



## BIRD COMMUNITIES ALONG A POST-DISTURBANCE SUCCESSIONAL GRADIENT IN ANDEAN FORESTS OF BOSQUE PEHUÉN PARK, ARAUCANÍA REGION, SOUTHERN CHILE

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**Abstract** · In southern Chile, the most diverse forest ecosystems are located between 36° and 40° S, in the same areas where agriculture and industrial forestry are concentrated. We studied bird assemblages in Bosque Pehuén Park (39°25'S), along a human disturbance gradient from early successional forest mixed with grasslands to barely disturbed old-growth forest. We surveyed birds across all of the disturbance gradients at 18 points from 860 to 1260 m a.s.l. using point-count methods. Each point was surveyed five times per year, during the Austral summer of 2015 and 2016. Our results confirmed that there is a group of forest birds strongly related to old-growth forest, while others were characteristic of open areas. Secondary forests shared bird species with both old-growth forests and disturbed areas, and presented lower abundance of forest bird specialists. The old-growth forest bird community proved to be small and was dominated by Thorn-tailed Rayadito (*Aphrastura spinicauda*, Furnariidae) and White-crested Elaenia (*Elaenia albiceps*, Tyrannidae). Most studies in this region have taken place in secondary forests, which are characterized by a lower presence of specialists and the inclusion of birds from open areas. Here, we provide a reference bird community for Andean forests, and we argue that bird communities in secondary forests are not a good control to analyze the effects of human disturbances. We emphasize the need to conserve the last remnants of the old-growth forest found in these regions.

**Resumen** · Comunidades de aves a lo largo de un gradiente de sucesión post-perturbación en los bosques andinos del parque Bosque Pehuén, región de la Araucanía, sur de Chile

En Chile, los bosques templados con mayor biodiversidad se encuentran entre 36° y 40°S, en las mismas áreas donde se concentran la actividad agrícola y las plantaciones forestales de árboles exóticos. Estudiamos los ensambles de aves en el parque Bosque Pehuén (39°25'S), a lo largo de un gradiente de perturbación humana desde bosques sucesionales tempranos mezclados con pastizales hasta bosques antiguos mínimamente perturbados. Usando puntos de escucha, registramos las aves presentes en 18 puntos distribuidos entre los 860 y los 1260 m s.n.m. cubriendo todo el gradiente de perturbación. Cada punto fue muestreado 5 veces por año, durante el verano austral de 2015 y 2016. Nuestros resultados confirmaron que hay un grupo de aves fuertemente relacionadas con bosques antiguos, mientras que otras fueron características de áreas abiertas. Los bosques secundarios compartieron especies de aves con bosques antiguos y zonas alteradas, y presentaron una menor abundancia de especialistas en aves de bosque. Se encontró que la comunidad de aves del bosque antiguo era pequeña, dominada por Rayadito Común (*Aphrastura spinicauda*, Furnariidae) y Fiofio Crestiblanco (*Elaenia albiceps*, Tyrannidae). La mayoría de los estudios en esta región se han llevado a cabo en bosques secundarios, que se caracterizan por una menor presencia de especialistas y la inclusión de aves de áreas abiertas. Aquí proporcionamos una comunidad de aves de referencia de los bosques andinos, y afirmamos que las comunidades de aves en los bosques secundarios no son un buen control para analizar los efectos de las perturbaciones humanas. Hacemos hincapié en la necesidad de conservar los últimos remanentes de bosques antiguos de estas regiones.

**Key words:** Forest birds · Forest disturbances · *Nothofagus* forests · Old-growth forest · Wildlife-habitat relationships

### INTRODUCTION

Human disturbances, such as the exploitation of old-growth forests and its replacement by secondary forests have detrimental effects on forest bird specialists. Forest degradation can deplete specific guilds of birds, such as understory birds, canopy specialists or cavity nesting birds (Thiollay 1999, Cockle et al. 2011), while favoring species that are able to tolerate and thrive in human-modified landscapes, homogenizing the biota (Devictor et al. 2008). Along disturbance gradients, bird diversity can be higher in ecotone zones; however, specialists may remain restricted to undisturbed habitats (O'Dea & Whittaker 2007).

South American temperate rainforests (SATRs) cover a narrow stretch of southern Chile and westernmost Argentina (Armesto et al. 1998). These forests are a biodiversity hotspot because of their high percentage of endemic species, and the threats they face, including land conversion to pastures, agricultural fields and exotic tree plantations (Olson & Dinerstein 1998, Mittermeier et al. 2005, Lara et al. 2012). The SATRs are inhabited by 40 bird species, with around 25 species strongly associated to old-growth forests (Vuilleumier 1985, Jaksic & Feinsinger 1991, Rozzi et al. 1996, Díaz et al. 2005). This bird assemblage is considered impoverished by glaciations and long-term isolation from other South American forests, representing a

Receipt 14 March 2017 · First decision 7 October 2017 · Acceptance 12 June 2019 · Online publication 2 August 2019

Communicated by Cintia Cornelius © Neotropical Ornithological Society

small and highly endemic bird community (Vuilleumier 1985). Due to their naturally low diversity, this community could serve as a good study model to understand the effects of human impacts on forest birds.

Bird species in SATRs are associated with specific structural elements: at least seven bird species depend on large old trees for foraging or nesting while five inhabit dense bamboo thickets in the forest's understory (Reid et al. 2004, Díaz et al. 2005, Willson et al. 2014, Altamirano et al. 2017). Habitat fragmentation decreases bird diversity in SATRs, specifically depleting understory bird abundance due to their inability to cross open areas (Willson et al. 1994, Sieving et al. 1996), while the transformation of old-growth to secondary forest is detrimental for birds associated to large trees, due to the loss of these trees with the consequent reduction of structural diversity in secondary forest (Díaz et al. 2005, Cornelius 2008, Altamirano et al. 2017).

In southern Chile, the most diverse forests in terms of plant and animals are located between 36°S and 40°S (Armesto et al. 1998, Villagrán & Hinojosa 2005), the same regions where most agricultural and industrial development occurs (Armesto et al. 1998). Most remnant forests are located in the Andean highlands since the lowlands have been converted into agricultural lands, pastures, exotic tree plantations and urban development, while the native forests that remain there are mostly second-growth patches (Armesto et al. 1998, 2010; Lara et al. 2012, Altamirano 2014). Old-growth forests in the highlands persist in inaccessible areas under more extreme climatic conditions, and are less diverse in plant and bird species than their lowland counterparts (Altamirano 2014).

