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# Riparian forest patches are critical for forest affiliated birds in farmlands of temperate Chile

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## ABSTRACT

There is ongoing debate among conservationists regarding the value of small habitat patches to sustain wild populations in farmlands. Our goal was to assess bird abundance in riparian forests differing in terms of size, configuration, landscape conditions and degradation level, to both inform the debate and to identify conservation strategies to maintain diverse agricultural landscapes. We conducted bird point-counts in 91 sites in 2016 across an agricultural valley in Chile. Using models that accounted for imperfect detection, we assessed variation in bird densities in riparian forests with different sizes and configuration, landscapes, and habitat characteristics. We found support in univariates models for our prediction that bird densities varied across riparian forest of various sizes and configuration for 10 of 16 bird species. However, when we added landscape and habitat characteristics to the model, we found that the densities of many of the birds were best explained by forest cover around their local (1 ha) and broader (50 ha) landscape combined with forests characteristics (e.g., invasive tree abundance). For example, Black-throated huet-huet and Chucao Tapaculo were positively associated with forest cover at the broader landscape (50 ha), but showed no response to number of patches, patch-size and Euclidean distance. Our results showed no evidence of negative fragmentation effect per se (i.e., after controlling for habitat area). While agricultural landscapes provide habitat for some species that use small forest patches, conservation strategies focusing on maintaining high level of forest cover and native vegetation are required to secure populations of forest affiliated species.

## 1. Introduction

Agriculture covers the largest portion of productive land on earth (Foley et al., 2005), which is why it is essential that agricultural landscapes host at least a portion of the planet's biodiversity (Tscharntke et al., 2005; Johnson et al., 2011). However, conservation planning in agricultural landscapes is challenging because there is limited land available for conservation (Foley et al., 2005), and, large patches of native habitat are often lacking (e.g., Tscharntke et al., 2005). A current debate in conservation has challenged the focus on protecting only large habitat patches because there is growing evidence that small habitat patches that remain in human dominated landscapes can also provide valuable habitat for many species of conservation concern (Hunter et al., 2017; Wintle et al., 2019; Riva and Fahrig, 2022). Furthermore, species may have different responses to habitat fragmentation (Miller-Rushing et al., 2019), i.e., the extent to which a constant habitat area occurs as continuous or as separated patches in a given landscape, with various species exhibiting positive, negative, or neutral responses (e.g., Haddad

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et al., 2015; Fahrig, 2017). In agricultural landscapes, forest habitat is scarce after deforestation and is frequently fragmented into small patches, including riparian forest patches that remain within open agricultural field and surrounded by varying degrees of other small forest (e.g., González et al., 2017). Riparian forest strips in agricultural landscapes can help maintain regional bird diversity (Bennett et al., 2014; González et al., 2017), and often support higher diversity of birds than other semi-natural habitat remnants within open fields, such as roadside vegetation (Hall et al., 2018). In agricultural landscapes, a bird species may use riparian forest patches for breeding and nesting, even if it is not a riparian specialist, because riparian strips may contribute to the minimum habitat area requirement of the species and have characteristics necessary to meet its life needs (Hall et al., 2018). Riparian forests patches can also function as movement corridors when they connect distant habitat patches (Lees and Peres, 2008; Gilbert-Norton et al., 2010), serving to improve the structural connectivity (the physical distribution of habitat) and functional connectivity (the extent that species can access habitats available in a given area; Rosenberg et al., 1997). However, ongoing deforestation due to human activities (e.g., unregulated logging, overgrazing, among others) can further shrink and fragment available habitat and transform existing fragments into smaller patches of riparian forests (Lees and Peres, 2008). It is likely that species with varying forest habitat requirements respond in different ways to such alterations (e.g., Boesing et al., 2021). Therefore, understanding the ability of different species to use riparian forest patches with varying conditions of degradation, habitat availability, and fragmentation of the forest in their surrounding landscape can both inform the current debate about the conservation value of small patches, and identify conservation strategies that maintain as many species as possible in agricultural landscapes.

In agricultural landscapes, where forest is scarce and fragmented, species may have limited ability to access isolated forest patches separated by the agricultural matrix, i.e., land cover such as crops, annual grasses and orchard that may reduce species movement. When forest habitat is fragmented into patches that are too small to sustain a population of a given bird species, individuals inhabiting them need to traverse agricultural cover to reach distant patches of forest (Rosenberg et al., 1997). For many birds, forest habitat fragmentation may not pose a problem (e.g., Vergara and Armesto, 2009; Fahrig et al., 2011; Fahrig, 2013) because birds are strong flyers, allowing them to move among multiple habitat patches (Fraser and Stutchbury, 2004; Fahrig et al., 2011). Then, species that can access those distant resources are generally positively associated with habitat availability in the landscape, rather than fragmentation (Fraser and Stutchbury, 2004; Vergara and Armesto, 2009). However, some species may respond to the size and configuration of remaining patches of forest. For example, small and isolated forest patches tend to have fewer species and lower abundance of birds with specialized habitat requirements, especially species that require interior conditions and may be reluctant to cross the surrounding open matrix (Castellón and Sieving, 2006; Lees and Peres, 2008; Boesing et al., 2021). Furthermore, in narrow forest patches, the adjacent matrix influences the biotic and abiotic conditions of the forest (Prevedello and Vieira, 2010; Vergara, 2011). Thus, edge habitats usually have more sunlight, less humidity, and, consequently, a different set of resources available than interior habitats (Ries et al., 2004). Edge habitats are closer to resources only available in the adjacent matrix than interior habitats, often increasing access to multiple resources (Ries et al., 2004). However, species may respond variously to edge conditions. For example, species adapted to interior conditions may not respond to additional resources that are more accessible in the edge habitat (e.g., no change in abundance between interior and edge habitat), while edge adapted species may increase in abundance at edges where they may access multiple resources (Ries et al., 2004). Also, species interactions can differ along forest edges, affecting patterns of competition or predation (Fagan et al., 1999). For example, forest edges often have higher rates of predation than forest interiors, which negatively affects forest interior-affiliated species that are not adapted to the higher predation pressure when they use edge habitat (Batáry and Báldi, 2004).

In addition to habitat amount and forest habitat fragmentation, human uses have transformed riparian forests in many other ways (Capon et al., 2013; González et al., 2017), including modification of plant community composition which may affect food provisioning for birds, e.g., reduction of plants that produce fruits (Rozzi et al., 1996), the loss of large trees that that support invertebrate food and provide nest sites (Altamirano et al., 2017), and decreased understory density (Reid et al., 2004; Díaz et al., 2005; Ibarra and Martin, 2015). Additionally, housing development, within or near riparian areas can degrade riparian forest because houses exacerbate the vegetation changes described above (Bar-Massada et al., 2014; Pidgeon et al., 2014), and increase road mortality and the risk of predation from generalist predators and pets (Lepczyk et al., 2013).

In the Temperate rainforest of South America, which is designated a Global Biodiversity Hotspot, the responses of birds to habitat amount, fragmentation and configuration varies greatly (e.g., Castellón and Sieving, 2006; Magrach et al., 2012; Vergara et al., 2012). Some forest bird species appear to tolerate the effect of habitat fragmentation, and can occupy landscapes where forests remain in patches of a wide range of sizes and shapes within an agricultural matrix (Vergara and Armesto, 2009; Vergara, 2011). However, observations suggest that not all forest patches remaining in the landscape are used by species, and that forest habitat specialists and generalists increase in density in forest of specific sizes or are connected by forested corridors (Vergara, 2011; Magrach et al., 2012; Vergara et al., 2012). For example, in agricultural landscapes, Black throated huet-huet and Thorn-tailed Rayadito showed higher density along forest strips 10 to 15 m wide and 350 to 550 m long than in open fields (Vergara, 2011). Additionally, some forest understory specialists, including Black throated huet-huet, Chucao Tapaculo, and Magellanic Tapaculo, were frequent in forest strips 25 to 50 m wide for dispersion and as breeding territories, while were rarely detected in narrower strips, < 10 m wide (Sieving et al., 2000). Also, some understory birds exhibit a degree of flexibility in their use of dense shrubby vegetation, including native Bamboo and other shrubs (Sieving et al., 2000; Castellón and Sieving, 2006). As agriculture expands and intensifies in South American temperate landscapes (Echeverría et al., 2006; Miranda et al., 2015), understanding responses of the avian community to riparian habitat availability, fragmentation, patch-area and configuration and habitat characteristics can guide conservation strategies aimed at maintaining birds' populations in this Global Biodiversity Hotspot.

