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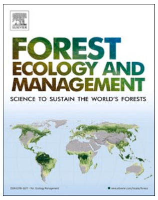

Native forest cover, fragmentation, and seasonality shape functional diversity in forest bird communities

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ABSTRACT

Biodiversity encompasses genetic, species, and ecosystem diversity, all of which are threatened by habitat loss and fragmentation driven by human activities. We evaluated how the replacement of native Maulino forest by pine (*Pinus radiata*) plantations affects forest bird communities, focusing on functional diversity and landscape configuration. The study was conducted in South Central Chile across 22 landscape units (4 km^2 each), where bird surveys were conducted during both the breeding and non-breeding seasons. Functional diversity was assessed using functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis). We recorded 26 forest bird species. Species richness was higher in native forests, where large tree users (LTU) dominated, whereas pine plantations favored shrub and vertical profile generalists. During the breeding season, FRic increased with native cover but declined with higher patch density, indicating that fragmentation constrains the functional breadth of communities. FEve and FDis showed weaker associations with landscape metrics, although fragmented forests tended to support more even but less functionally diverse assemblages. Seasonal patterns were evident, with of landscape structure being stronger in the breeding season. These results highlight the combined roles of habitat amount, configuration, and seasonal dynamics in shaping functional diversity. Conservation strategies should prioritize the retention of large tracts of native forest, limit further fragmentation, and maintain structural features such as mature trees to sustain key ecological functions.

1. Introduction

Biodiversity encompasses all forms of life on Earth, from genes to ecosystems, and is shaped by ecological and evolutionary processes. However, global biodiversity is undergoing unprecedented decline, largely driven by habitat loss and fragmentation resulting from human land-use change (Yuan et al., 2024). These processes reduce habitat connectivity, erode population sizes, and disrupt ecological interactions, undermining both species persistence and ecosystem functionality (Brooks et al., 2006; Pimm et al., 2014). Increasing evidence suggests that beyond species richness, such disturbances can severely affect functional diversity —the range and distribution of ecological traits in a community— with significant consequences for ecosystem stability and resilience (Cadotte et al., 2011; Mariano-Neto et al., 2023).

Reforestation with fast-growing, often exotic, tree species is a widespread response to deforestation and commercial demand for timber. Globally, over 290 million hectares have been reforested by 2020, mainly through monoculture plantations (FAO, 2020). However, these plantations frequently replace native forests, resulting in simplified vertical structure, reduced resource heterogeneity, and lower capacity to support diverse ecological functions (Yang et al., 2024). In central Chile, the Maulino forest—a biodiversity hotspot with high levels of endemism—has experienced extensive fragmentation and conversion to Monterey pine (*Pinus radiata*) plantations, raising concerns about biodiversity conservation in production-dominated landscapes (Echeverría et al., 2006).

The impact of such land-use changes on bird communities has been documented, but findings remain mixed. Some studies report limited changes in species richness across forest types (Vergara and Simonetti, 2004), while others show strong effects of landscape composition and configuration on bird assemblages and their functional roles (Magnago et al., 2014; Lisón et al., 2022). Functional trait-based approaches offer a

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promising framework to understand how birds respond to habitat alteration, as traits mediate ecological interactions such as resource use, mobility, and nesting behavior (Clavel et al., 2011). In forest ecosystems, functional diversity is particularly relevant for evaluating redundancy, ecological resilience, and the maintenance of ecosystem services under disturbance regimes.

In this study, we assess how forest bird functional diversity responds to the replacement of native Maulino forest by pine plantations. We specifically test the hypothesis that the amount of remaining native forest in the landscape has a positive effect on multiple indices of functional diversity—functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis)—at the scale of local bird assemblages. Our findings aim to inform conservation strategies that promote biodiversity and ecological function in forest production landscapes, highlighting the ecological value of native forest remnants in maintaining functional integrity.