The few studies that have documented the composition of forest bird communities in Andean forests in southern South America have found different dominance of birds, with strong associations between structural diversity and bird diversity (Estades 1997), and a strong association between the abundance of cavity-nesting birds and large old trees (Altamirano et al. 2017). However, very few studies relate forest disturbance (including the human exploitation that has transformed old-growth into secondary forests) with avian diversity in Andean forests (Ibarra et al. 2010, Altamirano et al. 2017). Here, we studied the current composition of bird species in forests subjected to human disturbances in the Bosque Pehuén Park, a privately protected area in the southern Andes (39°26'S). The disturbed areas of this park represent the same human disturbances as most areas throughout the southern Andes; nonetheless, this park still maintains a well-preserved belt of old-growth forest that is very valuable as a control area. We predicted that old-growth forest would host more birds associated with large-old trees and dense understory, while secondary forest, as well as shrublands and grasslands, would host a more diverse bird community, consisting mostly of habitat generalists. This study is the first report of an ongoing long-term monitoring program devoted to analyzing how bird communities of old-growth and secondary forest change in the long run in Bosque Pehuén Park.

## METHODS

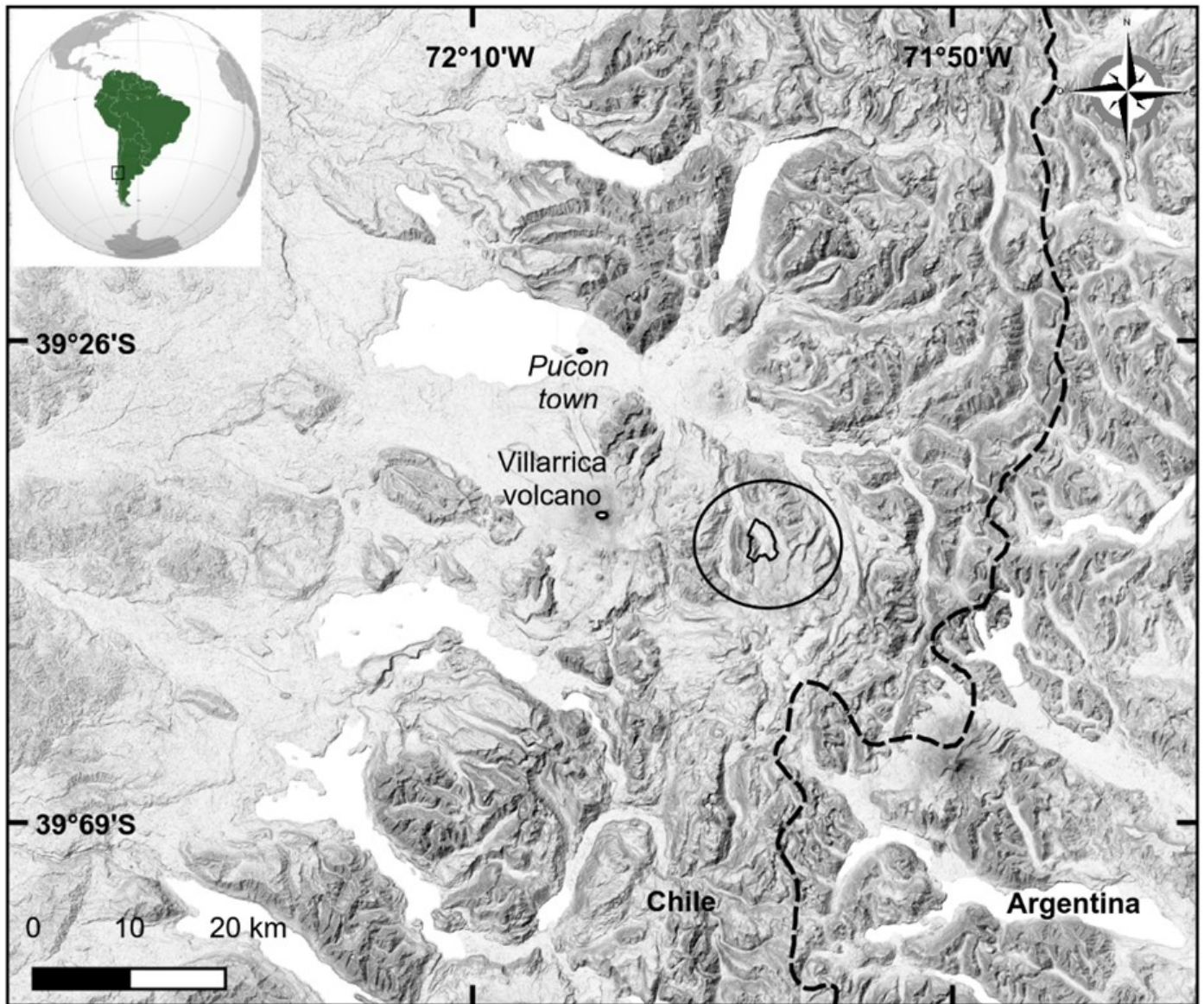
**Study site.** Our study was conducted in the Bosque Pehuén Park, a protected area of 882 ha owned by the Fundación Mar Adentro, a Chilean non-profit conservation organization.

This forest is located in the southern Chilean Andes (39° 25'52"S, 71°45'28"W), and from 860 to 1400 m a.s.l. (Figure 1). The climate in the area is cold temperate, with frequent snow cover in winter and occasional thunderstorms in summer. The annual temperature and annual precipitation recorded at the closest weather station in the city of Curarrehue (395 m a.s.l., 15 km away from the park) are 10.8°C and 2075 mm, respectively (Agromet 2012). The park has more extreme weather conditions than nearby lowland areas, with frequent snow in winter and lower temperatures due to its altitude and location in the Andean range.

Bosque Pehuén Park remained covered by an extensive old-growth undisturbed forest until the late 1960s, when it was no longer protected as part of Villarrica National Park and, instead, was given to settlers. Later, around 1978, this forest was subjected to intensive forestry exploitation; all of the trees that were useful for timber were logged. After two years of intensive exploitation, logging activities ceased and an extensive secondary forest developed. For 20 years after this exploitation, the lowlands were dedicated to cattle grazing (around 100 cows) and occasional logging, until 2006 when the land was acquired by the Fundación Mar Adentro, and the forests became a protected area. At this time, all of the logging and grazing activities were discontinued.

