	0.36*	5	-377.90	765.90	0.00	0.37
mod3	-0.62		0.43*	0.46*	3	-380.40	766.90	0.92	0.23
mod4	-0.75	0.21	0.46*	0.43*	4	-379.41	766.90	0.99	0.22
mod4mix	-0.8	0.18	0.38*	0.34*	6	-377.66	767.50	1.60	0.17
mod1mix	-0.79				3	-383.44	772.90	6.99	0.01
mod2mix	-0.91	0.21			4	-383.30	774.70	8.75	0.01
mod2	-0.65	0.28*			2	-414.69	833.40	67.48	0.00
mod1	-0.48				1	-416.90	835.80	69.87	0.00

Mottle-cheeked Tyrannulet

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	wi
mod4	-4.42	2.72*	-0.63*	-0.01	4	-146.89	301.90	0.00	0.83
mod4mix	-4.42	2.73*	-0.61*	-0.01	6	-146.87	305.90	4.07	0.11
mod2mix	-4.62	3.09*			4	-149.50	307.10	5.21	0.06
mod2	-4.4	2.97*			2	-154.67	313.40	11.49	0.00
mod3mix	-2.42		-0.46	0.34	5	-157.04	324.20	22.36	0.00
mod1mix	-2.53				3	-159.46	325.00	23.11	0.00
mod3	-2.27		-0.76*	0.43*	3	-160.80	327.70	25.78	0.00
mod1	-1.91				1	-177.49	357.00	55.12	0.00

White-crested Tyrannulet

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	wi
mod2mix	-2.48	1.11*			4	-221.60	451.30	0.00	0.40
mod4mix	-2.68	1.47*	0.14	-0.24	6	-219.82	451.90	0.56	0.30
mod4	-2.6	1.55*	0.14	-0.29*	4	-222.04	452.20	0.89	0.25
mod2	-2.32	1.17*			2	-226.26	456.50	5.25	0.03

Table 3.2 (Continued)

mod1mix	-1.81				3	-225.62	457.30	6.00	0.02
mod3mix	-1.82	0.12	0.12		5	-225.24	460.60	9.34	0.00
mod1	-1.47				1	-237.68	477.40	26.08	0.00
mod3	-1.48	0.05	0.01		3	-237.59	481.20	29.94	0.00

Tropical Parula

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	w _i
mod1mix	-2.71				3	-136.83	279.70	0.00	0.49
mod2mix	-2.5	-0.36			4	-136.58	281.30	1.53	0.23
mod3mix	-2.72		-0.30	-0.03	5	-135.91	282.00	2.24	0.16
mod4mix	-2.37	-0.61	-0.34	0.08	6	-135.34	282.90	3.16	0.10
mod1	-2.22				1	-142.47	286.90	7.22	0.01
mod3	-2.26		-0.27	-0.10	3	-141.04	288.10	8.42	0.01
mod2	-2.1	-0.22			2	-142.21	288.50	8.73	0.01
mod4	-2.06	-0.34	-0.29	-0.01	4	-140.57	289.20	9.51	0.00

Hepatic Tanager

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	w _i
mod1mix	-1.35				3	-285.73	577.50	0.00	0.34
mod1	-1.24				1	-288.31	578.60	1.10	0.20
mod2mix	-1.49	0.23			4	-285.31	578.70	1.19	0.19
mod2	-1.38	0.23			2	-287.58	579.20	1.66	0.15
mod3mix	-1.35		0.01	0.03	5	-285.70	581.50	4.02	0.05
mod3	-1.24		0.03	0.06	3	-288.08	582.20	4.70	0.03
mod4mix	-1.5	0.26	0.03	-0.01	6	-285.27	582.70	5.22	0.03
mod4	-1.39	0.25	0.05	0.01	4	-287.43	583.00	5.43	0.02

Sayaca Tanager

Model	Int.	TS	CO	DBH	k	logLik	AICc	Δ AICc	w _i
mod1mix	-2.98				3	-185.59	377.20	0.00	0.41
mod3mix	-2.89		0.14	0.50	5	-184.07	378.30	1.04	0.25
mod4mix	-2.32	-0.84	0.14	0.59*	6	-183.40	379.00	1.76	0.17
mod2mix	-2.72	-0.40			4	-185.46	379.00	1.78	0.17
mod4	-1.48	-0.74*	0.49*	0.64*	4	-203.85	415.80	38.55	0.00
mod3	-1.89		0.60*	0.53*	3	-208.14	422.30	45.09	0.00
mod2	-1.36	-0.55*			2	-223.46	451.00	73.71	0.00
mod1	-1.65				1	-226.43	454.90	77.63	0.00