Our goal was to assess how forest affiliated and generalist bird species respond to habitat availability, fragmentation and habitat characteristics of riparian forests in an agricultural landscape. We hypothesized that forest affiliated birds are positively associated with forest amount and negatively associated with fragmentation, while some generalist species may be negatively associated with forest amount and show no response to fragmentation. We also posed hypotheses for different habitat use guilds. Specifically, we expected to find that understory forest specialists that are poor flyers are less abundant in riparian forest patches that are small and isolated from other forest patches. Further, we expected that large tree users and canopy users that are good flyers would respond positively to specific characteristics of the habitat (e.g., tree size), and would not be strongly associated with patch size. Regarding habitat generalists, we hypothesized that their abundance would be higher in riparian forest patches that are relatively small, and that are surrounded by heterogeneous land covers. Our three objectives to identify which factors most influence density of forest affiliated and generalist birds, and to test our hypotheses are:

1. To describe the landscape and habitat characteristics of riparian forest of three spatial configuration classes: wide and large patches, forested strips, and small and isolated patches.

2. To assess the relationships of birds with riparian forest patch size and spatial configuration.
3. To determine which riparian forest attributes, i.e., landscape, patch size and spatial configuration or habitat characteristics, best explain species' densities.

## 2. Methods

### *2.1. Study area*

We studied riparian forests in an agricultural landscape in the temperate biome of Chile, South America (Fig. 1). Our study area is well suited to assess the response of birds to riparian forest fragmentation for the following reasons. First, the long history of deforestation reduces potential lag effects of recent forest clearing (Bierregaard et al., 1992). The most intense deforestation started in the mid-1800s with the expansion of wheat farming (Otero, 2006; Armesto et al., 2010). Then, from the 1970s to early 2000s forest clearing targeted mostly upland forests to plant exotic trees, grow crops and create pastures for livestock grazing (Miranda et al., 2015). Second, in this landscape riparian forest remains in patches of varying shapes, sizes and degree of isolation. Some riparian areas are fully deforested, despite a national law that requires 10 to 200 m of riparian forest be left intact to protect water quality (Ministerio de Agricultura, 2011; Romero et al., 2014). Third, the non-forested habitat is fairly homogenous (Prevedello and Vieira, 2010; Vergara, 2011), with pasture as the dominant open land cover (calculated from Zhao et al., 2016). We restricted our study sites to lowlands (< 450 m.a.s.l.) to control for variability due to altitude.

### *2.2. Study design*

Within the 200-m riparian zone, which we mapped from a publicly available hydrological network dataset (Ministerio de Bienes Nacionales, 2012), we randomly selected 91 sites separated by ≥1 km, to minimize spatial autocorrelation (Fig. 1). To choose variables to test our hypothesis that landscape fragmentation and the habitat characteristics and configuration of riparian forest can affects densities of the birds exhibiting greatest habitat specialization, we identified attributes known to influence bird abundances in temperate South American forests (Supplemental material B). In the field, we surveyed bird density and collected habitat attribute data, and calculated landscape characteristics from an existing land use-cover map.

### *2.3. Data*

#### *2.3.1. Bird density*

At each of the 91 sites, we located one point-count station. We conducted 139 surveys (43 sites were visited once, and 48 sites were visited twice) during the breeding season, i.e., from late-September to mid-December, of 2016. We surveyed birds from 6:30 to 11:00 am, recording all birds seen or heard vocalizing within a 50-m radius of the center of the point-count station during three consecutive 6 min periods (Ibarra and Martin, 2015). We only recorded birds using the forest habitat. For our analysis, for each species we used the maximum count of the three consecutive periods in subsequent models. To facilitate accounting for birds' detectability in models, we recorded date, time, air temperature, and wind speed, measured using a weather monitor

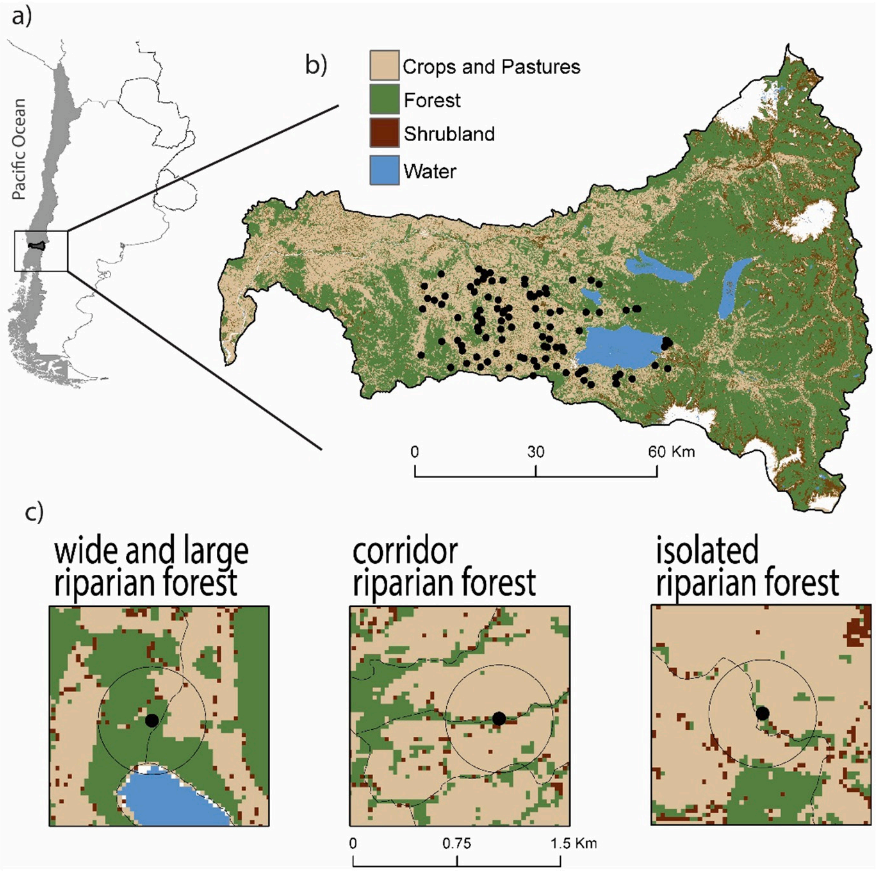

**Fig. 1.** a) Location of the Toltén watershed (black) in Chile. Our study area b) encompasses the central valley; a landscape dominated by pasture seeded for livestock grazing and secondary forest. Black dots indicate locations of 91 sites at which point-counts were conducted in riparian sites. c) Examples of wide and large, strips and small and isolated riparian forests. The open circle around each site is a 400-m buffer that we used to collect information about the landscape conditions surrounding point-count stations. Green patches are forest, tan indicates pasture and grassland, and brown is shrubland. The black lines are rivers.

(WindMate™ 300, Speedtech Instruments). Because we conducted point-counts close to the river, we also measured the noise of the river using a digital sound level meter (EXTECH Instruments 407,730). An assessment of the effectiveness of our design on capturing most of species on each riparian forest type, using a species accumulation curve, showed that richness values we recorded were at or very close to the asymptote in all three riparian forest types (Supplemental material A). We included nine forest affiliated species, one species affiliated with wetlands, one exotic species affiliated with urban areas, and the rest were generalist species, those species that were associated with multiple habitats, including forest (Table 1; Supplemental material G).

### 2.3.2. Riparian forest spatial configuration classes

We categorized riparian forest into three area and spatial configuration classes. We used a width of 120 m to separate between wide and large forest from corridor and isolated forest because forest that are narrower typically have internal abiotic condition that are different from forest interior in wider patches (Ries et al., 2004, 2017). We used a forest width threshold (~120 m) not a size threshold because we wanted to separate forest between corridor and wider patches, that would be most likely used as movement conduit versus wider patches that could be use as habitat. This approximation is different to other researchers that have classified fragments based on their minimum size to sustain a population (e.g., 100 ha for Chucao Tapaculo and 400 ha for Black-throated huet-huet; Castellón and Sieving, 2006), which leads to larger patch size to meet those requirements. Furthermore, in this agricultural landscape individuals may be using a combination of wide forest, corridors and isolated patches to meet their life requirements, so ultimately is relevant to consider individuals territory size, which tend to range from 1 to 4 ha for many of the species we studied (e.g., Botero-Delgadillo and Vásquez, 2016; Sieving et al., 2000). Considering this edge threshold, forest patches that were wider than 120 m in 2 perpendicular directions was labeled as 1) ‘wide and large’. We further subdivided the forest as follows: 2) ‘strips’ are narrow forest (<120 m), >100 m long, and connected to a ‘wide and large’ forest at one or both ends, and 3) ‘small and isolated’ is a narrow forest (< 120 m) of any

**Table 1**

Sixteen birds recorded in our study included in the analysis (see Supplemental material G. List of the 36 bird species that we registered during our surveys).

