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Structural complexity is a better predictor than single habitat attributes of understory bird densities in Andean temperate forests

Victoria C. Concha,[1] Julián Caviedes,[1,2] Fernando J. Novoa,[1,3] Tomás A. Altamirano,[1,3,4] and José Tomás Ibarra[1,3,5,*]

[1]ECOS (Ecosystem-Complexity-Society) Co-Laboratory, Center for Local Development (CEDEL) and Center for Intercultural and Indigenous Research (CIIR), Villarrica Campus, Pontificia Universidad Católica de Chile, Villarrica, Chile
[2]Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, Barcelona, Spain
[3]Cape Horn International Center for Global Change Studies and Biocultural Conservation (CHIC), Puerto Williams, Chile
[4]National Audubon Society, Audubon Americas, Chile
[5]Department of Ecosystems and Environment, Faculty of Agriculture and Natural Systems & Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile

*Corresponding author: jtibarra@uc.cl

ABSTRACT

The simplification of forest structural complexity, caused by anthropogenic land-use practices, is one of the main threats to understory specialist birds. We examined the association of both single structural attributes and structural complexity, with the density of 4 understory bird species in the Global Biodiversity Hotspot "Chilean Winter Rainfall-Valdivian Forests" of South America. Between 2011 and 2013, we surveyed habitat attributes and conducted bird point counts in 505 plots in Andean temperate ecosystems in Chile. In each habitat plot, we measured understory density, volume of coarse woody debris (CWD), number of snags, diameter at breast height (DBH) of trees, and leaf litter depth. With these attributes, we developed an index of stand structural complexity (ISC). On average, old-growth forests had higher values for understory density, CWD volume, DBH, and litter depth than secondary forests and open fields, and thus greater values of ISC. The density of understory birds was positively correlated with the ISC for the Rhinocryptidae *Pteroptochos tarnii*, *Scelorchilus rubecula*, and *Scytalopus magellanicus*. We also found a positive association between understory density and litter depth, with the density of the Furnariidae *Sylviorthorhynchus desmursii*. However, this latter species showed a negative association with the density of snags. Our results suggest the utility of using an index of structural complexity, rather than single or even additive habitat attributes, for determining the density of understory specialist birds. We recommend that management plans should promote the retention of habitat attributes that contribute to the structural complexity of temperate forests of South America and beyond.

Keywords: biodiversity hotspot, Chile, forest disturbance, habitat legacies, snags

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LAY SUMMARY

- We examined the association of forest structural attributes and structural complexity, with the density of four understory bird species from South American temperate forests.
- We surveyed 505 plots in Chile's Andean temperate ecosystems between 2011 and 2013, measuring various structural attributes and bird densities.
- We found that old-growth forests had higher values of structural complexity compared to secondary forests and open fields.
- The density of understory birds, including *Pteroptochos tarnii*, *Scelorchilus rubecula*, and *Scytalopus magellanicus*, was positively correlated with the index of stand structural complexity (ISC). There was also a positive association between understory density and leaf litter depth for the Furnariidae *Sylviorthorhynchus desmursii*.
- We highlight the importance of considering overall structural complexity for effective conservation planning, recommending the retention of habitat attributes that promote the structural complexity of temperate forests in South America and beyond.

La complejidad estructural es un mejor predictor que los atributos individuales de hábitat para la densidad de aves del sotobosque en los bosques templados andinos

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RESUMEN

La simplificación de la complejidad estructural del bosque, causada por prácticas intensivas de uso de la tierra por los seres humanos, es una de las principales amenazas para las aves especialistas del sotobosque. Examinamos la asociación tanto de atributos estructurales individuales del hábitat como de la complejidad estructural integrada, con la densidad de cuatro especies de aves del sotobosque en el Punto Caliente de Biodiversidad Global llamado "Bosques Valdivianos Chilenos de América del Sur." Entre 2011 y 2013, realizamos evaluaciones de atributos del hábitat en 505 parcelas y 505 puntos de conteo de aves en los ecosistemas templados andinos de Chile. En cada parcela de hábitat, medimos la densidad del sotobosque, el volumen de residuos leñosos gruesos (RLG), el número de árboles muertos en pie, el diámetro a la altura del pecho (DAP) de los árboles y la profundidad de la hojarasca. Con estos atributos, desarrollamos un índice de complejidad estructural del bosque (ICEB). En promedio, los bosques primarios tuvieron valores más altos para la densidad del sotobosque, el volumen de RLG, el DAP y la profundidad de la hojarasca que los bosques secundarios y los campos abiertos y, por lo tanto, valores mayores del ICEB. La densidad de las aves del sotobosque se correlacionó positivamente con el ICEB para las especies Rhinocryptidae *Pteroptochos tarnii, Scelorchilus rubecula* y *Scytalopus magellanicus*. También encontramos una asociación positiva entre la densidad del sotobosque y la profundidad de la hojarasca, con la densidad de la especie Furnariidae *Sylviorthorhynchus desmursii*. Sin embargo, esta última especie mostró una asociación negativa con la densidad de árboles muertos en pie. Nuestros resultados muestran la utilidad de utilizar un índice de complejidad estructural, en lugar de atributos de hábitat individuales o incluso aditivos, para determinar la densidad de las aves especialistas del sotobosque. Recomendamos que los planes de manejo forestal promuevan la retención de atributos del hábitat que contribuyen a la complejidad estructural de los bosques templados de América del Sur y más allá.

Palabras clave: Sitios calientes de biodiversidad, legados de hábitat, Chile, perturbación del bosque, árboles muertos en pie

INTRODUCTION

In forest ecosystems, the structural complexity of the habitat is essential for maintaining key ecological processes, such as pollination, seed dispersal, and the recruitment of woody plants (Luck et al. 2013, Lindenmayer 2019, Ibarra et al. 2020a). In structurally complex forests, there is greater availability of reproductive and feeding habitats for numerous organisms whose natural history depends on the forest (Ibarra and Martin 2015a, Caviedes and Ibarra 2017, Martins et al. 2017). At the local scale, structural complexity has been defined as "a measure of the number of different attributes present and the relative abundance of each of these attributes" (McElhinny et al. 2005). In addition, certain key structural habitat attributes have been identified as contributing to structural complexity. Referred to as "habitat legacies," these attributes can include the understory, coarse woody debris (CWD), standing dead trees (snags), large live trees, and leaf litter (McElhinny et al. 2005, 2006, Sabatini et al. 2015, Caviedes and Ibarra 2017).