Number of parameters (k), log-likelihood (logLik), sample-size-corrected Akaike's Information Criterion (AICc), weights (w_i) and coefficients are given for each model. Coefficients are presented in the log scale and those with an "*" are statistically significant at alpha 0.05. Models per species are ranked in ascending order by Δ AICc. 'mix' in model name indicates random effects version of structural models 1-4 (see methods). Int. - Intercept; TS - tree species planted (eucalyptus or pine); CO - canopy openness; DBH - diameter at breast height.

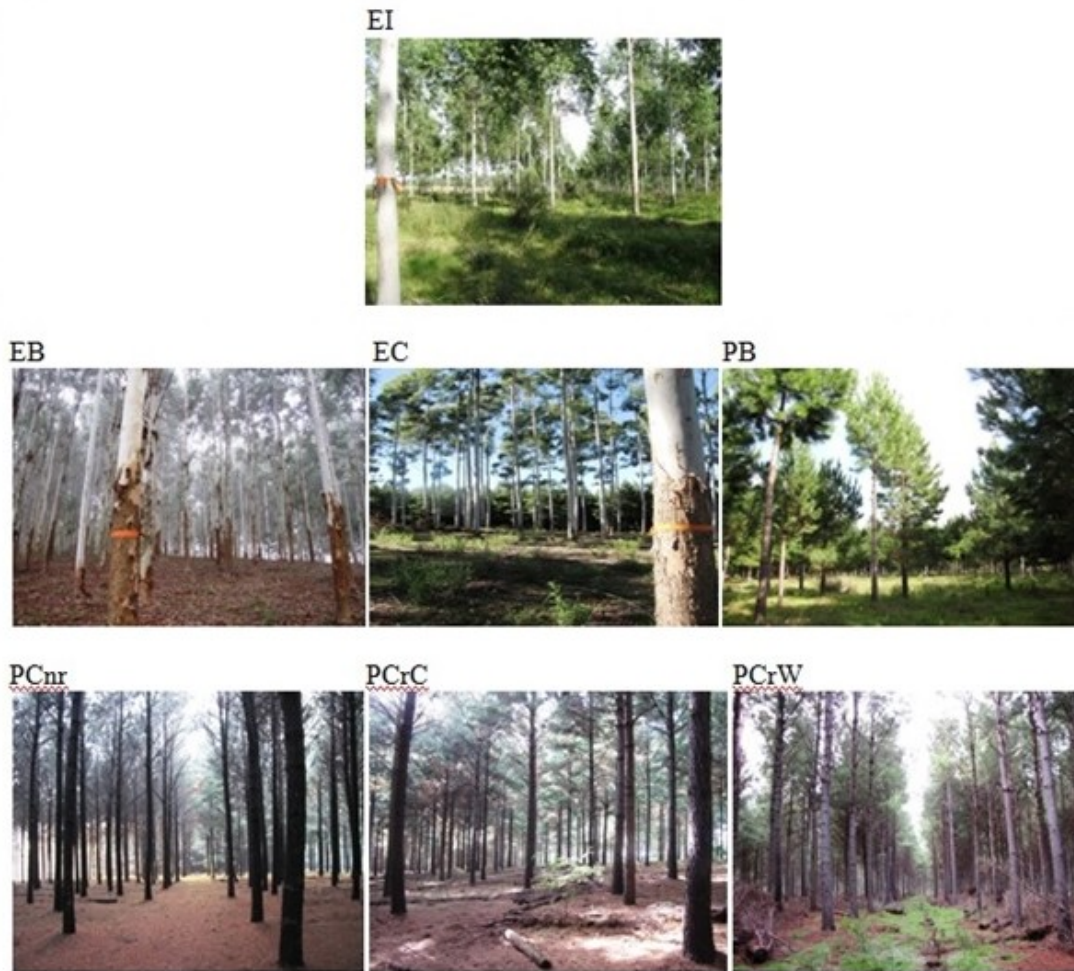


Figure 3.1 Forested habitat types used to develop bird-vegetation association models for selected passerines sampled during the 2013-2014 bird breeding season at study site in the Northern Campos Grasslands of Uruguay.

Habitat types: intermediate eucalyptus (EI); mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW).