As a result of this recent history of exploitation (in the last 40 years), all areas below 960 m a.s.l. are currently covered by a mosaic of secondary forests of *Nothofagus obliqua*, *N. dombeyi*, and *N. nervosa* (Nothofagaceae), shrubs, grasslands, and bamboo thickets of *Chusquea culeou* (Poaceae). There are extensive second-growth forests between 960 and 1030 m a.s.l., dominated by *N. nervosa* and *N. dombeyi* trees, that are approximately 40 years old and around 10 to 40 cm in diameter at the breast height (DBH), with basal areas of 80 m<sup>2</sup>/ha and around 1500 trees/ha (Díaz et al. 2017). These secondary forests have a disperse understory cover and abundant coarse woody debris partially originated by past logging activities. Between 1030 and 1200 m a.s.l. a belt of old-growth forest with low disturbance still persists; some trees there are more than 300 years old and greater than 1.5 m in DBH. The basal area reaches 113 m<sup>2</sup>/ha with around 400 trees/ha, dominated by *N. nervosa* and *N. dombeyi* trees (Díaz et al. 2017). Throughout this belt, the forest floor is covered by abundant coarse woody debris and dense understory, mostly bamboo thickets. Above 1200 m a.s.l., the old-growth forest is dominated by *N. dombeyi*, *N. pumilio*, and *Araucaria araucana* (Araucariaceae), and it is mixed with secondary forests, shrublands, and extensive grasslands with sparsely fallen logs from past fires. These grasslands most likely originated after ranchers burned the highland forests near the treeline, thus creating extensive pastures for cattle grazing (Quezada 2008, Díaz et al. 2017).

**Study design.** We traced an altitudinal transect from 860 to 1260 m a.s.l. across forests with different degrees of exploitation. Along this transect, we identified 18 points separated by a horizontal distance of 200 m (Figure 2). At each point, we conducted bird censuses using the point-count method (Ralph et al. 1995). This method consisted of recording all of the individuals seen or heard in a fixed radius of 50 m around the pre-identified point (Hutto et al. 1986). We recorded all individual birds detected in the radius (by their songs or by direct observation) for 8 minutes, following the protocol of



**Figure 1.** Map of the location of Bosque Pehuén Park (inside the circle), in the Andes of southern Chile, close to the city of Pucón, in the Araucanía region.

Willson et al. (1994, 1996) and Jiménez et al. (2000) for Chilean forest birds. All points were surveyed once a day for five days. Each point was surveyed on non-rainy days from dawn to two or three hours after dawn (07:00 to 09:00 am, GMT - 04:00) in January, 2015 and between January and March, 2016, during the summer of the Austral hemisphere. Censuses were conducted by three experienced observers. The census' times, dates and order of the observers were randomized to avoid any bias in the results.

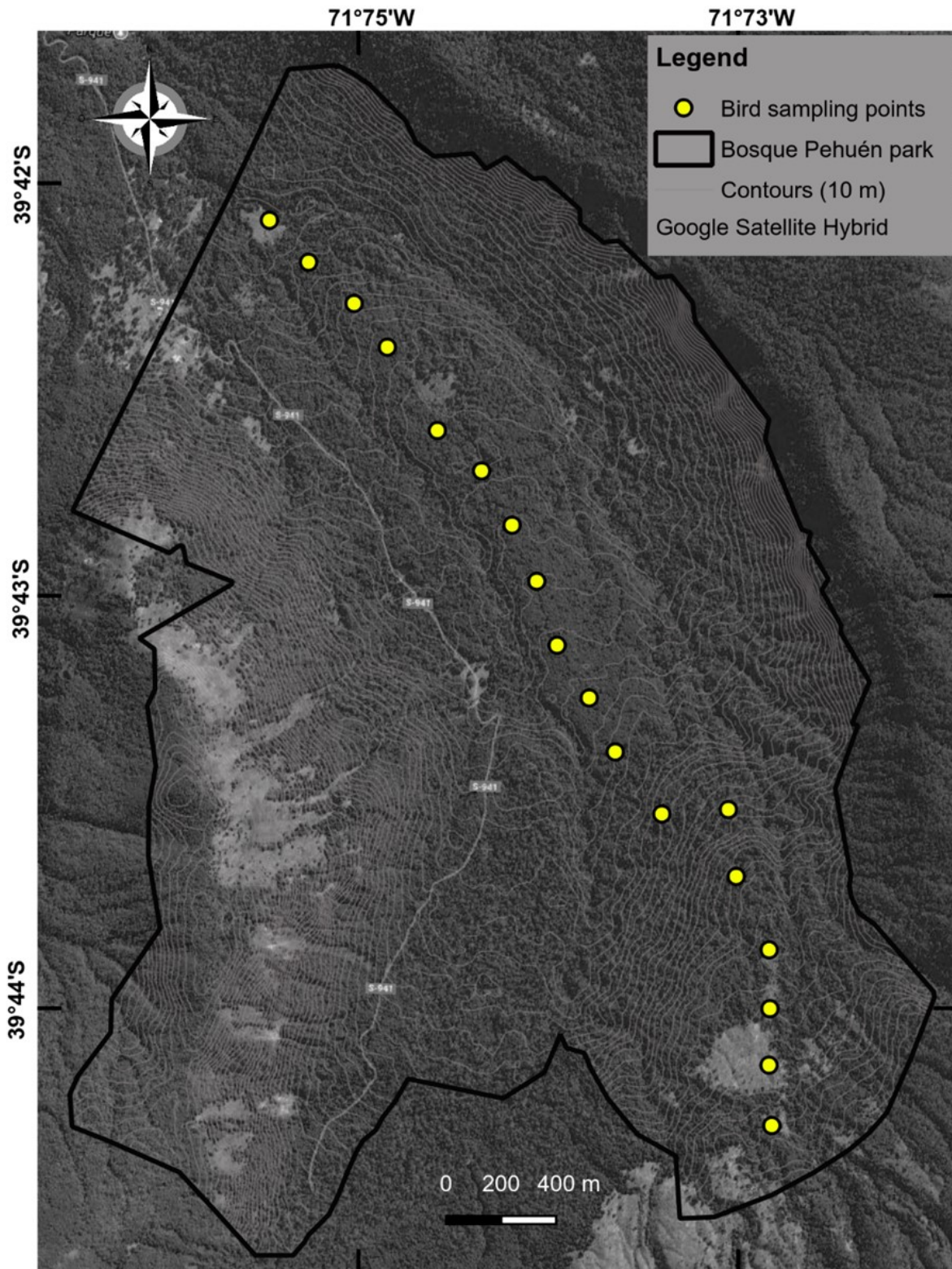
The transect crossed four main environments resulting from the past forest exploitation. Between 860 and 960 m a.s.l. there are shrublands, grasslands, and homogeneous and young secondary forests (hereafter referred to as SHRUB). The study area between 960 and 1030 m a.s.l. was covered by a more advanced secondary forest with scattered patches of old-growth forests (hereafter SECFOR). Between 1030 and 1200 m a.s.l. the transect crossed well-preserved old-growth forest (hereafter OLDFOR), and between 1200 and 1260 m a.s.l. there is a scattering of secondary forests, but shrublands and grasslands dominate this area (hereafter HIGSHRUB). The first four points were associated with the SHRUB, the following six points with the SECFOR, the next