2. Methods

2.1. Study area

The study was conducted on the bird community of the temperate forest in the South Central region of Chile, specifically in the administrative region known as "Del Maule." This region experiences a temperate climate with warm, dry summers (Peel et al., 2007). The average temperature is 13.9°C, with annual precipitation of 942 mm (Hajek and Di Castri, 1975). The research focused on a 7500 km^2 area of the "Roble-Hualo" forest type, distributed over the Coastal Range and known as Maulino forest. The study area extends from the Tregualemu River (35°58’ S, 72°44’ W) in the south to "Altos de Licanten" (34°58’ S, 72°02’ W) in the north. An important climatic factor considered in site selection was the varying oceanic influence due to topography.

2.2. Landscape units

The landscape units for the study were selected on the basis of a forest cover database from Arauco S.A., the largest forest company in Chile and South America (Arauco, 2017), the Chilean Government Forest Service’s updated Cartographic Forest Cover (CONAF-UACh, 2010), and QuickbirdTM imagery.

In total, 22 landscape units were defined within the study area. To encompass the breeding home range of most forest-dwelling passerines, landscape units of 4 km^2 were delineated (McGarigal and McComb, 1995; Villard et al., 1999). The selection process focused on continuous forest habitat, choosing only landscape units with at least 85 % forest cover to avoid disturbances from young or harvested stands. Since the majority of pine plantations in the region belong to Arauco Forest Company, including their land provided a representative sample of the area. To increase sample size, three additional landscape units from minor companies identified through satellite images were also included (Fig. 1).