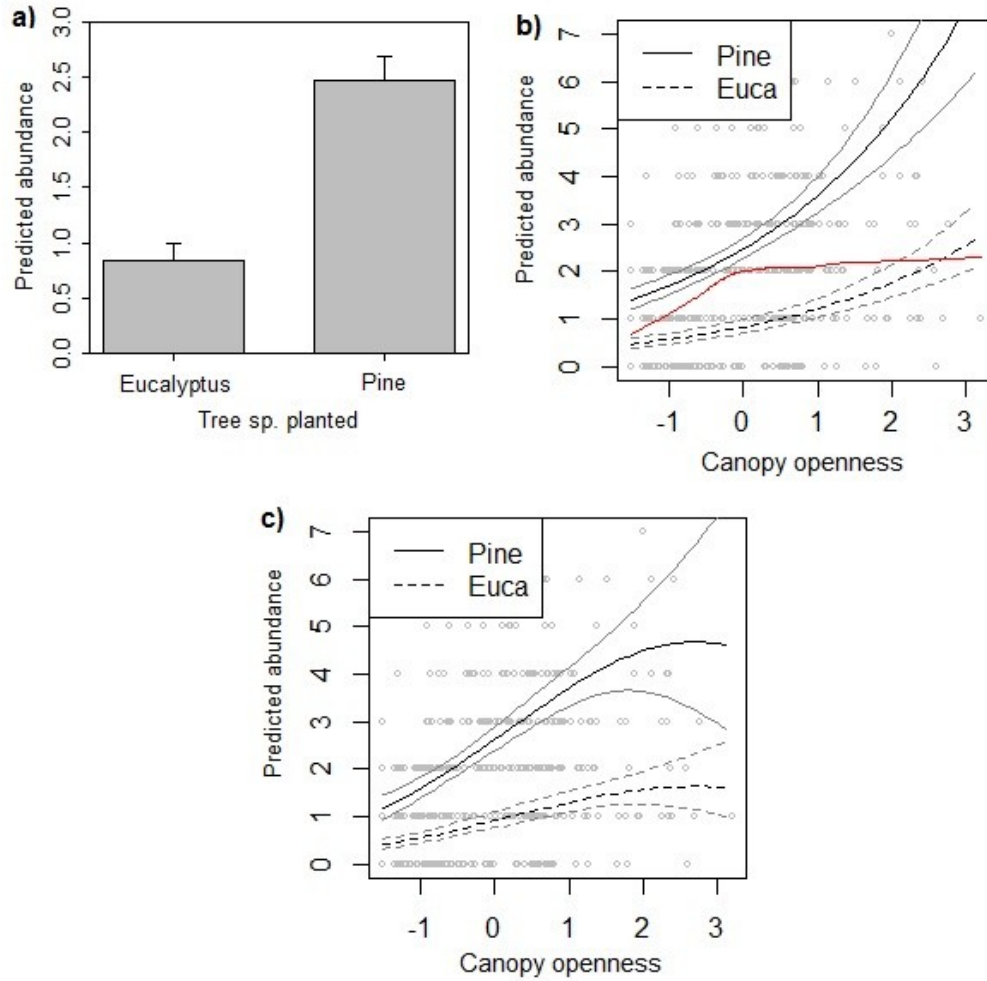


Figure 3.2 Predicted relative abundance for Rufous-collared Sparrow showing effect of tree species planted (a) and relationship of mean abundance per point count to canopy openness for the main effect only model (b) and quadratic effect model (c).

Dots represent observed counts. Red line represents the fit of the local polynomial regression averaged for pine and eucalyptus. Error bars and gray lines represent 95% CI. Canopy openness on standardized scale.