Structural complexity can vary depending on the type of forest, its successional stage, and disturbance regimes. For example, old-growth forests are generally characterized by their high structural complexity (Zenner 2004). However, the complexity of some secondary forests can also resemble that of old-growth forests due to a high presence of habitat legacies (Caviedes and Ibarra 2017). The persistence of these attributes after a disturbance may allow a level of structural complexity that facilitates regeneration of the vegetation (McElhinny et al. 2005, Caviedes and Ibarra 2017, Ehbrecht et al. 2017, Lindenmayer 2019, Novoa et al. 2021). Natural disturbances such as insect outbreaks, wildfires, or strong-wind events can affect a forest's structural complexity (Seidl et al. 2017). However, anthropogenic disturbances associated with intensive land-use practices are now one of the main threats to forest biodiversity worldwide (e.g., logging, livestock farming, and fires; Stephens and Wagner 2007, Gauthier et al. 2015). A direct consequence of these activities is the simplification of the forest's structure and composition (Sefidi et al. 2022). In addition, they homogenize stands by creating restrictions on the size and age of trees in intensively managed forests (Mishra et al. 2004, Miller et al. 2009, Asefa et al. 2017, Demarais et al. 2017, Prowse et al. 2017, Sefidi et al. 2022).

Indices of structural complexity serve as an objective measure with potential application to forest management (McElhinny et al. 2005, Sabatini et al. 2015, Caviedes and Ibarra 2017). Higher values indicate greater complexity (e.g., a greater presence and relative abundance of key structural attributes; Persiani et al. 2016). By increasing the availability of resources to a wide diversity of organisms (e.g., food items and reproductive sites), structural complexity may reduce negative relationships such as competition (Vergara and Simonetti 2003, Franklin and Van Pelt 2004, Vergara and Simonetti 2004, McElhinny et al. 2006, Ibarra et al. 2020a). However, it is not clear whether single structural attributes, or their combinations, are greater influences on the density of habitat specialist species.

Habitat specialist birds are particularly vulnerable to a reduction in forest structural complexity (Reid et al. 2004, Díaz et al. 2005). This guild has been reported to respond rapidly to anthropogenic disturbances (e.g., logging and burning of the forest) that affect its habitat, reflecting its sensitivity to the removal or simplification of structural attributes (Barlow et al. 2002, Carmona et al. 2002, Díaz et al. 2005, Flynn et al. 2009, Riffell et al. 2011, Ibarra and Martin 2015a, Soler et al. 2016, Altamirano et al. 2017, McFadden and Dirzo 2018, Navedo and Biscarra 2018, Díaz et al. 2019). For example, the presence of coarse woody debris and snags were found to be an important structural attribute for habitat specialist birds nesting in the loblolly pine (*Pinus taeda*) forests of South Carolina, USA. Species such as the *Pipilo erythrophthalmus* and *Piranga rubra* reproduced relatively less in sites where coarse woody debris was removed (Lohr et al. 2002). Similarly, small-diameter firs provide important understory vegetation, and their large-scale extraction appears to be related to a long-term decline in the population of *Poecile montana*, a specialist species of boreal forests in Fennoscandia (Eggers and Low 2014). Lastly, coarse woody debris volume and litter depth are thought to be crucial for the reproduction and feeding, respectively, for understory specialist birds in temperate forests of Chile (Reid et al. 2004, Díaz et al. 2005, 2006). Specifically, Chucao Tapaculos (*Scelorchilus rubecula*) and Magellanic Tapaculos (*Scytalopus magellanicus*) rely almost exclusively on cavities in fallen trees or coarse woody debris as nesting places (Altamirano et al. 2017). In other words, the sensitivity of specialist birds to alterations in their habitat could refer not only to the presence or absence of a particular structural attribute(s), but also to the importance of different combinations of habitat legacies that contribute to sites' structural complexity.

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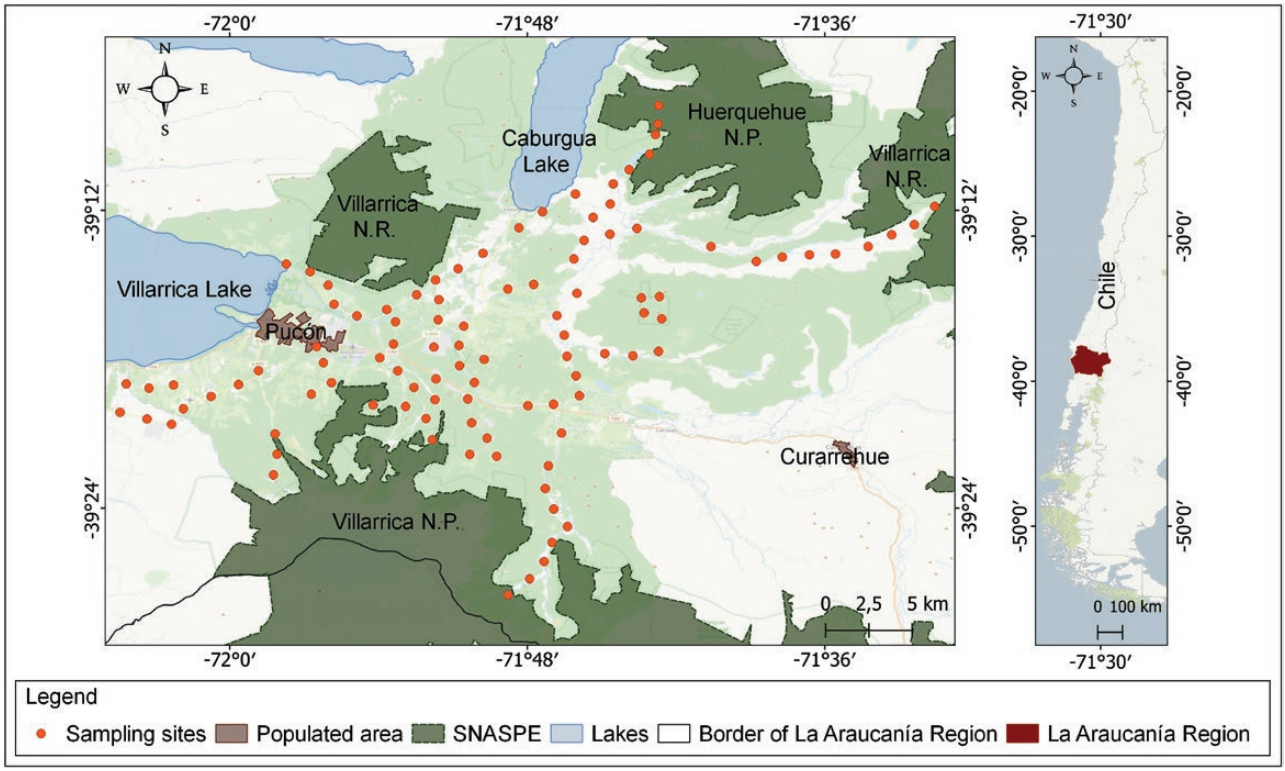

FIGURE 1. Study area 101 sampling sites (orange circles) in an environmental gradient in Andean temperate forests of southern Chile. Green = State Protected Areas (SNASPE, including N. P. National Park and N. R. National Reserve); blue = lakes; dotted line indicates the regional border.