| | Latin name | Common English name | UICN Habitat affinity | Habitat use guild | Sites present | Mean density (ind/plot) | Detection parameter | Estimated mean density with detection (ind/plot) |
|---|---|---|---|---|---|---|---|---|
| Trochilidae | | | | | | | | |
| 1 | *Sephanoides sephaniodes* | Green-backed Firecrown | Generalist | Vertical profile generalist | 77 | 1.29 | 0.42 | 3.09 |
| Rhinocryptidae | | | | | | | | |
| 2 | *Pteroptochos tarnii* | Black-throated Huet-huet | Forest | Understory user | 19 | 0.24 | 0.27 | 0.82 |
| 3 | *Scelorchilus rubecula* | Chucao Tapaculo | Forest | Understory user | 24 | 0.31 | 0.61 | 0.49 |
| 4 | *Scytalopus magellanicus* | Magellanic Tapaculo | Generalist | Understory user | 33 | 0.35 | 0.36 | 0.95 |
| Furnariidae | | | | | | | | |
| 5 | *Aphrastura spinicauda* | Thorn-tailed Rayadito | Forest | Large tree user | 60 | 1.22 | 0.52 | 2.3 |
| 6 | *Cinclodes patagonicus* | Dark-bellied Cinclodes | Wetland | Ground | 25 | 0.32 | 0.6 | 0.58 |
| 7 | *Pygarrhichas albogularis* | White-throated Treerunner | Forest | Large tree user | 39 | 0.47 | 0.44 | 1.07 |
| 8 | *Sylviorthorhynchus desmursii* | Des Murs’s Wiretail | Forest | Understory user | 24 | 0.22 | 0.03 | 7.41 |
| Tyrannidae | | | | | | | | |
| 9 | *Anairetes parulus* | Tufted Tit-Tyrant | Generalist | Shrub user | 68 | 1.36 | 0.5 | 2.75 |
| 10 | *Elaenia albiceps* | White-crested Elaenia | Forest | Vertical profile generalist | 83 | 3.24 | 0.2 | 16.43 |
| 11 | *Pyrope pyrope* | Fire-eyed Diucon | Forest | Vertical profile generalist | 44 | 0.47 | 0.16 | 2.95 |
| Troglodytidae | | | | | | | | |
| 12 | *Troglodytes aedon* | House Wren | Generalist | Shrub user | 63 | 1.2 | 0.57 | 2.09 |
| Turdidae | | | | | | | | |
| 13 | *Turdus falcklandii* | Austral Thrush | Generalist | Vertical profile generalist | 82 | 2.15 | 0.44 | 4.74 |
| Emberizidae | | | | | | | | |
| 14 | *Zonotrichia capensis* | Rufous-collared Sparrow | Generalist | Shrub user | 29 | 0.33 | 0.49 | 0.66 |
| Icteridae | | | | | | | | |
| 15 | *Curaeus curaeus* | Austral Blackbird | Generalist | Vertical profile generalist | 51 | 0.76 | 0.18 | 4.16 |
| Fringillidae | | | | | | | | |
| 16 | *Spinus barbatus* | Black-chinned Siskin | Generalist | Vertical profile generalist | 72 | 2.02 | 0.4 | 4.92 |

length that is separated from other forests ≥30 m. We used a 30-m threshold because at least one species is reluctant to traverse the open matrix (*Black-throated huet-huet*). Also, 30-m was the minimum distance that the land cover map allows us to use to separate between patches of forest. We collected width measures using a Google Earth image from 2016, which matches the year our field data was collected. To classify each site, we averaged three measures of forest width that we obtained using a straight-line perpendicular to the river. This classification resulted in 35 sites classified as 'wide and large', 39 classified as 'strips' and 17 classified as 'small and isolated'.

### 2.3.3. *Landscape characteristics*

We characterized land cover in the vicinity of our sites from a 30-m resolution landcover map (Zhao et al., 2016). We measured the proportion of the most dominant land cover types, native forest, pasture and shrubland, within circular plots of 60 and 400 m radius around each point-count station which represent the immediate vicinity (1 ha), and the broader neighborhood (50 ha) of each point-count station, respectively. We used these two buffer sizes because species respond to habitat around them at various scales (Vergara and Armesto, 2009; Moraga et al., 2019). Although, we note that two spatial scales may not capture the full range of scale effects that birds respond to (Moraga et al., 2019). Because the centers of point-count stations were at least 1 km apart, we have no overlap of the areas captured within the largest buffer size of 400 m radius. We obtained housing density (house/ha) by hand-digitizing house and other buildings within a 500 m of each center of point-count stations from the 2016 Google Earth image. To represent the level of fragmentation of the forest in the landscape, we calculated the "number of patches" within the 400-m buffer, using Fragstats (McGarigal and Marks, 1995). To have continuous variables to represent riparian patch and spatial configuration characteristics, we calculated "patch size" and "Euclidean distance to the nearest patch". In our study area, we found sites from a wide range of sizes: 37 % of the sites were smaller than 10 ha, 19 % of the sites ranged from 10 to 50 ha, 7 % of the sites ranged from 50 to 100 ha, 25 % of the sites ranged from 100 to 1000 ha and 12 % of the sites were patches larger than 1000 ha.

### 2.3.4. *Habitat characteristics*

We collected data on habitat characteristics following a protocol used previously in the study area, to facilitate comparability (Ibarra and Martin, 2015). We centered a circular plot (22 m diameter or 0.04-ha) on each point count station. Within the plot, we tallied number of trees and measured mean tree diameter at breast height for trees >12 cm in diameter (hereafter tree diameter). The information on species composition and number of trees of each species was used to calculate tree species richness, and relative abundance of non-native species (such as *Acacia dealbata* and *Salix viminalis*). To characterize the structure of the understory layer, we used two approximations. First, within the plot, we visually estimated vegetation cover at three height classes (0 to 5 m, 5 to 8 m and > 8 m). Second, we estimated density of the understory by averaging the number of branches touching a 3-m vertically pole in 10 sub-plots, located systematically 1-m apart along a line passing through the center of the plot.

## 2.4. *Data analysis*

### 2.4.1. *Variables correlation analysis*

We calculated Spearman rank correlation coefficients to assess collinearity between variables and excluded one of each pair having $r >$ 0.6 (Supplemental material C). For instance, we did not include percent of pasture because it was highly correlated with forest percent ($r > -0.7$), at both 1 ha and 50 ha scales. Also, we retained understory density instead of understory percent cover (i.e., vegetation cover of layer <5 m), because understory density represents the extent and complexity of the understory layer better (Díaz et al., 2005). We retained a few correlated variables to be able to text our specific hypothesis. First, we maintained forest percent at 1 ha and 50 ha, because forest affiliated species may respond differently to forest availability at various spatial scales (e.g., Moraga et al., 2019). We also maintained patch size, which was correlated at >0.7 with Forest at 1 ha, to contrast the importance of forest amount in a given landscape (continuous or fragmented) with continuous forest amount (i.e., patch-size). This preliminary variable selection procedure allowed us to reduce the list of variables to five landscape characteristics (forest within 60 m, forest within 400 m, shrubland within 400 m, house density and number of patches within 400 m), two patch characteristics (patch size and Euclidean distance to nearest neighbor) and four habitat characteristics variables (understory density, mean tree diameter, tree species richness and non-native trees abundance).

### 2.4.2. *Objective 1. To describe the landscape and habitat characteristics of riparian forests*

Prior to modeling bird densities, we quantified differences in landscape and habitat characteristic attributes among the three spatial configuration classes. We used one-way ANOVA to determine if there were significant differences among the classes and applied a post-hoc HSD-Tukey's test to detect differences between each pair of connectivity classes (Hothorn and Bretz, 2008).

### 2.4.3. *Objective 2. To assess variation in bird density with riparian forest spatial configuration classes*

We focused our analysis on 16 bird species for which we had sufficient data to model density, i.e., species that were present in at least 20 sites. We used data from sites with one visit and two visits because the models can apply the same detection parameter estimated from sites with two or more visit to bird occurrences at sites with one visit, without replication (Kéry and Royle, 2016). We first assessed the variation in density of each species related to riparian forest spatial configuration classes, using an N-mixture model with a Poisson distribution to account for imperfect detection of birds (Royle, 2004), with the package 'Unmarked' in R version 0.12–2 (Fiske et al., 2017). We used a standard detection model with noise from the river (decibels dB) and temperature (°C) (Ralph et al., 1995). To reduce the list of variables in the detection model, we used temperature instead of time of the day and ordinal date because temperature is a basic condition characterizing the environment and is typically associated with time of the day or ordinal date. To determine if overdispersion or lack of fit occurred in any of our univariate models, we performed a goodness of fit test using the overdispersion parameter $\hat{c}$ (Supplemental material D and E, in the package AICcmodavg 2.1-1) (Mazerolle, 2017).