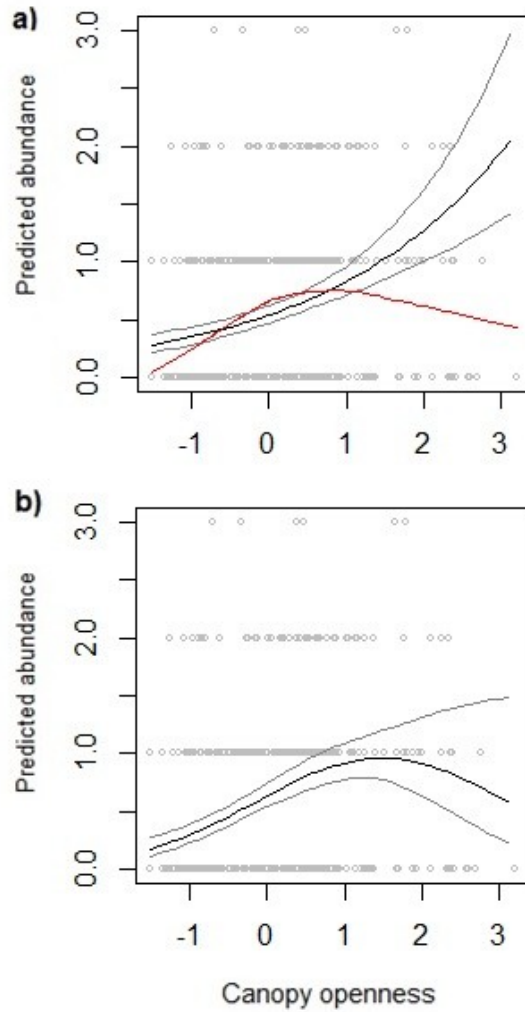


Figure 3.3 Predicted relative abundance per point count for House Wren showing response to canopy openness for the main effects only model (a) and quadratic effect model (b).

Dots represent observed counts. Red line represents the fit of the local polynomial regression. Gray lines are 95% CI. Canopy openness on standardized scale.

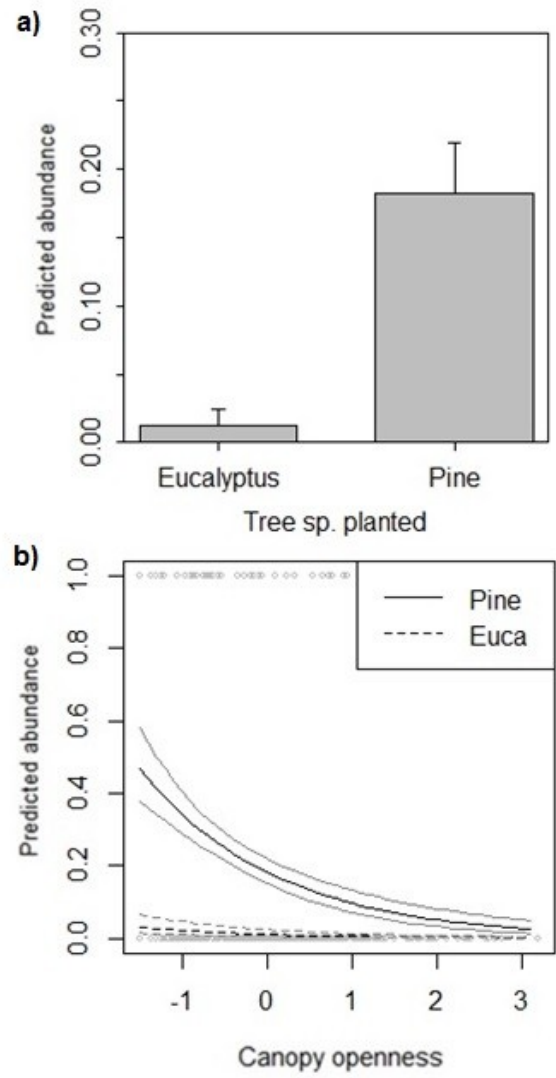


Figure 3.4 Predicted relative abundance for Mottle-cheeked Tyrannulet showing response to tree species planted (a) and relationship of mean abundance per point count to canopy openness (b).

Dots represent observed counts. Error bars and gray lines are 95% CI. Canopy openness on standardized scale.

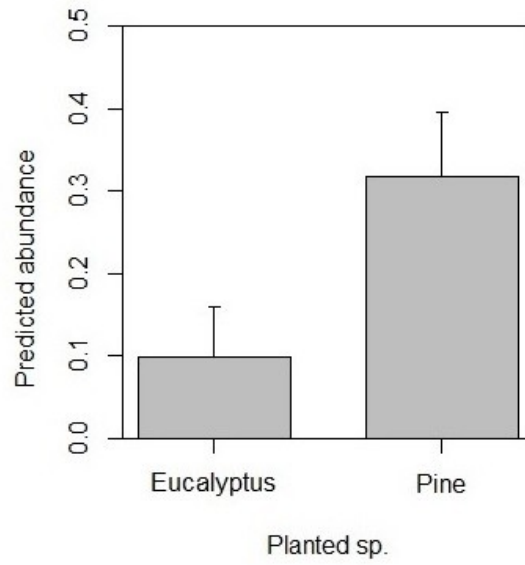


Figure 3.5 Predicted relative abundance for White-crested Tyrannulet showing response to tree species planted.