The temperate forests of South America are one of the world's 36 Biodiversity Hotspots (Noss 2016). Located between 35°S and 55°S, they are isolated from other South American forests by over 1,000 km (Vuilleumier 1967). Bird species such as Chucao Tapaculos, Black-throated Huet Huet (*Pteroptochos tarnii*), and Magellanic Tapaculos, all species of the Rhinocryptidae family, and Des Murs' Wiretail (*Sylviorthorhynchus desmursii*), a species of the Furnariidae family, inhabit southern temperate forests. These 4 bird species are generally considered "understory specialists" (Carmona et al. 2002, Díaz et al. 2005, Díaz et al. 2019, Altamirano et al. 2017). In recent decades, the degradation of native forest, the expansion of non-native tree plantations, and the historical use of human-induced fire to open new agricultural and livestock areas have caused a rapid loss of structural attributes that are key for the natural history of these birds (Ibarra and Martin 2015a, Soler et al. 2016, McFadden and Dirzo 2018, Novoa et al. 2021).

In this study, we evaluated the relationship between forest structural complexity and understory specialist birds in Andean temperate ecosystems of Chile. We developed an index of stand structural complexity and assessed its relationship with bird density for each understory specialist species. Specifically, we sought to answer the following question for each species: How are different forest structural attributes, individually and integrated into a complexity index, related to the density of understory specialist birds? We hypothesized that forest structural complexity would have a greater influence on the density of each understory bird species, than the habitat attributes per se. Testing this hypothesis will provide valuable information about the factors that structure biological communities, and this could be of great value for the design of forest management policies and practices that enhance biodiversity in a Global Biodiversity Hotspot.

MATERIALS AND METHODS

Study Area

We collected habitat variables and conducted bird point counts during the spring and summer months of 2011–2013 in the Araucarias Biosphere Reserve (Figure 1). The area has a temperate climate with a short dry season (<4 months) in summer and average annual precipitation of 1,945 mm (Luebert and Pliscoff 2006). It comprises 3 main vegetation formations distributed over an elevational gradient ranging from 220 meters above sea level (m.a.s.l.) to 1,400 m.a.s.l. The vegetation varies from low elevation forests (200–500 m.a.s.l.) with a predominance of *Nothofagus obliqua* and *Nothofagus dombeyi*, associated principally with *Laurelia sempervirens*, *Eucryphia cordifolia*, *Persea lingue*, and *Aextoxicon punctatum*. At intermediate elevations (500–900 m.a.s.l.), the forest is mixed with a predominance of *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *N. dombeyi* (Gajardo 1993). At high elevations (>900 m.a.s.l.), *Araucaria araucana* and *Nothofagus pumilio* predominate (Fuentes-Ramirez et al. 2018, Urrutia-Estrada et al. 2018). The understory is formed by a mixture of the species indicated above as well as, among others, *Dasyphyllum diacanthoides, Lomatia dentata*, *Fuchsia magellanica*, *Berberis darwinii*, *Rhaphithamnus spinosus*, and *Chusquea* spp, all species native to southern temperate forests.

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Focal Species

We focused on the understory specialists *S. rubecula*, *P. tarnii*, *S. magellanicus*, and *S. desmursii*. This guild is generally considered, in the literature, as vulnerable to land use change that reduces the supply of certain structural attributes of forests (Reid et al. 2004, Díaz et al. 2005). These species feed mainly on the invertebrates found in the understory, dead trees, and litter (Figure 2; Sieving et al. 1996, De Santo et al. 2002, Reid et al. 2004, Díaz et al. 2005, Altamirano et al. 2012b, Ibarra et al. 2017a, 2018, Medrano et al. 2020, Vergara et al. 2021). They frequently nest under the dense understory, especially bamboo (Díaz et al. 2005, Ibarra et al. 2017a). The areas of bamboo are often dense, impeding the movement of animals larger than 30 cm and protect these birds' nests and chicks from attacks by predators (De Santo et al. 2002, Vergara and Simonetti 2003, Reid et al. 2004, Altamirano et al. 2012a, Ibarra et al. 2017a). For the movement of bird individuals, a dense understory plays a key role in connectivity between fragments for the 4 focal species (Reid et al. 2004, Díaz et al. 2006, Vergara and Simonetti 2006, Willson 2006, Amico et al. 2008, Altamirano et al. 2012b). In addition, tree stumps and dead branches with a minimum diameter of 0.3 m have been associated with the presence of *P. tarnii* and *S. magellanicus* (Sieving et al. 1996, Vergara and Simonetti 2006, Amico et al. 2008). Furthermore, the 3 Rhinocryptidae use cavities in coarse woody debris with a diameter of between 61.3 and 193.8 cm, but *P. tarnii* could exceptionally nest 15 m from the ground. On the other hand, *S. desmursii* does not use cavities (Willson et al. 1994, De Santo et al. 2002, Willson 2006, Altamirano et al. 2012a, 2017).

Habitat Surveys

We selected 101 sites along the elevational gradient using QGIS 3.26.2 (Figure 1). We identified all the headwaters of the 19 sub-basins within the Villarrica watershed that were accessible by rural roads or hiking trails (Ibarra et al. 2014). We selected 13 sub-basins for which we had permission from land owners, locating the first site near the headwaters of each sub-basin and the remaining sites systematically at each 1.5 km down from the headwaters (Ibarra et al. 2014). At each of the 101 sites, we established 5 circular plots (0.04 ha; 11.2 m radius; $n = 505$), distributed every 125 m in an L-shaped transect (Ibarra et al. 2014). We included different types of habitats, comprising old-growth forest (>200 year; 64 plots), mid-successional forest (<80 year) with bamboo (102 plots), mid-successional forest (<80 year) with understory other than bamboo (99 plots), mid-successional forest (<80 year) without understory (44 plots), early successional forest (<20 year; 75 plots), arborescent shrubland (87 plots), and open field (28 plots).