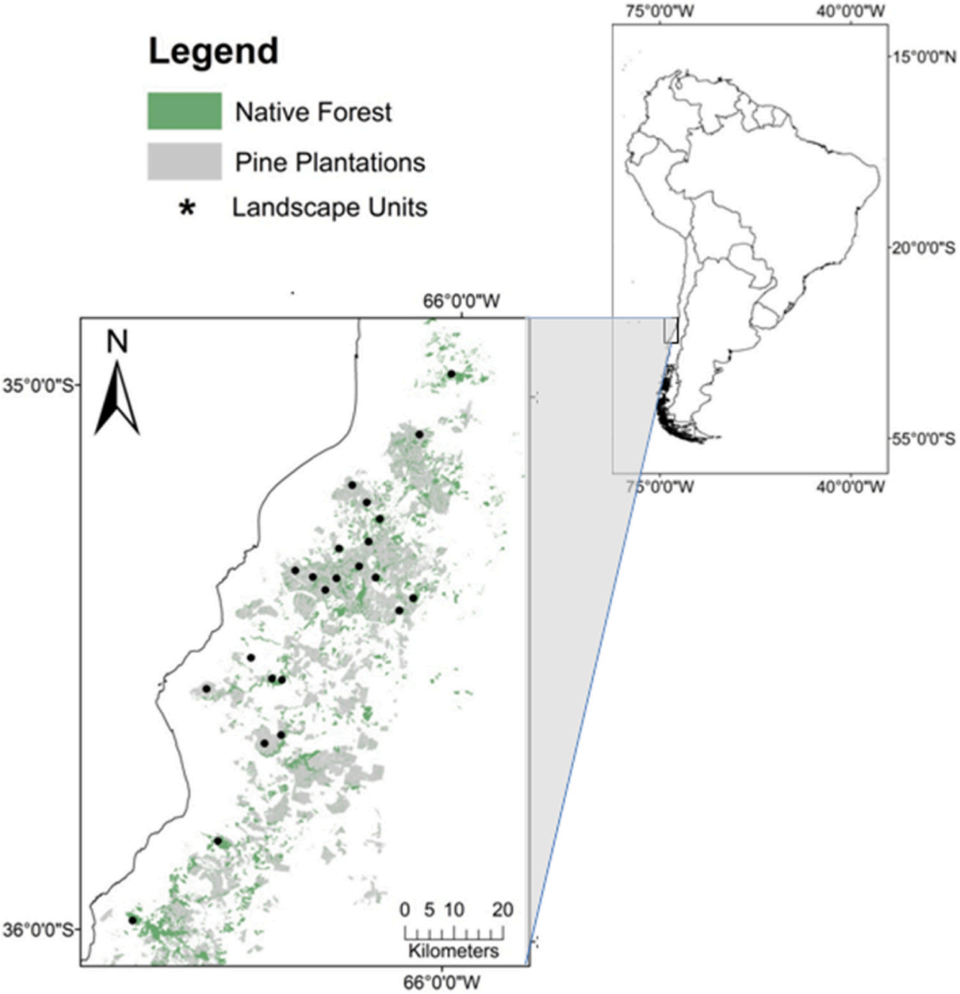

Fig. 1. Location of the study area in the central Chile region, showing the landscape units surveyed.

2.3. Landscape metrics

Many studies suggest that the presence of natural habitat patches within plantation stands can compensate in some way for the lack of a continuous natural forest stands (Dorp, Opdam, 1987; Olsson et al., 2001; Crozier and Niemi, 2003), and that the shape of remnant native forest fragments can also have a strong effect on some bird communities (Hawrot and Niemi, 1996; Lindenmayer et al., 2002). Using ArcGis (ESRI, 2011) over Arauco's forest cover Database and the Chilean Government Forest Service's updated Cartographic Forest Cover (CONAF-UACh, 2010) we prepared and constructed geographical information layers to estimate landscape attributes. To describe the landscape units in terms of their composition and fragmentation we worked on Fragstats 3.3 software (McGarigal et al., 2002) (see Supplemented material Table S1), from which we assessed the percentage of landscapes covered with native forest; native forest patch density, which corresponds with the number of native forest patches available per 100 ha of landscape; Normalized Landscape Shape Index, which represents the perimeter-to-area ratio for the native forest patches, and rescaled to a minimum and maximum value for comparison among landscapes. This landscape metric represents the aggregation of all native forest patches in the landscape, with values ranging from 0 for a non-fragmented landscape, to 1 for a fully disaggregated landscape. Core Area was defined using a depth-of-edge distance equal to 50 m. Connectivity is defined as the number of functional joins between patches of native vegetation based on 50-m-distance criterion.

2.4. Avian surveys

During the breeding season, from October to December, RT conducted bird counts on every landscape unit, considering every patch type. Bird density and species richness were estimated using the variable circular-plot method with a 50 m maximum observation radius. No observations were conducted on rainy or misty days. All birds seen or heard within the maximum radius were recorded, and their distance from the plot's center was estimated in 10 m increments to manage differences in detectability in each patch type (Buckland, 1987). With the exception of swallows and hummingbirds, birds flying over a plot were not considered.

In order to maximize the time spent in the sample plot, in relation to the time travelling between plots, two 5-min counts were conducted at every visit, separated by a 5-min period. We also included a 5-min period before the start of any count to minimize the effects of the arrival at the plots. All counts were carried out during the first 5 h after dawn by a single observer. To control for any seasonal effect, between the beginning and the end of the breeding season, all plots were visited twice and separated by a month. To assess any possible effect of pine plantation cover on the forest bird community during the winter, we surveyed a subsample of 13 landscape units during the month of July.

Using the software Distance 6.0 (Thomas et al., 2010), detectability curves were estimated for individual species in each vegetation type, and data were fitted to a hazard-rate or half-normal model curve (Buckland et al., 1993) considering the understory foliage volume as a covariate. However, detectability was assumed to be uniform (equal to 1) for those species with insufficient sample size to make a more informed decision.

To account for potential differences in vegetation structure and composition that could influence bird detectability and abundance, we characterized the vegetation at each census plot. Following the methodology of Estades and Temple (1999) for these forests, we estimated total foliage volume and foliage height diversity using a vertical stratification approach. Vegetation was assessed across five vertical strata (0–0.3 m, 0.3–2 m, 2–5 m, 5–10 m, and >10 m), and foliage volume was visually estimated within each stratum at each point count location. These data were used to compute an index of total understory foliage volume, which was then incorporated as a covariate in the detection function modeling performed in Distance 6.0.