Error bars represent 95% CI.

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CHAPTER IV

SYNTHESIS AND CONSERVATION IMPLICATIONS

Understanding habitat requirements of wildlife is essential for their conservation and management, particularly in human-modified landscapes. Afforestation has grown globally in response to demands for forest products, bio-energy, and carbon sequestration and forest restoration initiatives (Veldman et al. 2015, 2017). Consequently, it is key to understand how silvicultural practices may benefit native biodiversity while still meeting production goals. This is particularly important within grassland-dominated ecosystems, where tree plantations represent a very different structural and functional land cover type and effects on native wildlife communities is expected to be the greatest (Veldman et al. 2015).

Despite a notable expansion of commercial forestry during the past two decades in the Rio de la Plata Grasslands (RPG), little research has addressed biodiversity in afforested landscapes. Thus, for this research I developed a comparative bird-habitat approach to assess use of tree plantations in the Northern Campos grasslands of Uruguay. This research addressed avian biodiversity within native environments (grasslands and forests) and plantations of both pine and eucalyptus along representative succession stages, from newly planted to mature stands, and different stand thinning regimes. The link between these habitat types and the measurable bird responses was assessed by explicit evaluation of vegetation structure characteristics. I first assessed bird diversity

and composition in native environments and timber plantations and related bird community parameters (richness, evenness and composition) to vegetation structure gradients (Chapter II). I documented differences in diversity and composition of bird communities across native habitat types and plantations, and between plantations of different ages and thinning regimes. Native habitat types exhibited higher richness and were more variable than plantations. Bird communities found within plantations were composed of savanna, edge and forest species, with negligible occurrence of grassland birds.

Second, I developed bird-habitat models for selected avian species and assessed stand-level vegetation structure attributes influencing bird abundance patterns across pine and eucalyptus plantations (Chapter III). I found habitat generalists and savanna bird species benefited from open canopies, conditions commonly found in younger plantations or in older thinned plantations, while forest interior birds responded negatively to canopy openness. Contrastingly, edge and forest generalist species showed indiscriminate use of plantations. Overall, my results were consistent with previous research on birds in afforested landscapes of the RPG. Earlier work documented changes in avian diversity, bird abundance, and shifts in community composition, from grassland species assemblages to communities dominated by habitat generalists, edge and forest generalist species (Fillooy et al. 2010, Dias et al. 2013, Phifer et al. 2016, Jacoboski et al. 2016). However, past studies were based on a limited range of available vegetative conditions during the forestry cycle and native environments. Thus, my study represented not only the first characterization of bird communities in afforested landscapes in Uruguay, but

also an important contribution to understanding bird community and focal species' responses to afforestation over the RPG.

Where plantations replaced native forests or open environments (e.g. pasture or agricultural land) that were originally forests, properly managed plantations have shown to benefit native forest bird communities by providing surrogate habitat, connectivity and buffering edge effects (Miller et al. 2009, Felton et al. 2010, Volpato et al. 2010, Brockerhoff et al. 2013, Calviño-Cancela 2013, Law et al. 2014, Greene et al. 2016, Demarais et al. 2017). Similar mechanisms may also elicit use of plantations by bird species associated savannas and native forests in afforested environments of the RPG. My results suggest a mosaic of plantations of different tree species, age classes, and varied thinning practices harbored varying bird assemblages. Thus, if one of the aims of timber management is to promote overall bird diversity, standard forestry practices that maintain landscape heterogeneity and manage for stand structural complexity will likely meet conservation goals by promoting bird diversity (Lindenmayer and Hobbs 2004, Nájera and Simonetti 2010, Demarais et al. 2017).

It has been argued however that to properly assess the value of plantations to biodiversity, the original land cover type replaced by commercial forestry should be recognized along with the wildlife communities dependent on native conditions (Lindenmayer and Hobbs 2004, Stephens and Wagner 2007, Felton et al. 2010, Brockerhoff et al. 2008). In particular, over the RPG, plantations have largely replaced native upland grassland environments. Furthermore, grassland bird communities are endangered across the region, and most bird species of conservation concern in Uruguay are grassland specialists (Azpiroz et al. 2012a, Azpiroz et al. 2012b). Thus, grassland

communities and grassland specialist birds should be the ultimate target of conservation efforts in afforested landscapes over the RPG.