In each circular plot ($n = 505$), we measured attributes that have been reported as important for the life cycle of the focal species (Figure 1). They included (1) understory density, (2) coarse woody debris (CWD) volume, (3) number of snags, (4) tree diameter at breast height (DBH), and (5) litter depth (Caviedes and Ibarra 2017). For CWD with a diameter ≥ 7.5 cm, we measured its length and diameter at the center and, subsequently, calculated the volume (m^3 ha^{-1}) using the formula for the volume of a cylinder. We counted all trees and snags with DBH ≥ 12.5 cm and height ≥ 1.3 m (Ibarra et al. 2014). We measured understory density by the number of contacts by the vegetation intercepting a 3-m vertical pole for each vertical meter up to 3-m height and the litter depth by using a metal ruler (Díaz et al. 2006, Caviedes and Ibarra 2017). Understory density and litter depth were measured at 5 points, separated systematically at 5.6 m, within each plot. Values of each habitat attribute for the 5 plots were averaged and thus a single value was obtained for each of the 101 sites (Franklin et al. 2002). In addition, we determined the presence or absence of anthropogenic disturbances in each plot, specifically recording when a plot showed signs of fire, logging (remains of cut wood or stumps), or livestock activity (dung or browsed vegetation).

TABLE 1. Temporal and climatic covariate candidates for estimating the detectability and density of understory birds.

Type of covariate	Description
1. Time	Minutes since 0500 hours
2. Temperature	°C
3. Humidity	Relative humidity (0–100%)
4. Wind speed	Average wind speed (m s^{-1})
5. Cloud cover	Sky cloud cover. 0: Clear, 0.5: Partial cover, 1: Total cover
6. Playback	Acoustic playback

Bird Sampling

We conducted bird sampling during 2 reproductive seasons (2011–2012 and 2012–2013), between October and January. Point count stations were in the same plots used for habitat sampling, with the center of the plot at the center of the point count station. We sampled 81 sites (80.2%) in 2011–2012 and the remaining 20 (19.8%) in 2012–2013 (Ibarra and Martin 2015a). In each of the 101 sites, we established 5-point counts that were systematically spaced 125-m apart and lasted 6 min during which we recorded each individual seen and/or heard within a radius of 50 m (Bibby et al. 2000, Ibarra et al. 2017a).

To increase the detectability of understory specialist birds we performed playbacks. To avoid double counting at nearby stations. we reproduced playback at 3 out of the 5-point count stations. After the period of passive counting (the first 6 min), we reproduced the playbacks of the 4 understory specialist species. As each call by 30 s was followed by 30 s of listening in silence, the counting time for each station with playbacks totaled 15 min (Drever et al. 2009, Ibarra et al. 2017a). The distance to all the birds detected was estimated and grouped into 1 of 2 intervals for analysis (0–25 and 26–50 m; Bibby et al. 2000, Ibarra and Martin 2015a). We also registered temperature (°C), humidity (%), and wind speed (m s^{-1}) at each point count station (Table 1) using a portable weather monitor (Kestrel 4200, Kestrel-meters, Birmingham, MI), to assess the influence of these covariates on the detectability of each species.

Data Analysis

Construction of an index of forest structural complexity

To construct the index of forest structural complexity, we built upon the methodology proposed by Caviedes and Ibarra

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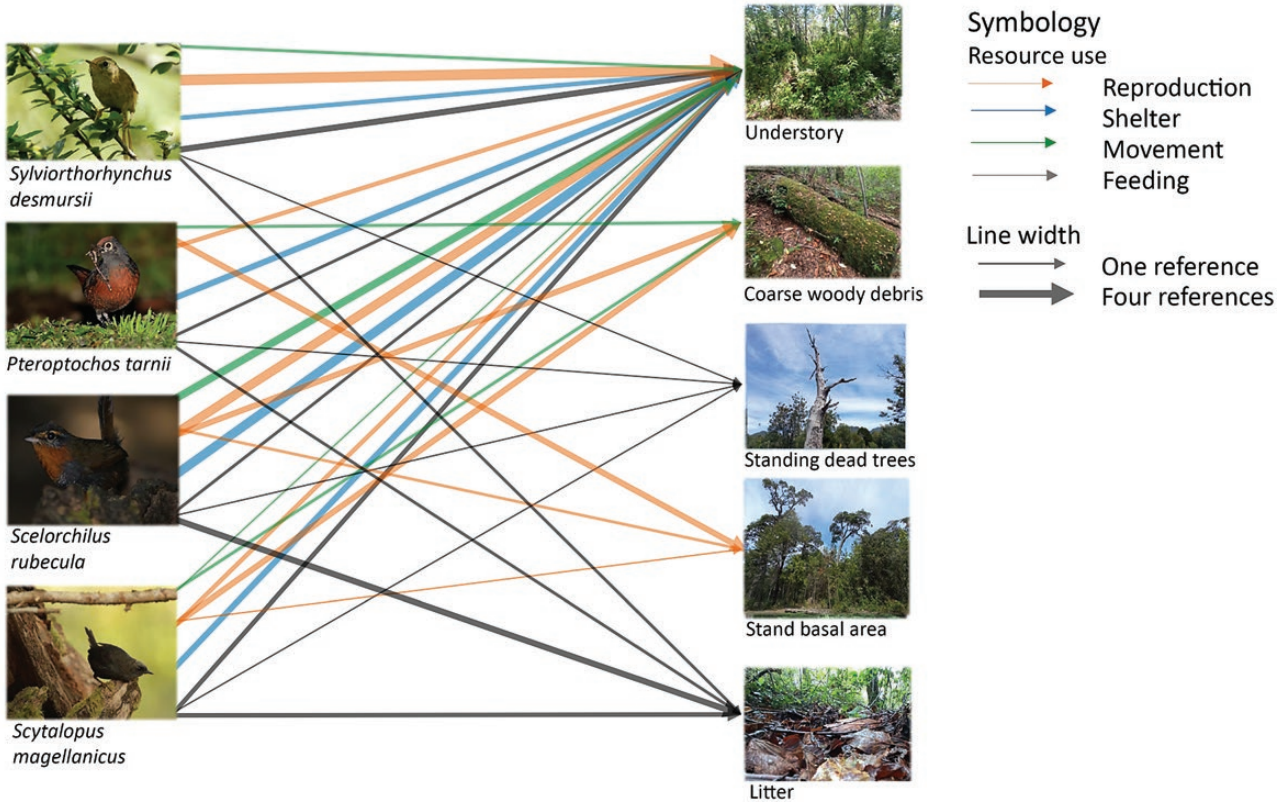

FIGURE 2. Theoretical network of our studied bird species. Lines represent the relationship between structural attribute's resource use by each species. The thickness of the line represents the number of authors who have described each relation. Green = movement, orange = reproduction, blue = shelter, grey = feeding.