We used a stratified sampling design to survey proportionally each forest type in every landscape unit. To ensure independence of samples and to minimize edge effects, point counts were no closer than 300 m from any other point and were located 25 m from stand boundaries for native forest plots. However, for pine plantation plots, they were set at 100 m from another patch type. In summary, distance constraints meant that all landscapes were sampled proportionally to patch types and forest cover, with c. 12 points per landscape unit. This sampling effort was adequate to estimate species richness and the density of most Chilean forest bird species, as the number of species and individuals plateaued at 8 points sampled (Jiménez, 2000).

2.5. Statistical analysis

To evaluate the effects of landscape composition and configuration on the functional diversity of forest bird communities, we modeled three complementary indices: functional richness (FRic), functional evenness (FEve), and functional dispersion (FDis) (Villéger et al., 2008). These indices were calculated at the point-count level using the FD package (Laliberté and Legendre, 2010), based on species trait data and relative abundances.

To address the hierarchical structure of the data, with multiple point counts nested within landscape units, we used generalized linear mixed-effects models (GLMMs) implemented in the lme4 package in R (Bates et al., 2015). In each model, we included landscape unit (ID_Landscape) as a random intercept to account for spatial autocorrelation and repeated measures within landscapes (Zuur et al., 2009). This general model structure was:

FRic_log (or FEve, FDis) $\sim$ PLAND_NF_s $+$ PD_NF_s $+$ NLSI_NF_s $+$ (1|ID_Landscape), family $=$ gaussian (link $=$ "identity")

The following landscape variables were used as fixed effects: the proportion of native forest (PLAND_NF), patch density (PD.NF), and normalized landscape shape index (NLSI.NF). Due to high collinearity among several landscape metrics (e.g., core area and PLAND_NF, $r > 0.9$), only variables with lower intercorrelations were retained (see Supplementary Table S1-S2). Specifically, we retained predictors with moderate correlations ($|r| \leq 0.7$). The complete Pearson correlation matrix, including p-values, is provided in Supplementary Table S2. To meet normality assumptions and reduce skewness, the FRic index was log-transformed (+0.01) prior to analysis. All predictor variables were standardized (mean $=$ 0, SD $=$ 1) before modeling to facilitate interpretation of effect sizes.

Response variables were continuous, so we assumed Gaussian error distributions with identity link functions. FRic values were strictly positive and right-skewed, so we tested both (i) a Gamma distribution with a log link and (ii) a log-transformation under Gaussian errors. The log-Gaussian model provided equal or better fit (based on AIC and residual inspection), and was therefore retained. Accordingly, FRic was log-transformed (+0.01), and coefficients should be interpreted as proportional changes in FRic after back-transformation.

Model assumptions were thoroughly assessed using the DHARMa package (Hartig, 2025). Specifically, we evaluated normality and homoscedasticity of residuals, dispersion, outliers, leverage, and influential points. We also examined the adequacy of random effects by checking for singular fits and estimating intraclass correlation coefficients (ICC) to quantify the variance explained at the landscape level. Diagnostic results are provided in Supplementary Figures S1–S3.

Sample sizes were $n = 231$ point counts across 20 landscapes for the breeding season and $n = 125$ for the winter dataset (see Tables 1 and 2). Model coefficients are reported with standard errors (SE), and p-values based on Wald t-tests. Visualizations of model effects were generated using the effects and jtools packages in R.

Finally, to assess functional trait composition at the community level, we calculated community-weighted means (CWM) for each trait using relative abundances of species at each point count (Lavorel et al.,

Table 1
Generalized linear mixed model results for the breeding season (fixed effects).