My results indicated young plantations with open canopies and older thinned plantations harbored bird assemblages that were more similar to open native environments (i.e. grasslands), and were associated with higher use and abundance of habitat generalists and savanna species than closed canopy stands. As such, favoring stand-structure attributes that elicit use by species typical of open environments would favor bird communities more similar to the ones being replaced. More open canopy conditions could be attained in established plantations via stand thinning, or by planting trees initially at lower densities. In addition, by thinning earlier, the amount of time stands persist in closed canopy condition could be minimized. Along this line, identification of community-level thresholds based on composite community metrics (e.g. evenness and species composition) could be an interesting target to assess management operations and how they influence bird communities.

However, my results also indicated that plantations had a limited capacity to harbor grassland bird species and, given the fast rate of tree growth in the region, suitable conditions may not be available long enough to sustain populations of grassland specialist birds. Further, bird assemblages in newly planted eucalyptus were more similar to those from lowlands than to those from upland grasslands. As a consequence, early plantation stages may not represent surrogate conditions for birds whose typical habitat is directly replaced by tree planting, i.e. upland grassland bird communities. Establishing and maintaining networks of connected upland grassland patches within plantations has been proposed as best alternative to improve grassland bird conservation in afforested

landscapes (Lipsev and Hockey 2010). Thus, the best conservation opportunities for grassland specialist birds within afforested landscapes in Uruguay and over the RPG may rely on management of unplanted upland grassland areas at the landscape level, rather than on standard forestry practices at the stand level. This concept is related to a "land-sparing" strategy for reconciling biodiversity and production goals in managed landscapes, which implies maintaining tracts of native vegetation without conversion as big as possible and use intensive high-yield management practices to minimize the area needed to achieve production goals (Balmford et al. 2005, Dotta et al. 2016, Phifer et al. 2016).

Future research that evaluates minimum area requirements and population dynamics of grassland specialist birds would inform the functional role of these interconnected grassland patches (i.e., size, shape and configuration) in promoting persistence and viability of native grassland birds. Furthermore, the spatial connectivity of grassland patches should be a primary criterion when designing plantation stands in this region, and in particular the connectedness with adjoining open grassland areas devoted to traditional activities such as cattle grazing. Loss of grassland specialist birds has been proposed as useful early indicator for landscape-scale transitions from grasslands to planted forests, and studies in this system are particularly needed to determine the proper scale and best arrangement of these dynamic landscape mosaics necessary to support viable populations of grassland specialist birds (Spies and Turner 1999, Bond and Parr 2010). In addition, research should include evaluating the emergent properties of establishing plantations in open environments, such as edge effects (Reino et al. 2009, Phifer et al. 2015), tree avoidance (Thomson et al. 2014), barriers to

movement (Villard and Haché 2012), nest predation and parasitism (Pietz et al. 2009, Ellison et al. 2013). Lastly, these prospects for research should control, or account for, the effects of cattle grazing intensities, as grazing-mediated changes in vegetation structure will have a major effect on incidence and abundance of grassland specialists birds in particular (Azpiroz and Blake 2015).

In sum, given the opportunities to manipulate vegetation structure at the stand level and plan the design of plantations from a landscape perspective, the results of this study will serve as guidelines for developing management strategies and future research for conservation of grassland bird communities while producing forest products in afforested landscapes in the RPG.

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APPENDIX A

BIRD COUNTS PER HABITAT TYPE AND SPECIES' INFORMATION

Table A.1 (Continued)