(2017). Constructing an index of forest structural complexity requires a stepwise approach, which we divided into four steps: (1) determining a comprehensive set of forest structural attributes; (2) establishing the core set of attributes to be included in the index; (3) sampling these attributes in a set of different sites, including different vegetation communities and habitat types; and (4) integrating the core set of attributes into an additive index. To address point one, we selected those attributes that were considered important for the life cycle of understory specialist birds in temperate forests (Figure 2). To identify the core set of attributes we selected those that (1) had low kurtosis (<2), (2) worked as a surrogate for other structural attributes, and (3) could be easily measured in the field (McElhinny et al. 2006). The 5 selected attributes included in the index were understory density, CWD, number of snags, DBH, and litter depth.

We improved the distribution of habitat attributes with a high kurtosis (>2) by transforming the raw data to logarithm ($x + 1$). We later rescaled each of the 5 attributes to a score from 0 to 10 by performing a regression analysis through quartiles, setting a score of 2.5, 5, 7.5, and 10 for the midpoints of each quartile, that is, the 12.5, 37.5, 62.5, and 87.5 percentiles (Sabatini et al. 2015, Caviedes and Ibarra 2017). The minimum score was 0, while the maximum score of 10 was attributed to the 87.5 percentile and above. We obtained the index of structural complexity for each plot by adding the rescaled values for each of the five attributes; an index closer to 50 had the highest structural complexity. Finally, we converted the index of forest stand structural complexity for the 505 plots into percentage. For further information about the methodology to build the index, see Caviedes and Ibarra (2017).

Probability of detection and density of focal species

To estimate detectability (p) and density (D), we analyzed point-count data using mixed multinomial-Poisson models (Royle et al. 2004). In these models, the estimated densities can be corrected by the probability of detection of each species as a function of the distance from the observer and other space-time covariates (Buckland et al. 2004, Royle et al. 2004, Ibarra et al. 2014). To estimate the detection and density of each species at all sites, we used maximum likelihood methods in R-Unmarked (Fiske and Chandler 2011, Ibarra and Martin 2015a). To model the detectability function, we used the multiple covariate distance sampling (MCDS) method in which the observer's distance (y) and one or more variables represented by the vector z determine the probability of detection in p (Marques et al. 2007).

To estimate the detectability and density of each species, we used the Akaike information criterion (AIC) for each point-count station to identify whether the half-normal or hazard ratio was the appropriate distance function for each species (Royle et al. 2004). We identified the half-normal as the most suitable detection function for each species. To estimate detectability, we used 6 covariates (Table 1) that potentially affect the detection function parameter: sampling time (minutes as from 0500 hours), temperature (°C), wind speed (m s^{-1}), cloud cover (0: clear, 0.5: partial cover, 1: total cover), relative humidity, and playback.

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Table 2. Means (SD) of the 5 structural attributes included in the structural complexity index and values of the structural complexity index in percentages.

Type of habitat	Structural complexity index (%)	Density of snags (stems ha^{-1})	Density of live trees (m^2 ha^{-1})	Density of understory (no. contacts)	Depth of litter (cm)	Volume of coarse woody debris (m^3 ha^{-1})
Old-growth forest	80.03 (9.10)	46.02 (33.20)	75.28 (35.62)	7.55 (3.87)	6.57 (3.7)	13.74 (23.79)
Secondary forest with bamboo understory	73.18(11.82)	55.01 (75.62)	41.67 (33.07)	5.49 (2.13)	6.31 (3.36)	11.34 (16.88)
Secondary forest with understory of other species	65.18(10.32)	44.11 (68.58)	34.76 (19.24)	4.72 (2.61)	5.23 (2.63)	4.41 (8.68)
Secondary forest without understory	55.66 (13.75)	35.20 (53.15)	35.22 (17.95)	1.70 (1.24)	2.98 (2.43)	5.85 (15.01)
Open field	34.38 (3.27)	0 (0)	2.21 (2.27)	0.42 (0.41)	0.41(0.41)	1.18 (1.23)

Relationship between habitat attributes and structural complexity with the density of focal species

Non-native tree plantations covered < 2% of the study area and we, therefore, excluded them from all analyses, evaluating bird density for each of the remaining plots (n = 499). Before estimating density, we tested for collinearity among covariates but none reached the established threshold value (r > 0.7). We also evaluated non-linear bird responses with the structural complexity index (Ibarra and Martin 2015a). To obtain the best density models (covariates that may influence the Poisson mean), we selected the most significant detectability covariates for each species and then added the habitat covariates individually and in different combinations to establish a set of 25 candidate models, which were compared based on the model weights (w_i) and the estimated coefficients based on AIC. The final confidence set was of 0.95 (Burnham and Anderson 2002, Ibarra and Martin 2015b). We performed all statistical analyses and created graphs using packages *unmarked*, *ggplot2*, and *polypoly* with R software version 4.2.0 (R Core Team 2021).

RESULTS

Habitat Attributes and Structural Complexity

The mean values of the 5 structural attributes selected varied depending on the type of habitat. Plots in old-growth forest stands had the highest mean values for understory density (7.55, SD = 3.87 # contacts), CWD volume (13.74, SD = 23.79 m^3 ha^{-1}), DBH (75.28, SD = 35.62 m^2 ha^{-1}), and litter depth (6.57, SD = 3.7 cm). The highest value for the density of snags (55.01, SD = 75.62 trunks ha^{-1}) was found in mid-successional forests with bamboo. The highest mean values of the structural complexity index (77.67%, SD = 11.15) were found in old-growth forest stands without visual signs of anthropogenic disturbance while the lowest mean value of the index (52.47%, SD = 16.28) corresponded to plots with the combined presence of fire, logging, and livestock activity (Table 2).