Index	Predictor	Estimate	Std. Error	CI low	CI high	p
FRic (log)	(Intercept)	-2.114	0.047	-2.213	-2.015	< 0.001
	PLAND NF (scaled)	0.142	0.067	-0.001	0.284	0.052
	PD NF (scaled)	-0.109	0.064	-0.245	0.026	0.107
	NLSI NF (scaled)	-0.020	0.051	-0.127	0.088	0.702
FEve	(Intercept)	0.705	0.008	0.688	0.722	< 0.001
	PLAND NF (scaled)	-0.014	0.012	-0.038	0.011	0.257
	PD NF (scaled)	0.019	0.011	-0.004	0.042	0.106
	NLSI NF (scaled)	-0.010	0.009	-0.029	0.008	0.250
FDis	(Intercept)	0.320	0.004	0.312	0.328	< 0.001
	PLAND NF (scaled)	-0.006	0.005	-0.018	0.005	0.235
	PD NF (scaled)	-0.001	0.005	-0.012	0.009	0.774
	NLSI NF (scaled)	-0.005	0.004	-0.013	0.004	0.266

Breeding models: n (FRic, FEve, FDis) = (231, 231, 231); groups = 20 landscape units. ICC = (FRic 0.04; FEve 0.08; FDis 0.10). R^2_marg / R^2_cond: FRic = 0.13 / 0.16; FEve = 0.12 / 0.19; FDis = 0.04 / 0.14.

Table 2
Generalized linear mixed model results for the non-breeding (winter) season (fixed effects).

Index	Predictor	Estimate	Std. Error	CI low	CI high	p
FRic (log)	(Intercept)	-2.330	0.086	-2.500	-2.159	< 0.001
	PLAND NF (scaled)	0.238	0.132	-0.024	0.499	0.074
	PD NF (scaled)	-0.029	0.098	-0.222	0.165	0.769
	NLSI NF (scaled)	0.231	0.128	-0.022	0.485	0.073
FEve	(Intercept)	0.715	0.018	0.674	0.757	< 0.001
	PLAND NF (scaled)	-0.003	0.029	-0.068	0.063	0.930
	PD NF (scaled)	-0.026	0.021	-0.074	0.022	0.248
	NLSI NF (scaled)	0.020	0.028	-0.043	0.082	0.491
FDis	(Intercept)	0.286	0.006	0.274	0.298	< 0.001
	PLAND NF (scaled)	0.013	0.009	-0.005	0.031	0.158
	PD NF (scaled)	-0.006	0.007	-0.019	0.007	0.369
	NLSI NF (scaled)	0.013	0.009	-0.005	0.031	0.146

Non breeding models: n (FRic, FEve, FDis) = (116, 116, 125); groups = 13 landscape units. ICC = (FRic NA; FEve 0.13; FDis NA). R^2_marg / R^2_cond: FRic = 0.03 / NA; FEve = 0.03 / 0.16; FDis = 0.02 / NA.

2008). These CWMs were used descriptively to examine trait filtering across the landscape gradient. All analyses were conducted in R version 4.5.1 (R Core Team, 2023), with a significance threshold of $\alpha = 0.05$.

In addition to the modeling of functional diversity indices, we tested differences in species abundance between native forest and pine plantations using Wilcoxon rank-sum tests (Z statistics reported). This non-parametric approach was selected due to unequal variances and unbalanced sample sizes between cover types, and provided a robust way to assess species-specific abundance shifts across contrasting habitat types.

Although bird count data were nested within landscape units, we opted for a non-parametric comparison for this specific analysis because the objective was to offer a complementary, species-level perspective on distribution patterns, rather than modeling the entire community structure. This approach was useful to identify species that may be particularly sensitive to habitat conversion or that disproportionately benefit from pine plantation cover.

2.6. *Selection of traits*

To characterize the role of the species in the community we considered a set of features that includes the widest range of ecological functions of each species, as well as characteristics of their autecology that might limit population density. Morphological and feeding traits were included to capture information about demands and strategies of food resource exploitation by species. The interaction of these two types of features strongly defines the trophic niche occupied by the species within a given community. Characteristics of species reproduction, migratory status or particular ecological functions were added as important features describing the ecological functionality of species, since they define limitations for the species itself or other species dependence on the functions performed by the species in question. The information for these traits was obtained from a literature review. For morphological measurements, records from Johnson et al. (1965) were specifically used. For later analyses we excluded traits that showed a high correlation (< 0.6). However, although body mass is highly correlated with other body measurements, this was included because this trait has a strong relationship with other traits (i.e. metabolic rate or life span) that might otherwise no longer be represented and could have a significant effect on the community. Finally, following Zhang et al. (2011) and based on life history and habitat use information for the forest species (Estades, 1997; Díaz, 2005; Díaz et al., 2005), we identified four habitat-use guilds. (see Supplemented material Table S3).