40	<i>Synallaxis frontalis</i>	Sooty-fronted Spinetail	Furnariidae	C	R	1	1	18	1	1
41x	<i>Synallaxis spixi</i>	Chieft Spinetail	Furnariidae	B	R	1	1	18	1	21
42x	<i>Syndactyla rufosuperciliata</i>	Buff-browed Foilage-Gleaner	Furnariidae	C	R	13	13			13
43	<i>Progne chalybea</i>	Grey-breasted Martin	Hirundinidae	A	M			8	10	18
44x	<i>Progne tapera</i>	Brown-chested Martin	Hirundinidae	A	M			2	1	3
45	<i>Pygochelidon cyanoleuca</i>	Blue-and-white Swallow	Hirundinidae	B	M			2	2	3
46	<i>Stelgidopteryx ruficollis</i>	Southern Rough-winged Swallow	Hirundinidae	B	M			2	2	6
47	<i>Tachycineta leucorrhoa</i>	White-rumped Swallow	Hirundinidae	B	M			8	8	14
48	<i>Agelaioides badius</i>	Bay-winged Cowbird	Icteridae	B	R	1	5	1	1	14
49x	<i>Cacicus chrysopterus</i>	Golden-winged Cacique	Icteridae	C	R			7	1	14
50	<i>Icterus pyrrhopterus</i>	Variable Oriole	Icteridae	C	R			1		1
51x	<i>Molothrus bonariensis</i>	Shiny Cowbird	Icteridae	B	R				8	8
52	<i>Pseudoleistes guirahuro</i>	Yellow-rumped Marshbird	Icteridae	B	R	3				3
53	<i>Mimus saturninus</i>	Chalk-browed Mokingbird	Mimidae	B	R	1				1
54x	<i>Anthus hellmayri</i>	Hellmayr's Pipit	Motacillidae	A	R			2	3	5
55	<i>Anthus lutescens</i>	Yellowish Pipit	Motacillidae	A	R				1	1
56x	<i>Basileuterus culicivorus</i>	Golden-crowned Warbler	Parulidae	C	R		5			16
57x	<i>Basileuterus leucoblepharus</i>	White-browed Warbler	Parulidae	C	R					21
58x	<i>Geothlypis aequinoctialis</i>	Common Miner	Parulidae	B	M	6	1	11	8	39
59x	<i>Parula pitagayumi</i>	Tropical Parula	Parulidae	C	R	4	1	1	8	77
60x	<i>Thamnophilus caerulescens</i>	Variable Antshrike	Thamnophilidae	C	R					10
61x	<i>Thamnophilus ruficapillus</i>	Rufous-capped Antshrike	Thamnophilidae	B	R					15
62	<i>Emberizoides herbicola</i>	Wedge-tailed Grass-Finch	Thraupidae	A	R					2
63x	<i>Embernagra platensis</i>	Great Pampa-Finch	Thraupidae	A	R					11
64	<i>Pipraeidea melanota</i>	Fawn-breasted Tanager	Thraupidae	C	R		1	3	1	5
65x	<i>Poospiza cabanisi</i>	Bearded Tachuri	Thraupidae	C	R		1	5	2	29
66x	<i>Poospiza nigrorufa</i>	Black-and-rufous Warbling-Finch	Thraupidae	B	R			4		6
67x	<i>Saltator similis</i>	Green-winged Saltator	Thraupidae	C	R	4	2	2	1	6
68x	<i>Sicalis flaveola</i>	Saffron Finch	Thraupidae	B	R					15
69x	<i>Sicalis luteola</i>	Grassland Yellowfinch	Thraupidae	A	R					24
70x	<i>Sporophila caerulescens</i>	Double-collared Seedeater	Thraupidae	B	M	3			13	16
71x	<i>Stephanophorus didematus</i>	Diademed Tanager	Thraupidae	C	R					6
72	<i>Tangara preciosa</i>	Chestnut-backed Tanager	Thraupidae	C	R					1
73	<i>Thraupis bonariensis</i>	Blue-and-yellow Tanager	Thraupidae	B	R					1
74x	<i>Thraupis sayaca</i>	Sayaca Tanager	Thraupidae	C	R		7	35	10	85
75x	<i>Volatinia jacarina</i>	Blue-black Grassquit	Thraupidae	A	M	26				29
76x	<i>Pachyrhamphus polychopterus</i>	White-winged Becard	Tityridae	C	M					5
77x	<i>Cistothorus platensis</i>	Grass Wren	Troglodytidae	A	R					6
78x	<i>Troglodytes aedon</i>	House Wren	Troglodytidae	B	R	38	16	14	55	317
79	<i>Turdus albicollis</i>	White-necked Thrush	Turdidae	C	R					2
80x	<i>Turdus amaurochalinus</i>	Creamy-bellied Thrush	Turdidae	C	R	2	1	3	15	50
81x	<i>Turdus rufigiventris</i>	Rufous-bellied Thrush	Turdidae	C	R		1	1	9	23

Table A.1 (Continued)