Composition and Detectability of Birds

We detected a total of 672 individual birds: *Scelorchilus rubecula* (n = 321), *Pteroptochos tarnii* (n = 149), *Scytalopus magellanicus* (n = 144), and *Sylviorthorhynchus desmursii* (n = 57). The detectability of *S. rubecula* (β = –0.3126, SD = 0.1757) and *S. magellanicus* (β = –0.4118, SD = 0.2261) was significantly negatively associated with wind speed (Table 2). The time at which observation took place (minutes after 0500 hours) was positively related to the probability of detection of *S. magellanicus* (β = 0.0022, SD = 0.0007) and *S. rubecula* (β = 0.0027, SD = 0.0006). Playback use showed a positive relationship with the detectability of *S. rubecula* (β = 0.2347, SD = 0.0771) and *P. tarnii* (β = 0.229, SD = 0.118). *S. desmursii* showed a positive relationship with the relative humidity of the air (β = 0.0118, SD = 0.00492).

Bird Densities

The best models (ΔAIC ≤ 2) indicated that the density of the species responded positively to the forest structural complexity index for *P. tarnii* (β = 0.0475), *S. rubecula* (β = 0.04999), and *S. magellanicus* (β = 0.0359; Tables 3 and 4), rather than to other single or additive habitat attributes. The best models also supported a positive association between the density of *S. desmursii* with understory (β = 0.09258) and litter (β = 0.010568). However, in the case of *S. desmursii*, there was a negative association with snag density (β = –0.00994; Figure 4). In addition, bird density differed between the 4 species: density of *S. rubecula* was 2.5 times greater than for *P. tarnii* and *S. magellanicus* (Figure 3), and 1.9 times greater than for *S. desmursii* (Table 4).

DISCUSSION

This study expands knowledge about the relationship between habitat specialist birds in Andean temperate forests and the structural attributes that shape their habitat. We found that forest stand structural complexity had more influence than the attributes per se on the density of 3 out of 4 focal species. The studied species of the Rhinocryptidae family (i.e., *S. rubecula*, *S. magellanicus*, and *P. tarnii*) responded positively, in terms of density, on sites with a higher presence and combination of habitat legacies (understory, coarse woody debris, snags, large live trees, and leaf litter). We, therefore, suggest that these 3 species may be, arguably, considered "habitat complexity specialists" rather than "understory specialists," as they are commonly termed in the literature (Reid et al. 2004, Amico et al. 2008, Rodríguez-Gómez et al. 2022). By contrast,

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Table 3. Species and covariates used to estimate detectability (*p*) and density (*D*) of specialist birds in Andean temperate forests, according to the selection of models based on the Akaike information criterion (AIC).

Detectability (*p*)								Density (D)					
Species	Season	Time	Temp	Wind	Hum	Cloud	Play	und	CWD	DBH	lit	tree	sci
Pteroptochos tarnii				–0.177			0.229*						0.0475***
				(0.206)			(0.118)						(0.00578)
Scelorchilus		0.00277		–0.31260*			0.23476***						0.0497***
rubecula		(0.000637)***		(0.175723)			(0.077179)						(0.00389)
Scytalopus		0.0022***		–0.4118*									0.0359***
magellanicus		(0.000796)		(0.226109)									(0.00532)
Sylviorthorhynchus					0.0118**			0.09258**			0.10568**	–0.00994***	
desmursii					(0.00492)			(0.03639)			(0.03348)	(0.00421)	

*Standard error in brackets.

***$p < 0.01$, **$p < 0.05$, *$p < 0.1$.

Time = time elapsed since 0500 hours, Temp = temperature (°C), Wind = wind, Hum = relative humidity, Cloud = cloud cover, Play = playback, sci = index of complexity, und = understory, CWD = coarse woody debris, lit = litter, tree = snags, DBH = diameter at breast height.

Table 4. Results of best-density models (ind ha^{-1}) as function of habitat attributes for understory specialists. WIND = wind, HUM = relative humidity, PLAY = playback, TEMP = temperature (°C), TIME = time elapsed since 5:00 hours, CLOUD = cloud cover, sci = complexity index, und = understory, CWD = coarse woody debris, lit = leaf litter, tree = dead standing trees, DBH = diameter at breast height.

Species	Structure of model	*K*	AIC_c	ΔAIC	w_i	LL
Pteroptochos tarnii	WIND + PLAY + sci	5	787.05	0.00	0.49	0.193
	WIND + PLAY + und + CWD + lit	7	787.78	0.73	0.82	0.200
	WIND + PLAY + und + CWD	6	791.21	4.16	0.89	0.189
	WIND + PLAY + und + CWD + tree	7	791.55	4.50	0.94	0.192
	WIND + PLAY + und + CWD + DBH	7	791.85	4.80	0.98	0.192
Scelorchilus rubecula	TIME + WIND + PLAY + sci	6	1,283.62	0.00	1.00	0.382
	TIME + WIND + PLAY + lit + tree + und	8	1,345.06	61.44	1.00	0.301
	TIME + WIND + PLAY + und + lit	7	1,353.08	69.46	1.00	0.285
	TIME + WIND + PLAY + und + CWD + lit	8	1,353.08	70.57	1.00	0.287
	TIME + WIND + PLAY + und + DBH	7	1,354	77.40	1.00	0.273
Scytalopus magellanicus	TIME + WIND + sci	5	832.14	0.00	0.95	0.148
	TIME + WIND + und + CWD + tree	7	839.84	7.69	0.97	0.141
	TIME + WIND + und + tree	6	840.99	8.85	0.98	0.134
	TIME + WIND + lit + tree + und	7	841.69	9.54	0.99	0.137
	TIME + WIND + und + DBH	6	843.35	11.21	0.99	0.129
Sylviorthorhynchus desmursii	HUM + lit + tree + und	6	431.35	0.00	0.57	0.121
	HUM + DBH + lit + tree	6	434.86	3.51	0.67	0.110
	HUM + lit + tree	5	434.89	3.55	0.76	0.103
	HUM + lit + tree + CWD	6	436.55	5.21	0.81	0.104
	HUM + DBH + lit	5	436.68	5.34	0.84	0.098

S. desmursii responded positively to litter depth and understory density individually, but negatively to a higher density of snags. All these results may be explained by the different requirements these species have in terms of feeding, reproduction, and shelter to fulfill their natural histories (Willson et al. 1994, Sieving et al. 1996, 2000, Reid et al. 2004).