### 2.4.4. *Objective 3. To determine which riparian forest attributes best describes species density*

In univariate models, we assessed the relationship of the density of each species with variables representing landscape (five variables), patch-area and spatial configuration (two variables) and habitat characteristics (four variables); in these models we used the same detection model for each species. All variables were scaled to be able to compare estimated coefficients of the multivariate model. To determine which variables to include in a multivariate model for each species, we selected variables that showed a significant relationship in their respective univariate models. Because we were testing multiple variables, we included all variables with a $p$-value ≤0.1, i.e., also those representing weak relationship. Second, we built one multivariate model with those previously selected variables for each species. We did not run further comparisons of models based on subsets of variables, because all the selected variables were relevant, and explained substantial amount of variability. Instead, we discussed the coefficients of our significant variables estimated in the multivariate model, and their influence on a given species. In addition, giving that variable selection procedures may be affecting the importance of variables that are relevant only when other variables are present in the model, we developed one global model that we applied to all species, to check consistency with our multivariate model procedure (Supplemental material F).

## 3. Results

### 3.1. Obj. 1. Landscape and habitat characteristics of riparian forest

Forest covered 64,099 ha, or approximately 37 % of our study region, but forest percent surrounding our point-count stations varied greatly among sites (Table 2). Forest percent within 60 m of the point-count stations was similar for strips and small and isolated riparian forests sites (45 % and 35 %, respectively), but significantly higher for wide and large riparian forests (78 %). Forest percent within 400 m was significantly different among all three riparian spatial configuration classes. It was highest for the wide and large riparian forest (43 %) and lowest for the isolated riparian forests (14 %). Number of patches was significantly smaller in wide and large patches (5.1 in wide and large and 7.5 and 8 in strips and small and isolated riparian forests, respectively). We found no difference across riparian forest classes for patch-area and configuration classes. Similarly, most habitat characteristics we measured did not differ among the three riparian forest patch-size and configuration classes. The only vegetation characteristic that differed significantly among riparian patch area and configuration classes was understory density (F = 3.73, *p*-value = 0.028), though the actual differences were small (3.34 ± 0.18 to 4.74 ± 0.08 branches/pole).

### 3.2. Obj. 2. Birds association riparian forest patch area and configuration classes

Density differed significantly for 11 bird species among the three-riparian forest patch-size and configuration classes (Figs. 2, 3). For three of five forest affiliated species, density (ind/plot) decreased significantly from wide and large to small and isolated riparian forest (Black-throated Huet-huet, Chucao Tapaculo, and Thorned-tailed Rayadito). Not a single Black-throated Huet-huet individual was found in a small and isolated riparian forest. For three of eight generalist bird species, density increased from wide and large riparian forest to small and isolated riparian forest (Black-chinned Siskin, House Wren, Rufous-collared Sparrow). Two species showed highest density in riparian forest strips, the White-throated Treerunner (a forest affiliate) and the Tufted Tit-Tyrant (a habitat generalist) (~1.5 and 3.5 individuals/plot, respectively). Five species did not differ among the three riparian forest patch-size and configuration classes: two forest affiliated, Des Murs's Wiretail and Fire-eyed Diucon, and three generalist species, Magellanic Tapaculo, Austral Thrush, and Austral Blackbird.

### 3.3. Obj 3. Attributes that influence each bird density

Forest percent was included in the multivariate models for 12 of 16 species. Forest percent in the vicinity of point-count station (i.e., within 60 m) was included in the multivariate model of 10 species and was a significant variable in the multivariate model for three species (Tufted Tit-Tyrant, Green-backed Firecrown, Magallanic Tapaculo; Table 3, Fig. 4). Forest percent in the broader neighborhood (i.e., within 400 m) was included in the multivariate model of eight species and was significant in six of them. For example, density (ind/plot) of Black-throated Huet-huet (mean ± SD = 0.89 ± 0.24; z = 3.68; p-value = 0.0002) and Chucao Tapaculo (mean ± SD = 0.38 ± 0.16; z = 2.30; p-value = 0.0212) were both significantly positively associated with forest within 400-m. In addition to forest percent, shrubland in the broader neighborhood (within 400 m) affected the density of seven species. Specifically, increasing shrub cover in the broader landscape had a negative effect on the density of Magallanic Tapaculo (mean ± SD = −0.76 ± 0.36; z = −2.13; p-value = 0.0331) and Des Murs's Wiretail (mean ± SD = −1.02 ± 0.54; z = −1.87; p-value = 0.0615).

The number of patches, our fragmentation variable, was included in the multivariate model of five species (Thorn-tailed Rayadito, Chucao Tapaculo, Green-backed Firecrown, House Wren, Fire-eyed Diucon; Fig. 4), but it was not a significant variable when other variables were present in the model. Similarly, Euclidean distance and patch size, were present only in the multivariate model of one species, Chucao Tapaculo and Black-chinned Siskin, respectively. None of these variables were significant when included in the multivariate model (Fig. 5).

Habitat characteristics, including mean tree diameter, tree richness and understory density, explained the density of forest affiliated birds

**Table 2**

Characteristics of landscapes and at plots associated with point-count stations in riparian forests classified as strips, isolated patch, or wide and large riparian forests. Shown are mean and standard error (se) and F and *p*-values for one-way ANOVA to detect differences in characteristics across riparian forest fragmentation classes. Differences between riparian forest fragmentation classes were estimated using post-hoc HSD-Tukey's test and are indicated by different letters (a, b or c). Forest percent within 60 m and 400 m was the most distinct characteristic across riparian forest fragmentation classes.

| | All sites | | | Strips | | | | Isolated | | | | Wide and large | | | | Anova | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* = 91 | | | *n* = 39 | | | | *n* = 17 | | | | *n* = 35 | | | | F | p-Value |
| | Mean | | SE | Mean | | SE | | Mean | | SE | | Mean | | SE | | | |
| *Landscape characteristics* | | | | | | | | | | | | | | | | | |
| Forest percent (1 ha)[a] | 52.69 | ± | 3.30 | 45.38 | ± | 3.87 | a | 35.31 | ± | 1.54 | a | 78.46 | ± | 0.69 | b | 24.38 | <0.001 |
| Forest percent (50 ha)[b] | 29.55 | ± | 1.84 | 26.45 | ± | 1.95 | a | 14.38 | ± | 0.55 | b | 43.49 | ± | 0.49 | c | 28.31 | <0.001 |
| Shrubland percent (50 ha)[b] | 9.7 | ± | 0.97 | 9.53 | ± | 1.42 | a | 13.69 | ± | 0.69 | a | 6.99 | ± | 0.22 | b | 3.19 | 0.046 |
| Number of patches (50 ha) | 6.7 | ± | 0.3 | 7.5 | ± | 0.5 | a | 8.1 | ± | 0.8 | a | 5.1 | ± | 0.4 | b | 7.78 | <0.001 |
| Housing density (houses/ha) | 0.64 | ± | 0.37 | 0.40 | ± | 0.21 | a | 0.28 | ± | 0.09 | a | 0.12 | ± | 0.03 | a | 1.51 | 0.227 |
| *Patch-size and configuration* | | | | | | | | | | | | | | | | | |
| Euclidean distance (m) | 97.8 | ± | 6.3 | 92.2 | ± | 8.2 | a | 109.6 | ± | 9.8 | a | 98.4 | ± | 12.7 | a | 0.49 | 0.611 |
| Patch size (ha) | 13,971.4 | ± | 5406.9 | 10,840.6 | ± | 7399.6 | a | 11.9 | ± | 8.0 | a | 24,240.4 | ± | 11,260.8 | a | 1.40 | 0.252 |
| *Habitat characteristics* | | | | | | | | | | | | | | | | | |
| Trees diameter (cm) | 25.86 | ± | 1.66 | 25.26 | ± | 1.26 | a | 27.29 | ± | 2.08 | a | 25.17 | ± | 1.14 | a | 0.49 | 0.612 |
| Understory density (branches/pole) | 3.65 | ± | 0.28 | 3.14 | ± | 0.05 | a | 3.34 | ± | 0.18 | ab | 4.74 | ± | 0.08 | b | 3.73 | 0.028 |
| Tree richness | 3.82 | ± | 0.25 | 4.03 | ± | 0.07 | a | 3.71 | ± | 1.89 | a | 4.34 | ± | 0.06 | a | 0.45 | 0.639 |
| Invasive tree abundance | 0.21 | ± | 0.04 | 0.19 | ± | 0.01 | a | 0.22 | ± | 0.12 | a | 0.19 | ± | 0.01 | a | 0.06 | 0.944 |

a indicates percent cover within 60 m of point count station. b indicates percent cover within 400 m of point count station.