3. Results

3.1. *Forest bird abundance under different cover types*

In total, 26 forest bird species were recorded in 1025 five-minute counts across the surveyed landscapes. Only one migratory breeder, the White-crested Elaenia (*Elaenia albiceps*), was detected, and it was the most abundant species in forest landscapes during the breeding season.

3.1.1. *Breeding season*

Population densities varied greatly between cover types for most species (Table S4). Total species richness was significantly higher in native forest than in pine plantations ($Z = 4.24$, $p < 0.001$). Three forest obligates—the Thorn-tailed Rayadito (*Aphrastura spinicauda*) ($Z = 6.24$, $p < 0.001$), White-throated Treerunner (*Pygarrhichas albogularis*) ($Z = 7.73$, $p < 0.001$), and Chestnut-throated Huet-huet (*Pteroptochos castaneus*) ($Z = 7.13$, $p < 0.001$)—were markedly more abundant in native forest and virtually absent from pine. Five species were significantly more abundant in pine plantations: Patagonian Sierra-finch (*Phrygilus patagonicus*) ($Z = -4.60$, $p < 0.001$), Black-chinned Siskin (*Spinus barbatus*) ($Z = -4.70$, $p < 0.001$), Rufous-collared Sparrow (*Zonotrichia capensis*) ($Z = -4.20$, $p < 0.001$), Southern House Wren (*Troglodytes aedon*) ($Z = -5.67$, $p < 0.001$), and Austral Thrush (*Turdus falklandii*) ($Z = -2.43$, $p < 0.05$). Except for the Rufous-collared Sparrow, these species—plus the White-crested Elaenia and Tufted Tit-tyrant (*Anairetes parulus*)—were among the most common pine specialists.

3.1.2. *Non-breeding season*

Species that were more abundant in native forest during the breeding season generally maintained this pattern in winter, as observed for the Thorn-tailed Rayadito ($Z = 5.29$, $p < 0.001$) and White-throated Treerunner ($Z = 4.69$, $p < 0.001$). In contrast, three species were more abundant in pine plantations: Southern House Wren ($Z = -4.88$, $p < 0.001$), Patagonian Sierra-finch ($Z = -3.27$, $p < 0.01$), and Fire-eyed Diucon (*Pyrope pyrope*) ($Z = -4.39$, $p < 0.001$).

3.2. Functional diversity responses to landscape structure

The effects of landscape structure on avian functional diversity varied between seasons and indices (Tables 1–2; Figs. 2–3).

During the breeding season, functional richness (log-transformed FRic) increased significantly with the proportion of native forest in the landscape (PLAND NF s: $\beta = 0.14 \pm 0.07$, $p = 0.037$). Patch density of native forest (PD NF s) showed a marginally non-significant negative effect on FRic ($p = 0.089$), and the Normalized Landscape Shape Index (NLSI NF s) had no detectable effect ($p = 0.697$).

Functional evenness (FEve) was marginally positively associated with PD NF s ($\beta = 0.02 \pm 0.01$, $p = 0.087$), whereas PLAND NF and NLSI NF showed no significant effects ($p > 0.2$). Functional dispersion (FDis) was not significantly influenced by any of the landscape metrics.

In the non-breeding season, FRic showed positive but marginally non-significant relationships with both PLAND NF ($p = 0.074$) and NLSI NF ($p = 0.073$). PD NF had no effect on FRic ($p = 0.769$). Neither FEve nor FDis showed significant or marginal associations with landscape variables.