Focal Species and Habitat

Each one of the selected habitat legacies has a relationship that has been identified as relevant for the natural history of our focal species. De Santo et al. (2002), Reid et al. (2004), Díaz et al. (2005, 2006); Vergara and Simonetti (2006) have suggested that a dense bamboo understory and the presence of coarse woody debris are good predictors of the abundance of understory specialists, because they use these attributes to move around and escape from predators. In particular, *S. desmursii* moves quickly through the dense vegetation between bamboo, shrubs, and trees of 1–2 m (Díaz et al. 2006, Altamirano et al. 2012a). Our results for *S. desmursii*, supported by a negative association with snag density and a positive association with the understory density and litter depth, are in line with this. *Sylviorthorhynchus desmursii* is an understory bird but also uses shrubland or "quilantales," which are areas dominated by bamboo *Chusquea* spp and areas with relatively fewer trees. This species does not use cavities, but builds hanging nests (Altamirano et al. 2012a), which may be linked to its negative relationship with snags. In our study area, snags are

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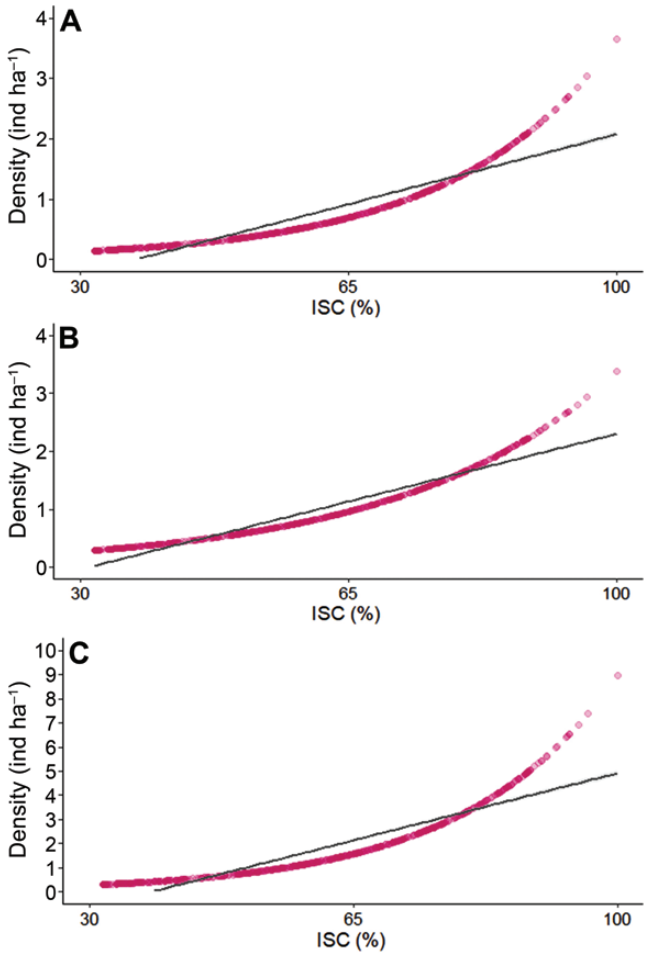

FIGURE 3. Density of three species of Rhinocryptidae increases with the stand structural complexity index: (**A**) *Pteroptochos tarnii*, (**B**) *Scytalopus magellanicus*, and (**C**) *Scelorchilus rubecula*.

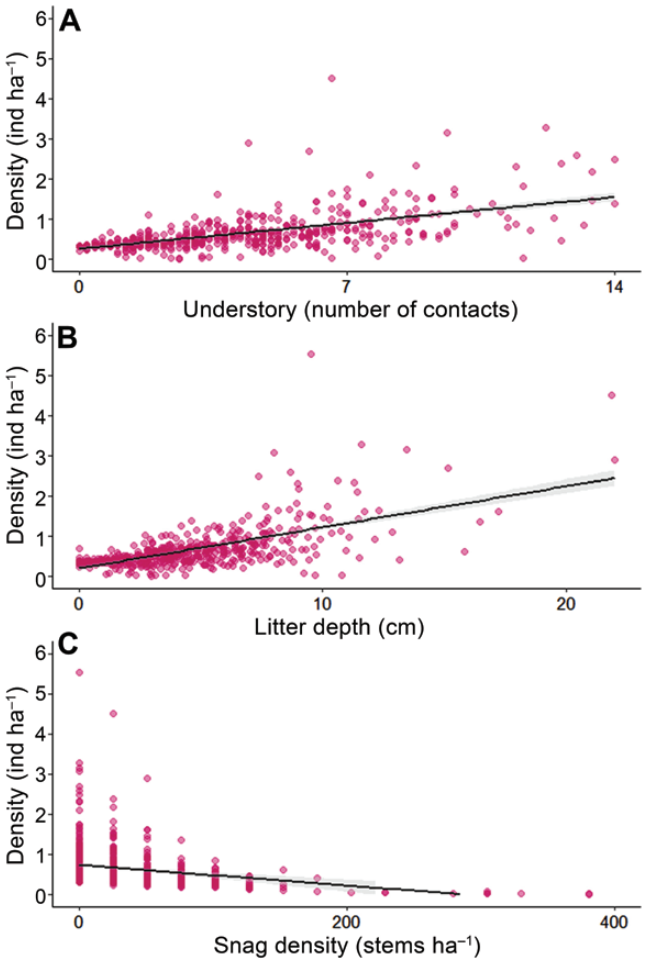

FIGURE 4. Density of *Sylviorthorhynchus desmursii* increases with (**A**) understory density and (**B**) litter depth and declines with (**C**) snag density.

frequent in secondary forests, where many times the density of even aged trees is high, and a dense and continuous understory (with bamboo and shrubs) is rare (Ibarra et al. 2020b).

On the other hand, we found stronger support for stand structural complexity rather than individual forest attributes explaining densities of Rhinocryptidae species. The combined presence of forest attributes is an important resource that allows these species to reproduce, feed, and find shelter (Vergara et al. 2017, Novoa et al. 2021). This suggests that the mechanisms underlying the negative effects of habitat disturbance on our focal species are likely operating in a multivariate way. For example, the presence of large decaying trees and snags in old-growth forests, as well as snags in second growth forests, can provide a crucial breeding resource for these species (Ibarra et al. 2020b), and is a factor of increasing structural complexity (Caviedes and Ibarra 2017). Specifically, cavities present in coarse woody debris are used for nesting by *S. rubecula* and *S. magellanicus* (91%, Altamirano et al. 2017), and *Pteroptochos tarnii* breed mainly in cavities available in large decaying trees (86%) (average DBH of 193.8 cm; Altamirano et al. 2017).