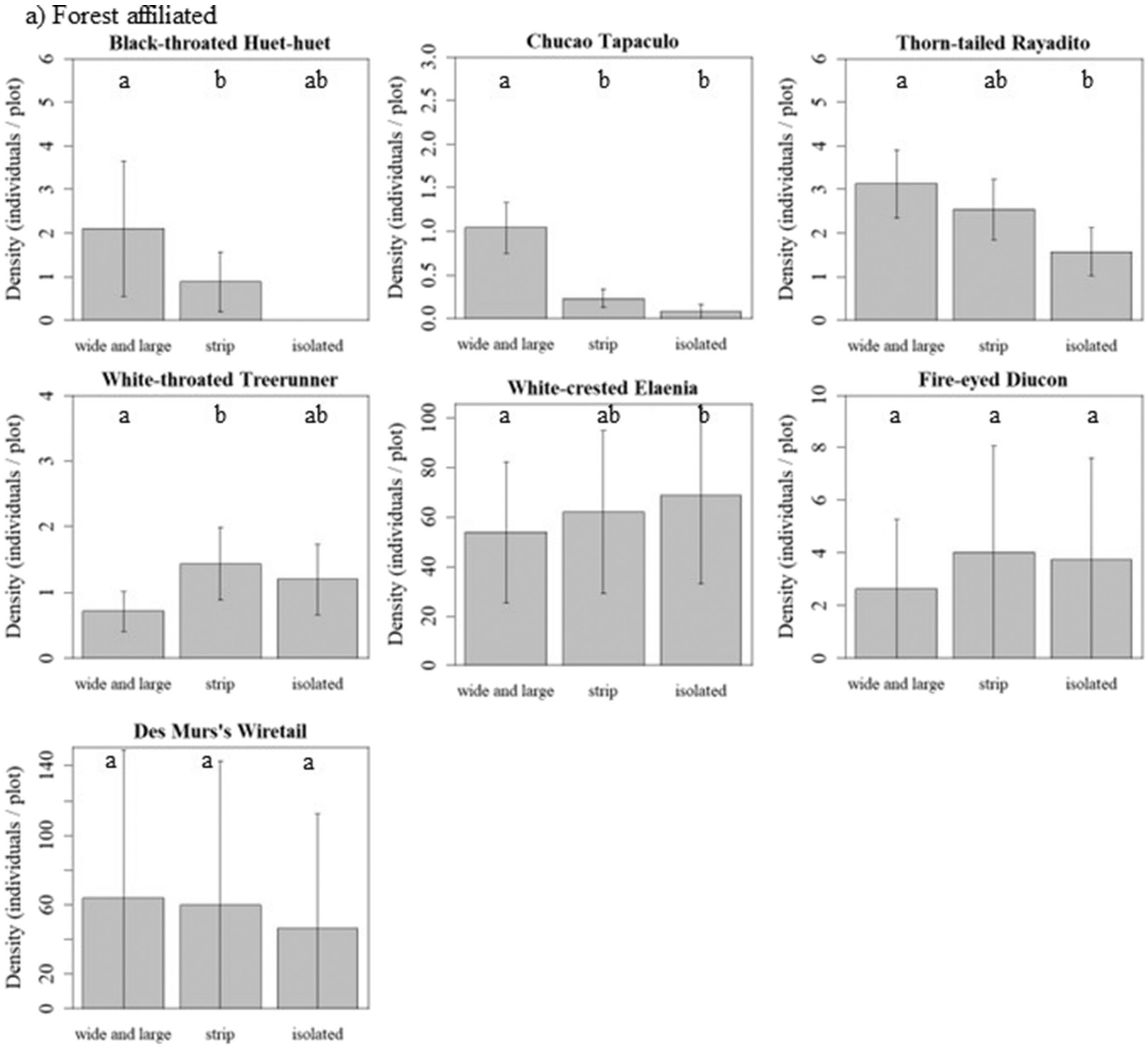

**Fig. 2.** Variation of bird density among riparian forest patch-area and configuration classes for seven a) forest affiliated species. Bar graph showed the mean bird density and Standard Error (vertical line) after accounting for imperfect detection. The letters above the bar graphs (a. b and c) indicate when the mean density of a given species changed significantly between riparian forest fragmentation classes; same letter indicate no significant difference and different letters indicate significant difference.

well (Fig. 6). For example, mean tree diameter was present in the best model of eight species. For five species, increasing mean trees diameter was associated with higher density, including White-throated Treerunner, which nest and feeds on trees. Three species were negatively associated with tree size (e.g., Magellanic Tapaculo). In addition, abundance of invasive trees was significantly associated with nine species, having a negative association with the five of these species, including Black-throated Huet-huet, White-throated Treerunner, Green-backed Firecrown, Austral Thrush, and Thorn-tailed Rayadito.

Our results, using a multivariate model, were consistent with results from a global model, including all 11 variables at once (Supplemental material F, Table 1). We found mostly consistency in terms of the direction of the relationship and the level of significance. Also, results from the global model were consistent in that number of patches, Euclidean distance and patch size showed little associations with birds' density.

## 4. Discussion

### 4.1. Bird response to forest percent

Our study in a Global Biodiversity Hotspot of southern South America shows that habitat amount was the most important factor explaining the density of birds of most species. Consistently with previous research (e.g., Vergara and Armesto, 2009), we found that forest specialist species can use small remnant of forest, either narrow strips and/or small and isolated patches, when forest in the surrounding landscape to those patches can support the presence of the species. While our results showed that the abundance of forest affiliated species is lower in small remnants of forest habitat than in wide and large tracks of forest, these remaining forest patches may be helping to sustain the populations of forest affiliated bird species in agricultural areas, where land suitable for habitat protection is limited. Our results support the

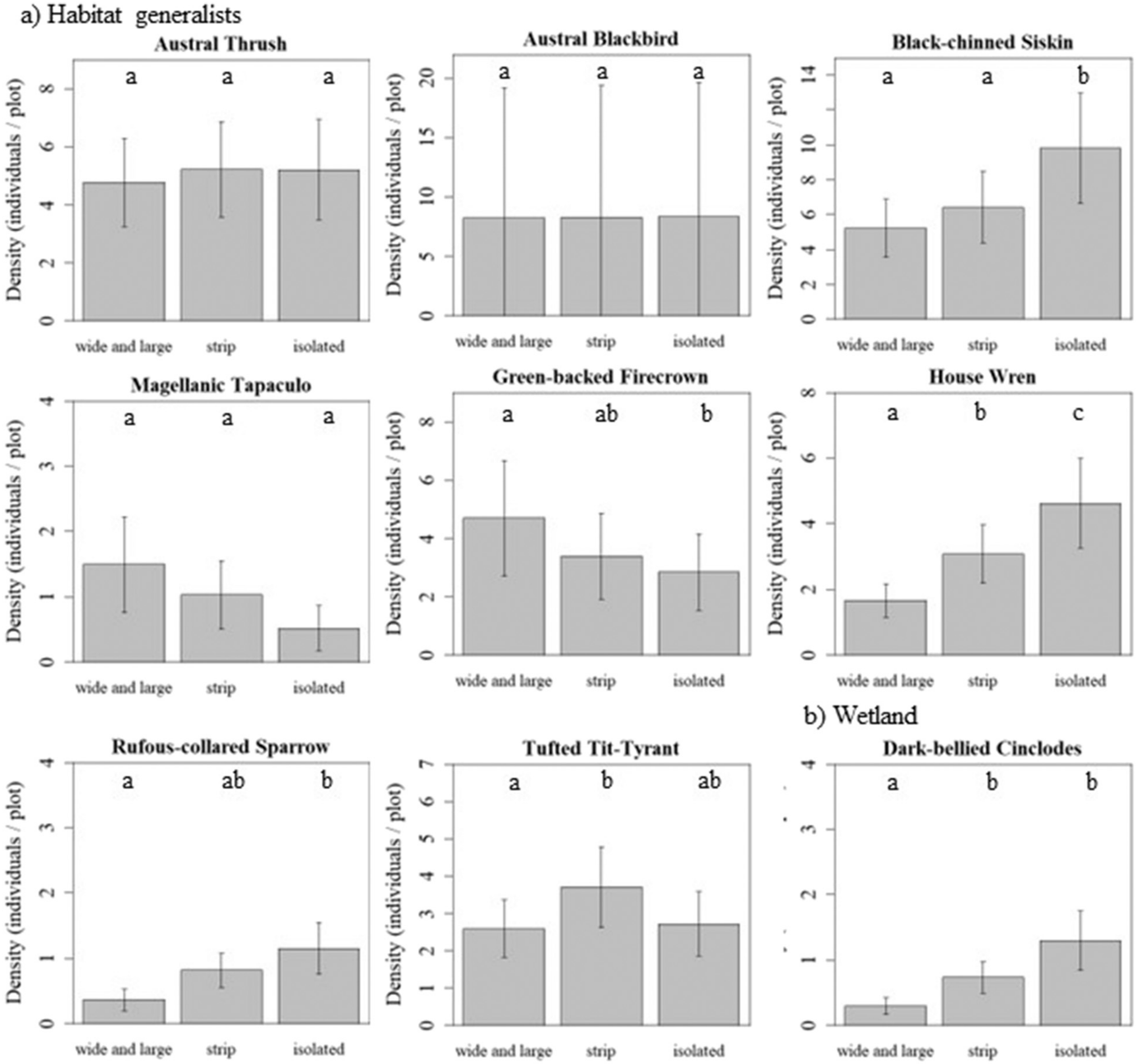

**Fig. 3.** Variation of bird density among riparian forest fragmentation classes for nine a) habitat generalists, one b) urban area and one c) wetland affiliated species. Bar graph showed the mean bird density and Standard Error (vertical line) after accounting for imperfect detection. The letters above the bar graphs (a. b and c) indicate when the mean density of a given species changed significantly between riparian forest fragmentation classes; same letter indicate no significant difference and different letters indicate significant difference.

argument that habitat amount, and not fragmentation per se, is the most important factor determining species abundance (e.g., Fahrig, 2017), and provides evidence supporting the conservation value of small remnant patches of habitat for bird conservation in agricultural land (Hunter et al., 2017; Wintle et al., 2019; Riva and Fahrig, 2022). Our work strongly suggests that restoring or newly establishing even small patches of forest in agricultural land, where forest was once widespread, can help reduce ongoing biotic homogenization (Le Viol et al., 2012; Riva and Fahrig, 2022).