Overall, these results suggest that the proportion of native forest in the landscape plays a key role in maintaining functional richness, particularly during the breeding season, while the responses of evenness and dispersion are more variable and weaker. The positive trends for NLSI in winter may reflect structural heterogeneity effects that become more relevant when bird communities are less constrained by breeding. In addition, there is clear variation in functional guild dominance depending on the degree of substitution or fragmentation of native forests by pine plantations. As shown in Fig. 4, the guild "Large Tree Users" (LTU) dominates in landscapes with greater native forest cover and in those with lower patch density, i.e., less fragmented forests, with statistically significant differences in both cases ($F_{3,251} = 3.148$, $p = 0.025$ for forest cover; $F_{3,251} = 4.512$, $p = 0.004$ for patch density).

4. Discussion

As expected, forest bird species richness was higher in native forests than in pine plantations. Differences in abundance between habitat types were primarily driven by species' habitat specialization. Forest obligate species were significantly more abundant in native forests, with some completely absent from pine plantations, indicating a species filtering process in altered landscapes. Conversely, generalist species, such as the Patagonian Sierra-Finch and House Wren, were more abundant in pine plantations, highlighting the homogenization effect of these modified habitats. Similar processes of functional biotic homogenization, where specialist species are replaced by generalists, have been reported in other temperate forests of Chile, with deforestation reducing both functional richness and specialization (Ibarra and Martin, 2015).

Seasonal fluctuations in species densities were evident, likely influenced by migration, regional movements, and changes in territorial behavior. The White-crested Elaenia was the only confirmed migratory breeder, while the Patagonian Tyrant and Fire-eyed Diucon were recorded during the non-breeding season, supporting their classification as austral migrants. Furthermore, some resident species exhibited seasonal habitat shifts, with the Black-chinned Siskin and Austral Blackbird moving to agricultural areas during winter. These patterns underscore the dynamic nature of forest bird communities and the importance of considering seasonal effects when assessing landscape impacts on biodiversity.

The proportion of native forest was the most influential factor shaping functional richness (FRic), particularly during the breeding season. This indicates that landscapes with higher native forest cover support more ecologically diverse bird assemblages. Patch density showed a marginally negative effect on FRic, suggesting that greater fragmentation limits the functional breadth of communities even when forest cover remains. Interestingly, these effects were weaker or absent in the non-breeding season, likely because seasonal movements reduce the dependence of bird communities on local habitat configuration during winter.

Functional evenness (FEve) exhibited only weak relationships with landscape metrics, showing a marginally positive effect of patch density in the breeding season. Functional dispersion (FDis) was not significantly associated with any landscape variable in either season, indicating that redundancy in functional traits may be relatively robust to changes in landscape composition at the spatial scale considered.

An additional pattern emerged from the analysis of functional guilds: the dominance of the Large Tree Users (LTU) guild in landscapes with greater native forest cover and in less fragmented landscapes (lower patch density). This pattern, supported by statistically significant differences in both comparisons, highlights the critical role of mature forest stands in sustaining bird species that depend on large trees for foraging, nesting, or other life-history requirements. The reduction of LTU dominance in fragmented or plantation-dominated landscapes suggests a loss of ecological functions tied to structural forest complexity. Similar trends have been observed in other forested ecosystems, where habitat