four points with the OLDFOR, and the last four points with the HIGSHRUB (Figure 2).

The local forest bird community is small, comprised of around 25 species (Díaz et al. 2005), all of which are easily identifiable by direct observation or by their vocalizations. In general, these birds are not afraid of humans. In addition, we were not interested in obtaining absolute measures of population densities; instead, we aimed to compare the bird species assemblage as a whole with others forests, comparing birds among a similar type of ecosystems. Consequently, following Buckland et al. (2011), we assumed that any bias associated with bird detectability was constant among treatments and preferred the classical point-count method over other density estimations for the characterization of bird communities.

We characterized the disturbance gradient using Landsat satellite images from Google Earth (Google Inc.) for the year 2015. For each of the 18 census points, we defined a circle with a radius of 50 m, and based on the image we defined what percentage of the circle was covered by grassland, shrubs, secondary forest and old-growth forest. Subsequently, we validated our classification comparing what we classi-



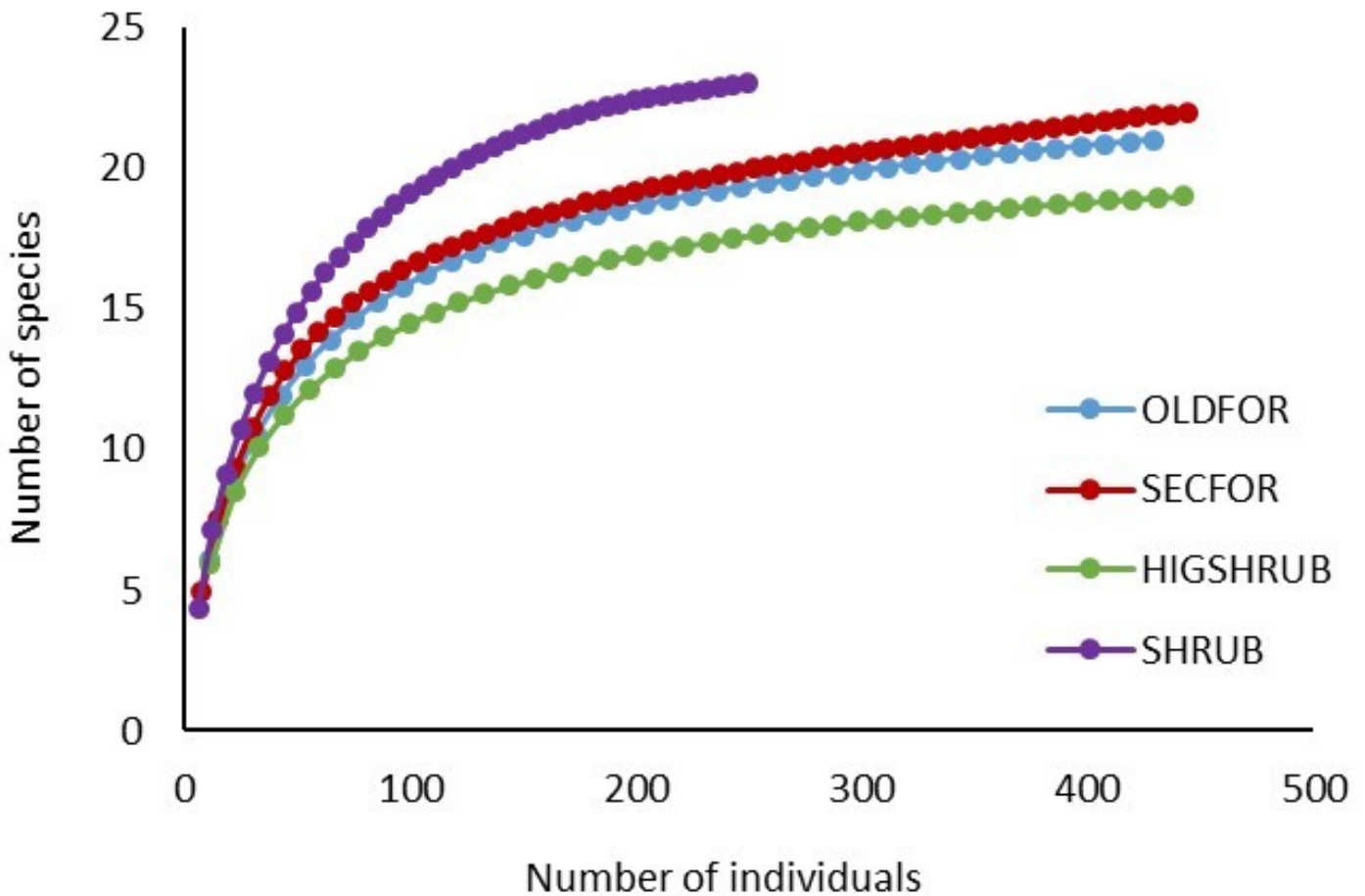


**Figure 2.** Map of the Bosque Pehuén Park showing the location of each sampling point (yellow points), along an altitudinal gradient from 860 to 1260 m a.s.l.; indicated are contours each 10 m altitude. Forests are in dark grey and the open areas and shrublands are in light grey.

fied as different habitat in the images with what we found in the field. On a smaller scale, we characterized the DBH (diameter at breast height in cm) of all of the trees with diameters > 5 cm in a 20 m long and 2 m wide transect across the center of each plot. We also assessed the abundance of large living trees and large snags (> 80 cm DBH) in a 10 m radius around the central point.