One mechanism that may explain the lower density of forest birds in strips and small isolated patches is the influence of having separated resources within an individuals' territory (Fahrig, 2013). Habitat fragmentation can force birds to establish relatively larger territory sizes than typical due to reduced resource density (e.g., trees and food; Haskell et al., 2002; Fraser and Stutchbury, 2004). Increasing the foraging area reduces the amount of time an individual spends in any one area. We speculated that birds using narrow strips and small and isolated patches hold larger territories and may use the riparian forest strip as movement corridors (e.g., Sieving et al., 2000), which may explain our finding of lower density in those riparian forest classes. Furthermore, the amount of forest in our study area varied across the landscape, but overall forest covered around 37 % of the landscape. This proportion of forest is likely too low to sustain stable populations of other forest specialist bird species that require large contiguous forests, such as the Magellanic Woodpecker (*Campephilus magellanicus*), Chilean Hawk (*Accipiter bicolor*) and Rufous-legged Owl (*Strix rufipes*) (Trejo et al., 2006; Ojeda and Chazarreta, 2014; Ibarra et al., 2014). The agricultural landscape that we studied has likely already lost species that require large tracts of forest.

Habitat generalist bird responses to forest percent were largely negative, similarly to previous research (Vergara and Armesto, 2009), but there was not a significant relationship with forest percent in the vicinity of point-count stations. One possible explanation for this is that for most of the habitat generalist species we studied, forested habitat and open matrix can provide complementary resources to meet life requirements. Habitat generalist bird species that spend most of their time

**Table 3**
Estimate of variables coefficient, standard error (SE), z value and p-value for a multivariate model. Models were built using variables with a p-value <0.1 from univariate model. Detection model was set with temperature and river noise as representative factors affecting species detection in our study. We assigned *** to p-values ≤ 0.01, ** to 0.01 < p-values ≤ 0.05, and * to 0.05< p-values ≤ 0.1, meaning very strong evidence, strong evidence and moderate evidence against the H0, respectively.

| | | Estimate | SE | z | P-value | |
|---|---|---|---|---|---|---|
| Tufted Tit-Tyrant | | | | | | |
| ∼Density | Intercept | 1.12 | 0.28 | 4.04 | 0.000 | *** |
| | Forest (1 ha) | −0.17 | 0.09 | −1.94 | 0.052 | * |
| | Tree size | −0.35 | 0.17 | −2.04 | 0.041 | ** |
| | Understory density | −0.12 | 0.09 | −1.38 | 0.168 | |
| ∼Detection | Intercept | −0.27 | 0.49 | −0.55 | 0.580 | |
| | River noise | −0.28 | 0.16 | −1.72 | 0.085 | * |
| | Temperature | 0.11 | 0.14 | 0.74 | 0.456 | |
| Thorn-tailed Rayadito | | | | | | |
| ∼Density | Intercept | 0.90 | 0.37 | 2.42 | 0.016 | ** |
| | Number patches (50 ha) | 0.00 | 0.12 | 0.03 | 0.979 | |
| | Forest (1 ha) | 0.16 | 0.12 | 1.31 | 0.189 | |
| | Forest (50 ha) | 0.01 | 0.12 | 0.08 | 0.939 | |
| | Shrub (50 ha) | −0.29 | 0.18 | −1.63 | 0.103 | |
| | Tree size | 0.31 | 0.19 | 1.63 | 0.104 | |
| | Tree richness | 0.01 | 0.10 | 0.14 | 0.888 | |
| | Invasive trees | −0.49 | 0.17 | −2.82 | 0.005 | *** |
| ∼Detection | Intercept | −0.48 | 0.58 | −0.83 | 0.408 | |
| | River noise | −0.20 | 0.15 | −1.33 | 0.184 | |
| | Temperature | −0.18 | 0.14 | −1.27 | 0.203 | |
| Black-chinned Siskin | | | | | | |
| ∼Density | Intercept | 1.92 | 0.40 | 4.83 | 0.000 | *** |
| | Patch size (ha) | −0.05 | 0.11 | −0.42 | 0.672 | |
| | Forest (1 ha) | 0.10 | 0.10 | 1.08 | 0.279 | |
| | Forest (50 ha) | −0.39 | 0.10 | −3.75 | 0.000 | *** |
| | Tree size | 0.53 | 0.13 | 3.95 | 0.000 | *** |
| | Understory density | 0.14 | 0.06 | 2.28 | 0.023 | ** |
| | Tree richness | −0.05 | 0.08 | −0.67 | 0.506 | |
| | House density | 0.46 | 0.24 | 1.93 | 0.054 | * |
| ∼Detection | Intercept | −1.01 | 0.54 | −1.86 | 0.064 | * |
| | River noise | −0.22 | 0.10 | −2.08 | 0.037 | ** |
| | Temperature | 0.22 | 0.12 | 1.89 | 0.059 | * |
| Dark-bellied Cinclodes | | | | | | |
| ∼Density | Intercept | −0.60 | 0.27 | −2.17 | 0.030 | ** |
| | Forest (1 ha) | 0.12 | 0.22 | 0.56 | 0.578 | |
| | Forest (50 ha) | −0.45 | 0.25 | −1.83 | 0.067 | * |
| | Understory density | −0.48 | 0.23 | −2.13 | 0.033 | ** |
| | Invasive trees | 0.39 | 0.15 | 2.61 | 0.009 | *** |
| ∼Detection | Intercept | 0.06 | 0.54 | 0.11 | 0.909 | |
| | River noise | 0.66 | 0.41 | 1.61 | 0.108 | |
| | Temperature | 0.12 | 0.34 | 0.36 | 0.720 | |
| Austral Blackbird | | | | | | |
| ∼Density | Intercept | 2.11 | 1.33 | 1.59 | 0.111 | |
| ∼Detection | Intercept | −2.35 | 1.45 | −1.62 | 0.104 | |
| | River noise | −0.30 | 0.12 | −2.53 | 0.011 | ** |
| | Temperature | −0.11 | 0.11 | −0.98 | 0.325 | |
| White-crested Elaenia | | | | | | |
| ∼Density | Intercept | 3.93 | 0.40 | 9.88 | 0.000 | *** |
| | Forest (1 ha) | −0.09 | 0.06 | −1.41 | 0.160 | |
| | Forest (50 ha) | −0.04 | 0.06 | −0.60 | 0.546 | |
| | Shrub (50 ha) | 0.07 | 0.05 | 1.59 | 0.112 | |
| ∼Detection | Intercept | −2.71 | 0.43 | −6.34 | 0.000 | *** |
| | River noise | −0.06 | 0.06 | −1.03 | 0.303 | |
| | Temperature | 0.14 | 0.05 | 2.58 | 0.010 | *** |
| Black-throated Huet-huet | | | | | | |
| ∼Density | Intercept | 0.53 | 2.75 | 0.19 | 0.847 | |
| | Forest (50 ha) | 0.38 | 0.16 | 2.30 | 0.021 | ** |
| | Tree size | −1.21 | 0.38 | −3.21 | 0.001 | *** |
| | Understory density | 0.37 | 0.16 | 2.29 | 0.022 | ** |
| | Invasive trees | −1.19 | 0.52 | −2.30 | 0.021 | ** |
| ∼Detection | Intercept | −2.76 | 2.89 | −0.95 | 0.341 | |
| | River noise | −0.46 | 0.22 | −2.13 | 0.033 | ** |
| | Temperature | −0.02 | 0.22 | −0.09 | 0.926 | |
| White-throated Treerunner | | | | | | |
| ∼Density | Intercept | 0.99 | 1.56 | 0.64 | 0.524 | |
| | Tree size | 0.93 | 0.28 | 3.27 | 0.001 | *** |
| | Tree richness | 0.27 | 0.14 | 1.88 | 0.060 | * |
| | Invasive trees | −0.38 | 0.23 | −1.70 | 0.090 | * |
| ∼Detection | Intercept | −1.84 | 1.85 | −1.00 | 0.320 | |
| | River noise | −0.15 | 0.16 | −0.94 | 0.347 | |
| | Temperature | −0.20 | 0.17 | −1.16 | 0.245 | |
| Chucao Tapaculo | | | | | | |
| ∼Density | Intercept | −1.51 | 0.69 | −2.19 | 0.029 | ** |
| | Euclidean Distance (m) | 0.18 | 0.14 | 1.35 | 0.177 | |
| | Number patches (50 ha) | 0.43 | 0.32 | 1.34 | 0.180 | |
| | Forest (1 ha) | 0.11 | 0.28 | 0.41 | 0.682 | |
| | Forest (50 ha) | 0.89 | 0.24 | 3.68 | 0.000 | *** |
| | Understory density | 0.17 | 0.17 | 0.99 | 0.323 | |
| | Tree richness | −0.02 | 0.22 | −0.10 | 0.921 | |
| | Invasive trees | −0.53 | 0.34 | −1.58 | 0.113 | |
| | House density | −3.12 | 4.19 | −0.74 | 0.456 | |
| ∼Detection | Intercept | −0.10 | 0.67 | −0.16 | 0.876 | |
| | River noise | 0.07 | 0.37 | 0.19 | 0.849 | |
| | Temperature | 0.25 | 0.34 | 0.73 | 0.465 | |
| Magellanic Tapaculo | | | | | | |
| ∼Density | Intercept | −0.21 | 0.60 | −0.35 | 0.726 | |
| | Forest (1 ha) | 0.50 | 0.20 | 2.56 | 0.011 | ** |
| | Shrub (50 ha) | −0.76 | 0.36 | −2.13 | 0.033 | ** |
| | Tree size | −0.80 | 0.34 | −2.37 | 0.018 | ** |
| ∼Detection | Intercept | −1.06 | 0.80 | −1.31 | 0.189 | |
| | River noise | −0.36 | 0.24 | −1.46 | 0.144 | |
| | Temperature | 0.29 | 0.31 | 0.95 | 0.344 | |
| Green-backed Firecrown | | | | | | |
| ∼Density | Intercept | 1.48 | 0.74 | 2.01 | 0.044 | ** |
| | Number patches (50 ha) | −0.03 | 0.10 | −0.32 | 0.752 | |
| | Forest (1 ha) | 0.22 | 0.10 | 2.26 | 0.024 | ** |
| | Shrub (50 ha) | −0.03 | 0.12 | −0.25 | 0.801 | |
| | Invasive trees | −0.21 | 0.12 | −1.83 | 0.067 | * |
| ∼Detection | Intercept | −1.04 | 1.02 | −1.02 | 0.309 | |
| | River noise | 0.16 | 0.13 | 1.18 | 0.236 | |
| | Temperature | −0.21 | 0.13 | −1.59 | 0.113 | |
| Des Murs’s Wiretail | | | | | | |
| ∼Density | Intercept | 2.24 | 1.32 | 1.70 | 0.089 | * |
| | Shrub (50 ha) | −1.02 | 0.54 | −1.87 | 0.062 | * |
| | Tree size | 0.72 | 0.38 | 1.88 | 0.060 | * |
| | Understory density | 0.16 | 0.15 | 1.07 | 0.285 | |
| | Invasive trees | −0.18 | 0.32 | −0.55 | 0.585 | |
| ∼Detection | Intercept | −4.29 | 1.29 | −3.34 | 0.001 | *** |
| | River noise | −0.34 | 0.21 | −1.61 | 0.108 | |
| | Temperature | −0.07 | 0.21 | −0.33 | 0.743 | |
| House Wren | | | | | | |
| ∼Density | Intercept | 1.23 | 0.43 | 2.85 | 0.004 | *** |
| | Number patches (50 ha) | 0.00 | 0.10 | −0.01 | 0.990 | |
| | Forest (1 ha) | 0.04 | 0.12 | 0.32 | 0.751 | |
| | Forest (50 ha) | −0.45 | 0.14 | −3.31 | 0.001 | *** |
| | Shrub (50 ha) | 0.00 | 0.11 | −0.04 | 0.967 | |
| | Tree size | 0.48 | 0.19 | 2.51 | 0.012 | ** |
| | Understory density | −0.17 | 0.10 | −1.75 | 0.080 | * |
| | Tree richness | −0.05 | 0.12 | −0.45 | 0.653 | |