82x	<i>Camptostoma obsoletum</i>	Southern Beardless Tyrannulet	Tyrannidae	C	R	1	2	2	2	6	4	3	18				
83x	<i>Elaenia parvirostris</i>	Small-billed Elaenia	Tyrannidae	C	M		1			47	11	7	66				
84	<i>Knipolegus cyanirostris</i>	Blue-billed Black-Tyrant	Tyrannidae	C	R					1	1		2				
85x	<i>Lathrotriccus euleroi</i>	Euler's Flycatcher	Tyrannidae	C	M					3			3				
86	<i>Machetornis rixosa</i>	Cattle Tyrant	Tyrannidae	B	R	2						1	3				
87x	<i>Myiarchus swainsoni</i>	Swainson's Flycatcher	Tyrannidae	C	M		4			4	1		9				
88x	<i>Myiodynastes maculatus</i>	Streaked Flycatcher	Tyrannidae	C	M		5	2	1	2	9	3	28				
89x	<i>Myiophobus fasciatus</i>	Bran-coloured Flycatcher	Tyrannidae	B	M						4	2	6				
90x	<i>Phylloscartes ventralis</i>	Mottle-cheeked Tyrannulet	Tyrannidae	C	R		2	8	23	19	16		76				
91x	<i>Pitangus sulphuratus</i>	Great Kiskadee	Tyrannidae	B	R	7	9	4	2	13	2	9	75				
92	<i>Pyrocephalus rubinus</i>	Vermilion Flycatcher	Tyrannidae	B	M			1				3	4				
93	<i>Sarapa icterophrys</i>	Yellow-browed Tyrant	Tyrannidae	B	R				1			1	2				
94x	<i>Serpophaga nigricans</i>	Sooty Tyrannulet	Tyrannidae	A	R						3		3				
95x	<i>Serpophaga subcrissata</i>	White-crested Tyrannulet	Tyrannidae	B	R	17	5	8	3	30	10	11	138				
96x	<i>Tyrannus melancholicus</i>	Tropical Kingbird	Tyrannidae	B	M	3	6	9	4	3	2	1	4				
97x	<i>Tyrannus savana</i>	Fork-tailed Flycatcher	Tyrannidae	B	M	8		1			2	9	11				
98x	<i>Xolmis cinereus</i>	Grey Monjita	Tyrannidae	B	R				1			2	3				
99x	<i>Xolmis irupero</i>	White Monjita	Tyrannidae	B	R							2	4				
100x	<i>Cyclarhis guianensis</i>	Rufous-browed Peppershrike	Vireonidae	C	R		3				13		16				
101x	<i>Vireo olivaceus</i>	Red-eyed Vireo	Vireonidae	C	M		9	5			7		21				
102x	<i>Colaptes campestris</i>	Field Flicker	Picidae	B	R	1	3					3	19				
103x	<i>Colaptes melanochloros</i>	Green-barred Woodpecker	Picidae	B	R	3		1	7	2	1	1	15				
104	<i>Picumnus nebulosus</i>	Mottled Piculed	Picidae	C	R						1		1				
105x	<i>Veniliornis spilogaster</i>	White-spotted Woodpecker	Picidae	C	R		1	8	10	5	14	5	44				
106	<i>Myiopsitta monachus</i>	Monk Parakeet	Psittacidae	B	R								5				
107	<i>Rhea americana</i>	Greater Rhea	Rheidae	A	R				3		1		4				
108	<i>Athene cucularia</i>	Burrowing Owl	Strigidae	A	R							1	1				
109	<i>Nothura maculosa</i>	Spotted Tinamou	Tinamidae	A	R	1					1	1	3				
110x	<i>Rhyncotus rufescens</i>	Red-winged Tinamou	Tinamidae	A	R	8					2	2	12				
						337	178	203	266	380	176	307	598	379	409	213	3,446

Counts were summarized by taking maximum count obtained across repeated visits at same point. ID: species identification number (those with 'x' were recorded in $\geq 5\%$ of points for at least one habitat type). HP - habitat preference of species: grasslands (A), generalists (B), forest (C). MS - migratory status of species: breeding resident (R), breeding summer migrants (M). Total individuals per species, total individuals per habitat type and grand total are provided. Habitat types: newly planted eucalyptus (EA), intermediate eucalyptus (EI), mid-rotation eucalyptus (EB), mature eucalyptus (EC), mid-rotation pine (PB), unthinned mature pine (PCnr), selectively thinned mature pine (PCrC), systematically thinned mature pine (PCrW), native forest (NF), lowland grassland (LG), upland grassland (UG).