**Data analysis.** We conducted a rarefaction analysis to define both the effectiveness of the sampling effort and to compare

bird species richness among the four studied environments. Rarefaction curves allow for the comparison of environments while avoiding the over-estimation of species richness in areas where more data is available. Also, rarefaction avoids the bias in the number of species detected due to the increased probability of species detection in areas where birds were more abundant, by plotting the number of species detected in function of the number of individuals observed. Consequently, in this study rarefaction permitted better comparisons among different areas, despite the fact that



**Figure 3.** Rarefaction analysis between the number of individuals and the number of bird species recorded in point-counts in the Bosque Pehuén Park, Chile. Data from 2015 and 2016 were pooled. Abbreviations mean: HIGSHRUB: Grasslands, shrublands and forest in the highlands; OLDFOR: Old-growth Forest; SECFOR Secondary Forest; and SHRUB: Grassland, shrublands and forest in lowlands. This figure showed that SHRUB host the highest number of bird species, followed by OLDFOR and SECFOR, while the lowest species richness was in HIGSHRUB.

surveys failed to detect all possible species (Gotelli & Colwell 2011). This procedure includes Monte Carlo simulations as well, which deliver an average value of species richness with a confidence interval of 95% (Colwell 2006). Rarefaction analyses were conducted using the software EstimateS Win 8 (Colwell 2006).

We compared the similarities and/or differences in species composition in different environments using the Bray-Curtis similarity index, with EstimateS Win 8 software. This index involves the presence/absence of species and the abundance of individuals to make more informed comparisons (Chao et al. 2004). If the value obtained is close to 1, the environments are considered to be similar to one another, whereas if this value is close to zero the environments are assumed to be different in terms of species composition and abundance. We compared the species composition among environments by conducting a Permutational Multivariate Analysis of Variance (Permanova), a non-parametric alternative to a multivariate analysis of variance (Anderson 2008) using the vegan package (Oksanen et al. 2018) in R (R core team 2015). Permanova allowed us to compare differences in bird composition and abundance among environments, by evaluating the differences between groups, testing if their centroids were equivalent. Since we were not interested in the yearly variations in bird populations, we controlled for the year effect in order to focus the comparison only among environments. Finally, we used Non-metric Multidimensional Scaling (NMDS) to relate bird species with the amount of old-

growth forest, secondary forest, shrubs and grassland at each point along the transect. The Bray-Curtis distance was used as a measure of ecological similarity for NMDS ordination. PAST (Hammer et al. 2001) was used for NMDS analyses.

## RESULTS

**Bird species.** We recorded 29 bird species belonging to 16 families (Table S1, Supplementary Material online). Nine bird species were endemic to the SATR, and 11 were restricted to southern South American habitats (Table S1). The rarefaction analysis indicated that the sampling effort recorded over 90% of the species that could be found in each environment. The rarefaction analysis also showed that the environment with the highest number of bird species was SHRUB, followed by OLDFOR and SECFOR, which presented similar levels of species richness. The environment with the lowest species richness was HIGSHRUB (Figure 3). Total abundance was greater in OLDFOR and HIGSHRUB, followed by that in SHRUB and SECFOR (Table S1).

The Permanova results showed differences in species composition among these four environments (Table S1, Table 1). The White-crested Elaenia (*Elaenia albiceps*) was the most abundant bird in all four environments, representing between 18% and 32% of all of the individuals observed. The Thorn-tailed Rayadito (*Aphrastura spinicauda*) was the second-most abundant bird in OLDFOR, SECFOR, and SHRUB,

**Table 1.** Results from Permanova analyses, comparing bird abundance and composition among four environments in Bosque Pehuén Park, southern Chile: 1) Old-growth forest (OLDFOR), 2) Secondary forest (SECFOR), 3) Grasslands, shrublands, and forest in lowlands (SHRUB), and 4) Grasslands, shrublands, and forest in highlands (HIGSHRUB).

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F	P
Environment	3	0.9711	0.32369	3.649	< 0.001
Residuals	32	2.8386	0.08871		
Total	35	3.8097			

while the Black-chinned Siskin (*Spinus barbatus*) was the second-most abundant bird in HIGSHRUB. The third-most abundant bird varied among environments; in OLDFOR it was the Patagonian Sierra-Finch (*Phrygilus patagonicus*), in SECFOR and SHRUB it was the Green-backed Firecrown (*Sephanoides sephanioides*), and in HIGSHRUB it was the House Wren (*Troglodytes aedon*), the latter being rarely recorded in the other environments (Table S1).

White-crested Elaenia, Chucao Tapaculo (*Scelorchilus rubecula*), and Thorn-tailed Rayadito were recorded in most point-counts along the altitudinal gradient, while House Wren, Austral Thrush (*Turdus falcklandii*), Austral Blackbird (*Curaeus curaeus*), and Tufted Tit-tyrant (*Anairetes parulus*) were present mostly in points dominated by shrubs (Figure 4). The remaining species were mostly recorded in one or two specific environments. Magellanic Woodpecker (*Campophilus magellanicus*) and Black-throated Huet-huet (*Pteroptochos tarnii*) were occasionally recorded in the OLDFOR and SECFOR (Table S1). The Bicolored Hawk (*Accipiter bicolor*) was recorded only in the SECFOR, while the Des Murs' Wiretail (*Sylviorthorhynchus desmursii*) was only registered in the OLDFOR (Table S1). The remaining species were mostly recorded in one or two specific environments.

Bird species composition showed different levels of similarity among environments. The bird species composition of the SECFOR was more similar to that found in the OLDFOR than that of the other environments (Table 2), while SHRUB differed the most, especially when compared to OLDFOR and HIGSHRUB (Table 2).

**Vegetation structure and cover.** The OLDFOR had a higher basal area and the greatest number of large trees and snags of all of the environments, with 1.82 m<sup>2</sup> of basal area/point, and 0.75 large trees or snags/point (Table 3), followed by SECFOR with a basal area of 0.58 m<sup>2</sup>/point and 0.33 large trees or snags/point. HIGSHRUB had lower basal areas and fewer large trees and snags, while SHRUB showed practically no large trees or snags (Table 3).