Forest structural attributes such as litter, snags, coarse woody debris, and understory are not only crucial for breeding purposes, but also for the presence of invertebrates, which are the main food item of these 4 specialist bird species (Sieving et al. 1996, De Santo et al. 2002, Reid et al. 2004, Díaz et al. 2005, Altamirano et al. 2012a, Ibarra et al. 2017b, Navedo and Biscarra 2018, Medrano et al. 2020, Vergara et al. 2021). For example, *S. rubecula* and *P. tarnii* dig for food in the litter (Altamirano et al. 2017). Insectivorous birds are highly sensitive to alterations in habitat structure (Boves et al. 2013, Stratford and Stouffer 2013), because the latter has been associated with changes in the availability of arthropods (Sam et al. 2019).

The supply of structural attributes varies across the world's forest systems. The differences can be attributed to the different types of forest, successional stages, and disturbance regimes (Paratori et al. 2023). By providing a relatively greater number of niches for a wide diversity of organisms, complexity might reduce the incidence of ecological interactions such as predation and competition (Vergara and Simonetti 2003, Franklin and Van Pelt 2004, Vergara and Simonetti 2004, McElhinny et al. 2006, Ibarra et al. 2020a). Southern temperate forests are dominated by species of trees from the Nothofagaceae family, which have high rates of wood decay associated with insect attacks and the presence of fungi (Veblen et al. 1996, Ojeda et al. 2007). To understand the underlying mechanisms behind the importance of stand structural complexity in increasing the density of habitat specialist birds, future studies should assess how structural attributes,

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acting across spatial and temporal scales, influence food, nesting, and shelter opportunities for birds in southern temperate forests and beyond.

Our focal species *S. rubecula*, *P. tarnii*, S. *magellanicus*, and *S. desmursii* are endemic species of lesser conservation concern (IUCN 2022). However, in recent decades, the degradation of native forest, the expansion of non-native tree plantations, and the historical use of fire to open up agricultural and livestock areas have been identified as causing a rapid loss of structural attributes that are key for the natural history of these birds (Ibarra and Martin 2015b, Soler et al. 2016, McFadden and Dirzo 2018, Novoa et al. 2021). A meta-analysis suggests that it is necessary to retain between 40% and 60% of structural attributes if secondary forests are to maintain an assemblage of birds similar to that of relatively undisturbed native forests (Basile et al. 2019). In our study, the mean structural complexity of plots subject to the combined presence of fire, logging, and livestock farming was 52.5%. Our findings indicate that particular attention should be paid to the retention of structural attributes as, for example, the number of logs (coarse woody debris) positively predicted bird abundances across sites over a long latitudinal gradient (~450 km) (Rodríguez-Gómez et al. 2022).

Implications for Conservation

Chilean native forests were deforested and degraded at an alarming rate during the second half of the 20th century (Armesto et al. 1998, Zamorano-Elgueta et al. 2015). In areas under forest management, it is still common that bamboo, coarse woody debris, and snags are removed (Ibarra et al. 2018). Chile's national forestry policy promoted, for decades, the expansion of non-native tree plantations and facilitated the degradation of native forests through logging operations that eliminate large living trees (Altamirano et al. 2017, Ibarra et al. 2017b). The Chilean law for native forest recovery and promotion does not consider snags or fallen trees (i.e., coarse woody debris); Law Nº 20.283; MINAGRI 2008). Moreover, these attributes are generally perceived as "dirty and unhealthy" forest characteristics and a sign of "poor management." They are often the first attributes to be removed and harvested for firewood (Ibarra et al. 2020b).

Current forest management practices use methodologies such as the estimation of ages of different forest stands, a measure that provides few details about the structural complexity of the forests being managed (Martin et al. 2020). The retention of a forest's structural attributes, including large decaying trees, snags, and coarse woody debris, along with dense understory and litter rich in decaying organic material, can have a positive influence on both forest biomass and numerous wildlife species that require structurally complex forests (Basile et al. 2019, Rappa et al. 2022). Our results suggest that a structural complexity index is useful for predicting the density of several habitat specialist birds in a Global Biodiversity Hotspot. We recommend that management practices should promote the retention of these structural attributes that together contribute to structural complexity. Thus, this recommendation supports the recently published and officialized Bird Conservation Strategy in Chile, which promote the retention of important structural attributes to improve the forest management sustainability (MMA—ONU Medio Ambiente, 2022).

We show that, for 3 of our 4 focal species, there is no single structural attribute that is important in isolation but, instead, they require habitat complexity of at least 65% to 80%. While we acknowledge that forest monitoring and management is not always an easy endeavor for stakeholders, we recommend two non-mutually exclusive approaches for these tasks. First, managers can assess the potential role of "habitat complexity specialists" as focal species for conservation planning; their presence may represent both sustainable management practices and the availability of structurally complex forest stands in managed areas (Castellón and Sieving, 2012). In these forests, for instance, the presence of the Rufous-legged Owl (*Strix rufipes*) has been indicative of a high diversity of avian functional diversity and endemism (Ibarra and Martin, 2015b). Second, application of the forest structural complexity index to guide forest management could serve as an innovative and relatively straightforward approach to sustainable silviculture in temperate forests.

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Ethics statement

We followed the IOU Code of Ethics (https://www.internationalornithology.org/iou-code-ethics). We thank the Chile's National Forest Service (CONAF) for allowing us to work in State Protected Areas (Permit #11/2012 IX).

Conflict of interest statement

Authors declare that no conflict of interest or direct financial benefits from publication exist.

Author contributions

J.T.I., and J.C. conceived the idea, design, and experiment. J.T.I., T.A., J.C., F.N., and V.C. performed the experiments (collected data, conducted the research). V.C., J.T.I., J.C., T.A., and F.N. wrote the paper. J.T.I., J.C., and V.C. developed or designed methods. V.C., J.C., and F.N. analyzed the data. J.T.I. contributed substantial materials, resources, or funding.

Data availability

Analyses reported in this article can be reproduced using the data provided by Concha et al. (2023).

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