(*continued on next page*)

**Table 3** (*continued*)

| | | Estimate | SE | z | P-value | |
|---|---|---|---|---|---|---|
| | Invasive trees | 0.20 | 0.11 | 1.83 | 0.067 | * |
| | House density | 0.30 | 0.31 | 0.97 | 0.332 | |
| ~Detection | Intercept | −0.77 | 0.65 | −1.18 | 0.238 | |
| | River noise | −0.42 | 0.17 | −2.38 | 0.017 | ** |
| | Temperature | 0.30 | 0.15 | 1.99 | 0.046 | ** |
| Austral Thrush | | | | | | |
| ~Density | Intercept | 1.68 | 0.34 | 4.94 | 0.000 | *** |
| | Invasive trees | −0.13 | 0.08 | −1.68 | 0.093 | * |
| ~Detection | Intercept | −0.47 | 0.54 | −0.88 | 0.381 | |
| | River noise | −0.08 | 0.11 | −0.69 | 0.489 | |
| | Temperature | 0.09 | 0.11 | 0.87 | 0.384 | |
| Fire-eyed Diucon | | | | | | |
| ~Density | Intercept | 1.59 | 1.61 | 0.99 | 0.322 | |
| | Number patches (50 ha) | 0.10 | 0.15 | 0.66 | 0.512 | |
| | Forest (1 ha) | −0.12 | 0.15 | −0.79 | 0.432 | |
| | Shrub (50 ha) | 0.10 | 0.12 | 0.77 | 0.444 | |
| | Tree richness | −0.19 | 0.17 | −1.15 | 0.251 | |
| ~Detection | Intercept | −2.26 | 1.80 | −1.26 | 0.209 | |
| | River noise | −0.31 | 0.16 | −1.88 | 0.059 | * |
| | Temperature | 0.03 | 0.14 | 0.23 | 0.821 | |
| Rufous-collared Sparrow | | | | | | |
| ~Density | Intercept | −0.36 | 0.31 | −1.14 | 0.255 | |
| | Forest (50 ha) | −0.45 | 0.21 | −2.09 | 0.037 | ** |
| | Understory density | −0.40 | 0.20 | −2.00 | 0.046 | ** |
| ~Detection | Intercept | −0.43 | 0.52 | −0.84 | 0.404 | |
| | River noise | −0.12 | 0.32 | −0.36 | 0.720 | |
| | Temperature | 0.74 | 0.31 | 2.36 | 0.018 | ** |

in the open matrix, such as Black-chinned Siskin, may use the adjacent forest for protection, to find food or as stepping-stones (sensu Saura et al., 2011) while moving from one habitat patch to another (Estades and Temple, 1999; Boesing et al., 2021). Similarly, habitat generalist birds that spend most of their time in the forest or shrubby vegetation, such as House Wren, may use the adjacent open matrix for foraging (Estades and Temple, 1999). Therefore, while small increases of forest in the immediate vicinity of point count stations may not affect the density of these species, landscape dominated by forest may reduce the ability of individuals to access complementary resources found in open habitat.

### 4.2. *Riparian forest patch-area and configuration*

The density of the Huet-huet was highest in wide and large forest and it was lower in riparian strips, a sign that the species can use those narrow habitats. However, we did not find a single individual in small and isolated riparian forest. Our results are consistent with previous studies that have shown that Black-throated Huet-huet avoids crossing open vegetation such as crops and pastures (Castellón and Sieving, 2006), similar to the Chestnut-throated Huet-huet (*Pteroptochos castaneus*, Rhinocryptidae), its sister species (Castillo et al., 2018). During dispersal, individual Black-throated Huet-huets rarely move between separated forests across the intervening open land (Castellón and Sieving, 2006), and a reproductive pair needs at least 10 ha of connected forest to maintain a breeding territory (De Santo et al., 2002). This suggests that large forests or narrow strips between smaller patches of habitat are necessary for this species to persist. Edge effects are less important because Black-throated Huet-huet can successfully nest, feed, and disperse in narrow forest strips (De Santo et al., 2002). Our results are consistent with findings in the Amazon, where connected riparian forest retained significant avian phylogenetic diversity in a palm oil agricultural landscape (Cardoso et al., 2021).