In terms of vegetation cover, over 80% of OLDFOR's surface was found to be covered by old-growth forests (Table 3), but stands of old-growth forests were present in low proportions in all of the remaining environments. SECFOR was dominated by secondary forests with around 25% of its surface covered by scattered patches of old-growth forests. Finally, HIGSHRUB and SHRUB were found to be covered by secondary forest, shrublands, and grasslands. However, HIGSHRUB showed a higher coverage of grasslands and shrublands than SHRUB, while the latter was covered by nearly 50% of scattered patches of secondary forests (Table 3).

**Relationship between vegetation cover and birds.** The

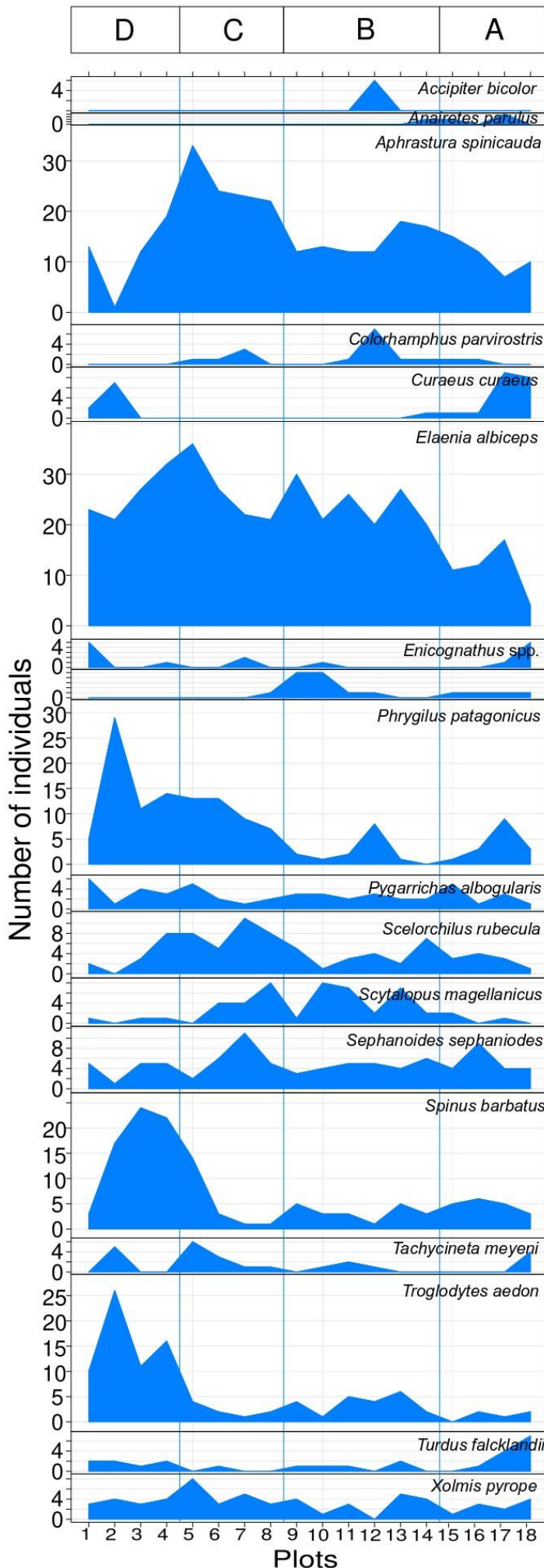
NMDS showed several associations between bird species and the specific vegetation cover in the study area. Thorn-tailed Rayadito, Chucao Tapaculo, Green-backed Firecrown, Magellanic Woodpecker, Black-throated Huet-huet, Black-chinned Siskin, Magellanic Tapaculo (*Scytalopus magellanicus*), and White-crested Elaenia were strongly associated with the points dominated by old-growth and second-growth forests (Figure 5). On the contrary, Austral Thrush, House Wren, and Chilean Blackbird were clearly associated with points dominated by grass and shrubland. The Fire-eyed Diucon (*Xolmis pyrope*) was observed moving frequently between grasslands and the canopy of old-growth forests. Finally, a group of birds consisting of Patagonian Sierra-Finch, Striped Woodpecker (*Veniliornis lignarius*), Chilean Swallow (*Tachycineta meyeni*), and Chilean Pigeon (*Patagioenas araucana*) were observed moving from forests to openings (Figure 5).

## DISCUSSION

Our results indicate that bird species richness, abundance, and composition have been affected by forest disturbances. Most birds in HIGSHRUB were open area species, such as the House Wren, while most birds in OLDFOR were species associated with the understory and large trees. SECFOR and SHRUB presented subsets of old-growth forest birds and birds from open areas. One example of OLDFOR bird is the Thorn-tailed Rayadito, one of the most abundant species closely associated with the large old trees it requires for nesting (Díaz et al. 2005, Cornelius 2008, Altamirano et al. 2017). Similarly, the Des Murs' Wiretail is strongly associated with the *Chusquea* understory (Díaz et al. 2006), and was registered only in OLDFOR due to the dense understory of *Chusquea culeou* found there. All species belonging to the Rhinocryptidae, such as the Chucao Tapaculo, were associated with dense understories and the presence of fallen logs (Reid et al. 2004, Willson et al. 2014), and were clearly associated to OLDFOR as well. House Wren and Patagonian Tyrant (*Colorhamphus parvirostris*) were more abundant in the HIGSHRUB, preferring the mosaic of open areas, thickets and the trees of secondary forests. The Bicolored Hawk, a forest raptor, was only registered in SECFOR but could use the other forest habitat types as well. In fact, the two species of hawks observed present home ranges much larger than our surveyed points, and could include different habitat types. The characteristics of this particular secondary forest, with heterogeneous canopy, and scattered old trees and snags could be more habitable to these hawks than other more homogeneous secondary forests lacking old trees and snags.

These results are consistent with previous studies of Díaz et al. (2005), Willson et al. (1994, 2014), Altamirano (2014) and Altamirano et al. (2017) since they confirm that the forest bird community inhabiting OLDFOR shows clear habitat-





**Table 2.** Bray-Curtis similarity index of bird communities present in the four different environments in the Bosque Pehuén Park, southern Chile. Abbreviations: HIGSHRUB – Grasslands, shrublands and forest in highlands; OLDFOR – Old-growth forest; SECFOR Secondary forest; SHRUB – Grasslands, shrublands and forest in lowlands.

	HIGSHRUB	OLDFOR	SECFOR	SHRUB
HIGSHRUB	1	0.68	0.66	0.599
OLDFOR		1	0.747	0.584
SECFOR			1	0.681
SHRUB				1

associations with structural elements characteristic of old-growth forests. The use of structural elements to understand the presence of specific birds in particular habitats represents an opportunity to conserve and restore degraded environments for birds; i.e., if these elements are conserved, we can expect that birds associated with them will also be present.

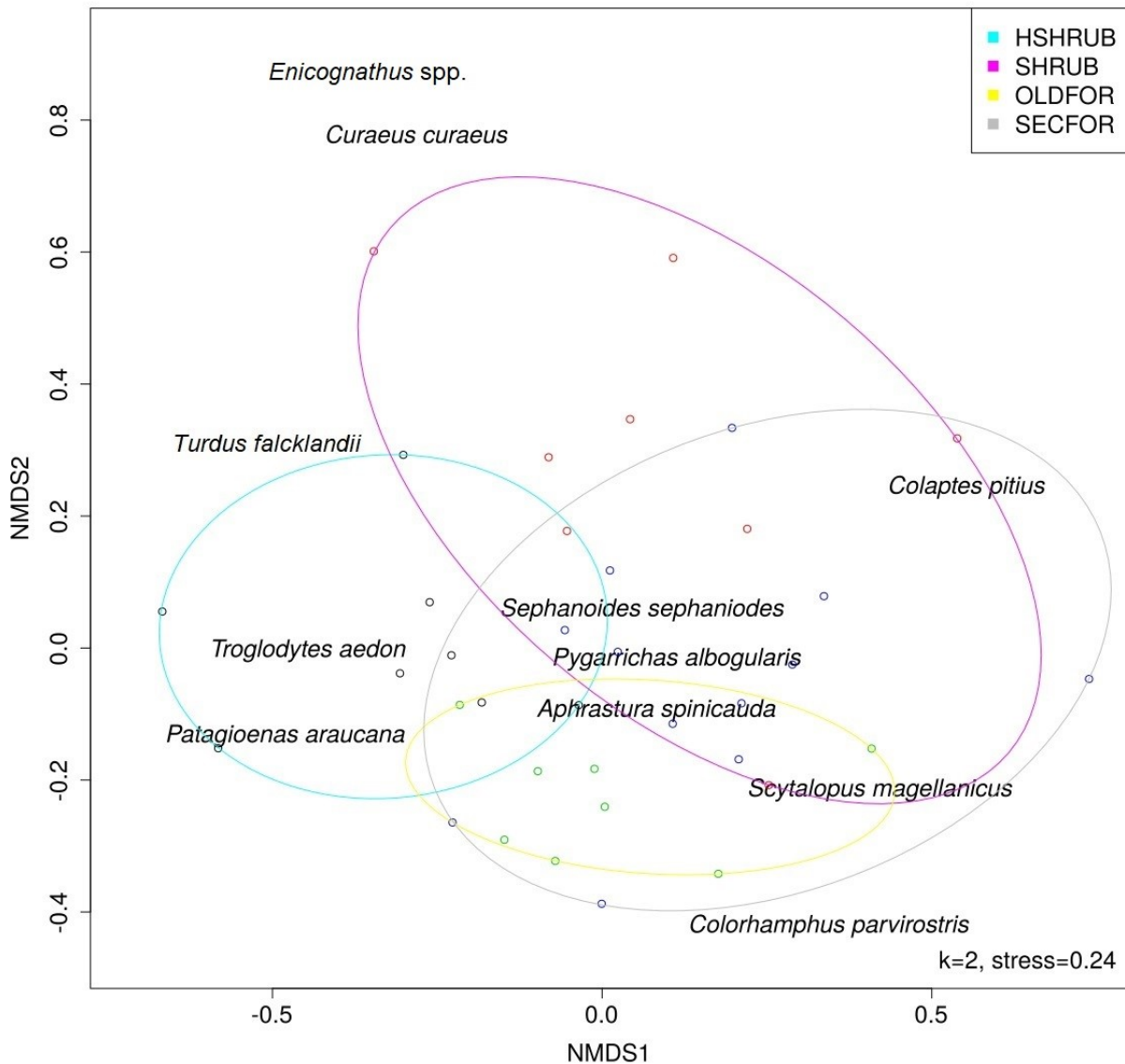
Vuilleumier (1985) recognized that the number of bird species in SATR is small, considering it a depauperated community resulting from geographical isolation and a significant reduction in forest cover during the Quaternary glaciations (Villagrán & Hinojosa 2005). In contrast, birds from open areas are more diverse, with some species invading forests from grasslands, such as the finches (Vuilleumier 1985). In the old-growth forests of Chiloé Island, bird communities reach between 20 and 25 species, largely dominated by White-crested Elaenia, Thorn-tailed Rayadito, Fire-crown Hummingbird, and Chucao Tapaculo (Willson et al. 1994, Díaz et al. 2005). In old-growth Araucaria forests, Ibarra et al. (2010) found a similar number of species, dominated also by White-crested Elaenia, Thorn-tailed Rayadito, and Fire-crown Hummingbird. In Bosque Pehuén Park, old-growth forests were dominated by Thorn-tailed Rayadito and White-crested Elaenia, but with lower abundance of Fire-crown Hummingbird and Chucao Tapaculo than the lowland coastal old-growth forests of Chiloé Island. The bird community found in secondary forests of Bosque Pehuén also was a subset of birds in old-growth forest, similar to what has been described in lowland coastal forests (Díaz et al. 2005).

Other studies have frequently compared bird diversity between native forests and different types of gradients and land use, without considering the influence of the human disturbance history and plant composition of forest bird communities. For instance, Estades (1997) described the forest bird distribution along an altitudinal gradient. How-

**Figure 4.** Distribution of vegetation cover and dominant bird species throughout the 18 points of bird surveys in the Bosque Pehuén Park, southern Chile. The letters indicate each environment: **A:** Grassland, shrublands, and forest in lowlands; **B:** Secondary forest; **C:** Old-growth forest; and **D:** Grasslands, shrublands, and forest in the highlands. This figure showed that forest bird species, such as White-crested Elaenia (*Elaenia albiceps*), Chucao Tapaculo (*Scelorchilus rubecula*), and Thorn-tailed Rayadito (*Aphrastura spinicauda*), were recorded in most point-counts along the altitudinal gradient but concentrated in forests, while House Wren (*Troglodytes aedon*), Austral Thrush (*Turdus falcklandii*), Austral Blackbird (*Curaeus curaeus*), and Tufted Tit-tyrant (*Anairetes parulus*) were present mostly in points dominated by shrubs.