### 4.3. *Habitat characteristics*

All riparian forest, including large and wide riparian forest, had vegetation characteristics that are typical of secondary and degraded forest in agricultural landscapes, e.g., mean tree diameters are small and non-native species are frequent. This is typical for riparian forests in agricultural landscapes elsewhere, due to livestock grazing, selective logging, historical clear-cut, exotic plant invasion, and changes in river flow due to dam construction are widespread causes of forest degradation (Martin and Mcintyre, 2007; Capon et al., 2013; González et al., 2017). As a result, many riparian forests have a simplified understory, lack old trees, and coarse woody debris and snags in different states of decay, and have soil compaction, and reduced vegetative litter, and highly impoverished plant communities (Nagy et al., 2015). Forest degradation can be a problem for birds that rely on specific vegetation characteristics (e.g., Caviedes and Ibarra, 2017). We found that mean tree diameter was the best explanatory variable for the density of one habitat specialist, the White-throated Treerunner, consistent with previous studies (Ibarra and Martin, 2015). In addition, we found that several species decreased in density in forests dominated by non-native invasive trees, a new finding for our study area, but one that has been previously reported for birds in North America (e.g., Nelson et al., 2017).

### 4.4. *Caveats and limitations*

Even though we collected data only during one breeding season, rarefaction curves indicate that we captured most species present within each riparian forest type (See supplementary information). We also found consistent results between the two approaches we applied, a multivariate model with selected variables and a global model, all variables included. Furthermore, our results were consistent with previous estimates of bird density and species' known associations with landscape and habitat characteristics (Vergara and Armesto, 2009; Ibarra and Martin, 2015). We focused our study on species for which we had sufficient data to incorporate detectability in estimates of density and assessed the fit of our models to test for goodness of fit. Our assessments showed that models had little overdispersion and that one or more of the variables we measured were able to explain variation in bird's density. We did not find baseline detection estimates for our species to compare our results with previous findings (because detection was either not estimated or not reported) (e.g., Estades and Temple, 1999; Ibarra and Martin, 2015; Vergara and Armesto, 2009). We note that some of our estimated detection parameters were quite low (e.g., the lowest was 0.03 for Des Murs's Wiretail).

## 5. Conclusion

We studied birds in remnants of the once-continuous forest that covered much of the temperate region of Chile prior to European colonization. Our results provide data useful for establishing conservation strategies that can support populations of forest affiliated species which are sensitive to forest habitat loss, but that have persisted within the agricultural landscape for 170+ years, thus keeping biotic homogenization at bay (e.g., Le Viol et al., 2012). One conservation strategy is to focus on bolstering habitat for the most sensitive bird species, those whose populations exhibit the clearest signal in response to landscape and habitat characteristics. In our study area, these are the understory specialist birds that depend on higher amount of forest in the landscape (Black-throated Huet-huet) and other specialist species that responded strongly to specific characteristics of the vegetation, e.g., tree size and invasion by non-native trees. An existing regulation in Chile (Ministerio de Agricultura, 2011) enforces maintaining intact riparian forest along natural watercourses to protect water quality. Our results suggest that this additional vegetation can also help maintain forest affiliated species by adding forest cover where forest cover is low. In addition, it would be

**Fig. 4.** Association of 16 birds with landscape characteristics forest within 60 m (1 ha), forest within 400 m (50 ha), shrubland within 400 m (50 ha), number of patches (50 ha) and house density. The x-axis shows the coefficient of multivariate models for each species. The 95 % confidence interval is shown as a horizontal line. Relationships where the line did not include zero are significant.

beneficial to encourage landowners to halt degradation of riparian forest. For example, establishing stock ponds for cattle away from riverbanks, fencing to reduce livestock access to riparian forest, and implementing silvicultural activities to maintain trees of various native species and varying sizes could help reduce degradation of riparian forests (Johnson et al., 2011) and foster the continued presence of forest specialist bird species within the agricultural landscapes of temperate Chile.

## CRediT authorship contribution statement

**Isabel M. Rojas:** Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Volker C. Radeloff:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition. **Jennifer D. McCabe:** Writing – review & editing, Methodology, Formal analysis. **J. Tomás Ibarra:** Writing – review & editing, Methodology, Conceptualization. **Anna M. Pidgeon:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

## Declaration of Generative AI and AI-assisted technologies in the writing process

We did not use of artificial intelligence in scientific writing and any other aspect of this manuscript.

## Declaration of competing interest

There are no direct financial benefits for the authors that could result from the publication of this manuscript.

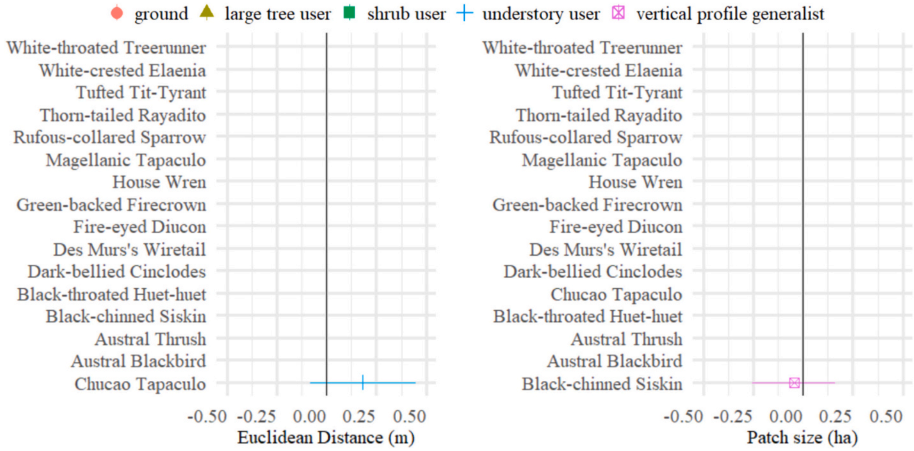

**Fig. 5.** Association of 16 birds with patch-area and configuration metrics (patch size and Euclidean distance). The x-axis shows the coefficient of multivariate models for each species. The 95 % confidence interval is shown as a horizontal line. Relationships where the line did not include zero are significant.

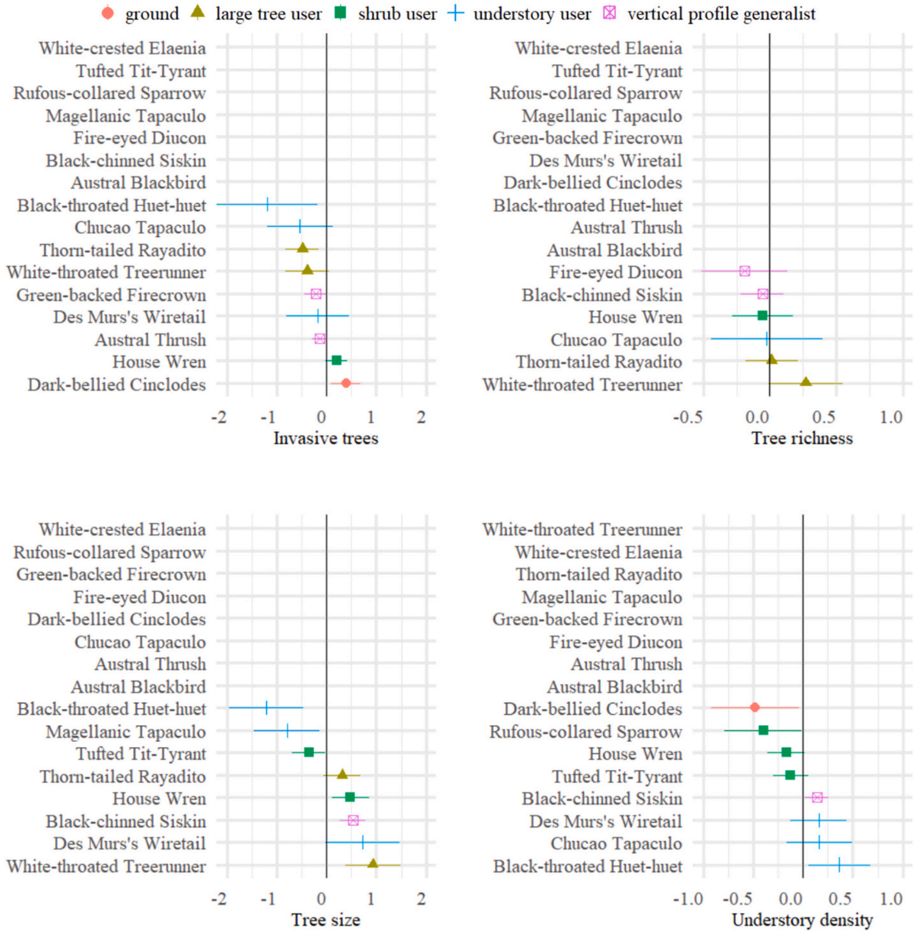

**Fig. 6.** Association of 16 birds with habitat characteristics (tree richness, understory density, tree size and Invasive tress). The x-axis shows the coefficient of multivariate models for each species. The 95 % confidence interval is shown as a horizontal line. Relationships where the line did not include zero are significant.

## Data availability

Data will be made available on request.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110727.

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