**Table 3.** Average ( $\pm$  SE) basal area of living trees, number of large trees and snags per transect, and vegetation cover (%) in the four environments defined in the Bosque Pehuén Park, southern Chile. Abbreviations: HIGSHRUB – Grasslands, shrublands, and forest in highlands; OLDFOR – Old-growth forest; SECFOR – Secondary forest; and SHRUB – Grasslands, shrublands, and forest in lowlands.

Characteristics of the environments surveyed	HIGSHRUB	OLDFOR	SECFOR	SHRUB
Basal area (m <sup>2</sup> )	0.12 $\pm$ 0.08	1.82 $\pm$ 1.53	0.58 $\pm$ 0.21	0.23 $\pm$ 0.15
Large old trees and snags (N individuals/ transect)	0.25 $\pm$ 0.29	0.75 $\pm$ 0.29	0.33 $\pm$ 0.30	0
Old-growth forest cover (%)	17.5 $\pm$ 7.3	83.8 $\pm$ 6.4	24.2 $\pm$ 2.6	22.5 $\pm$ 9.6
Second-growth forest cover (%)	32.5 $\pm$ 11.2	16.3 $\pm$ 6.4	72.5 $\pm$ 3.7	57.5 $\pm$ 15.0
Grassland cover (%)	43.8 $\pm$ 14.0	0	0	17.5 $\pm$ 20.2
Shrubland cover (%)	6.3 $\pm$ 4.3	0	3.3 $\pm$ 3.7	2.5 $\pm$ 2.9



**Figure 5.** Non-parametric multidimensional scaling (NMDS) between the different types of vegetation cover and the abundance of each bird species in Bosque Pehuén Park, southern Chile. The plot shows the association between the type of vegetation cover and the different bird species. Data from 2015 and 2016 were pooled. Abbreviations: HIGSHRUB – Grasslands, shrublands, and forest in highlands; OLDFOR – Old-growth forest; SECFOR – Secondary forest; SHRUB – Grassland, shrublands, and forest in lowlands.

ever, the forest studied corresponded to a secondary forest, dominated by trees lower than 15 meters tall. Estades & Temple (1999) studied bird communities in a fragmented landscape dominated by pine tree plantations, comparing birds in native secondary forests with those in exotic tree plantations; they concluded that plantations support even more birds than forests. Similarly, Vergara & Simonetti

(2004) compared bird abundance in exotic tree plantations and fragmented forests, concluding that species responses to fragmentation was species specific, and that several bird species could be supported by exotic tree plantations. All of these studies have been conducted in secondary forests, which lack large old trees, have lower abundance of forest birds, and can include bird species characteristic of open



areas when the forest is in its early successional stages (e.g., Díaz et al. 2005). Additionally, these plantations presented understories and early successional forests developing below the canopy of exotic pine trees; i.e., birds may have been living in the forest structures that were developing below the pines. Our results indicate that even an accurate comparison of a plantation's bird composition with that of nearby forests can lead to inappropriate conclusions regarding the importance of plantations for forest bird conservation. Researchers may compare exotic tree monocultures with secondary forests that represent incomplete native forests, or they could be assuming that many bird species are living in the exotic tree monocultures, when in reality birds are living in the early successional forests that develop below the crown of the exotic tree plantations. Further studies comparing the effects of forest fragmentation created by tree plantations should include forest plant composition and structure, as well as type and intensity of human disturbance (Jaña-Prado et al. 2006), since the avian assemblage of secondary forests cannot represent that of original old-growth forests.

**Implications for conservation.** Our results suggest that the number of species is not a good indicator for forest bird conservation, while few studies have been conducted in undisturbed forests that truly represent the original forest bird community. The Andean forests of south-central Chile have historically been exploited and degraded, mostly in recent decades (Lara et al. 2012, Miranda et al. 2015). The secondary forests that remain dominate the landscape in southern Chile and are common in many public and privately protected areas.

The presence of vegetation structures and biological legacies are key to the presence of bird species, and can help to define reference ecosystems. Fallen trunks and standing dead trees (Willson et al. 1994, Altamirano 2014), understory cover (Reid et al. 2004), and large old trees (Díaz et al. 2005) represent resources and offer habitat for many specific bird species (Khanapostani et al. 2012). Old-growth forests used to dominate many landscapes, and many regions no longer have remnants of these original forests (Camus 2006). In most mountainous forests worldwide, lowlands have been especially disturbed by humans (Nogués-Bravo et al. 2008), and a significant part of our knowledge on bird composition has originated from secondary forests. Nonetheless, as our study showed, it is likely that no bird species is a specialist of secondary forests. Today, extensive secondary forests lack the ancient trees that offer nesting sites to birds (Cockle et al. 2011), and habitat and/or food to insects (Ellwood & Foster 2004, Díaz et al. 2012), plants (Nadkarni et al. 2004, Díaz et al. 2010), and other animals (Lindenmayer et al. 2014). Consequently, secondary forests should not be considered as a control to study the effects of human disturbances on bird communities, especially in areas of the world like south-central Chile, with high endemism and high pressure for the transformation of remnant forest into pine and eucalyptus plantations. Thus, for forest birds, the old-growth forest is irreplaceable, and it is likely that what has been observed in birds is true for other animal groups as well. Therefore, conservation, management, and restoration plans must prioritize the conservation of the old-growth forests and biological legacies to ensure the long-term conservation of biodiversity.

## ACKNOWLEDGMENTS

We are grateful to the Fundación Mar Adentro for providing all of the facilities and funds necessary to conduct this study. We are particularly grateful to Madeline Hurtado, Diego Urrejola, Pamela Hurtado, and Nicole Ellena for their permanent support; to Christine Harrower for providing helpful comments and advice to improve the quality of the manuscript, and especially to Guillermo Méndez (also known as Don Segundo) and his family for their hospitality and assistance in the field.

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