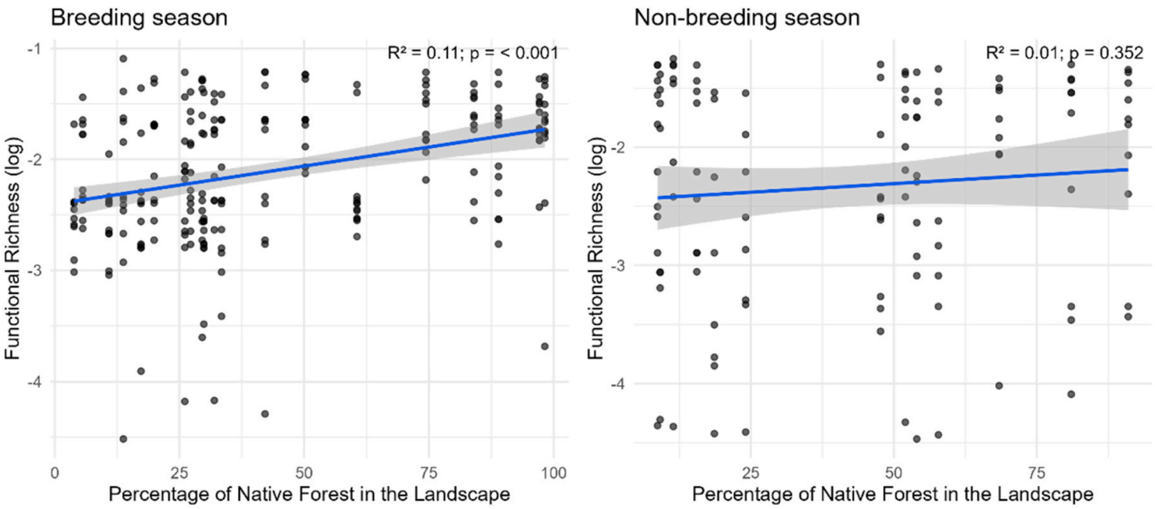

Fig. 2. Effects of native forest cover (PLAND NF s) and patch density (PD NF s) on species richness during the breeding and non-breeding seasons. Left panels: species richness increases with the proportion of native forest in the landscape in both seasons. Right panels: patch density of native forest shows a negative relationship with species richness in both seasons. Lines represent model predictions from GLMMs (Table 1), with 95 % confidence intervals (shaded areas). Points represent observed values for individual count points.

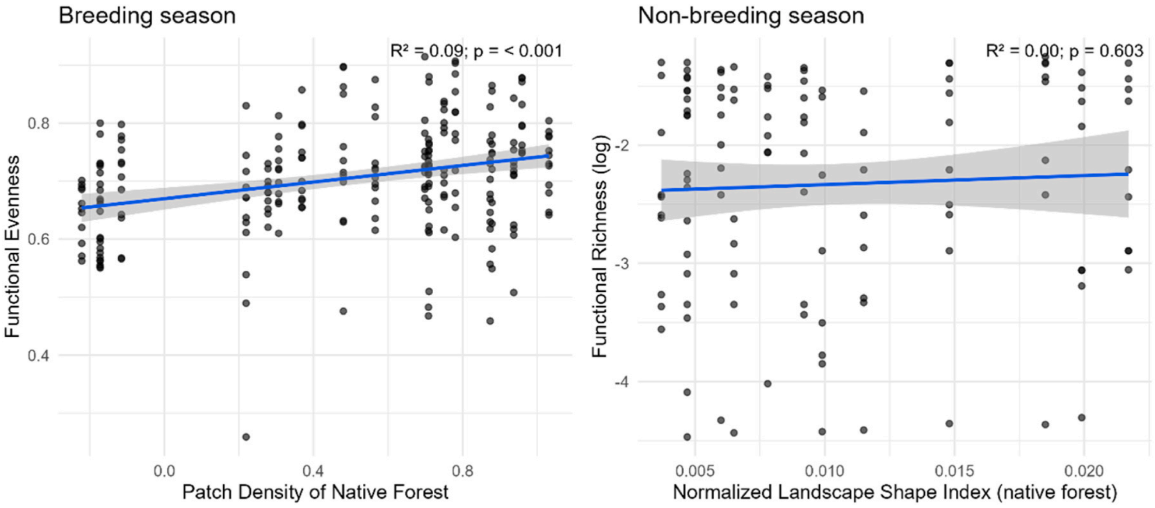

Fig. 3. Relationships between functional diversity indices and landscape metrics during breeding and non-breeding seasons. Top row: Functional richness (log-transformed FRic) increases with the proportion of native forest in the breeding season, with a marginal positive trend in winter. Middle row: Functional evenness (FEve) shows a marginal positive association with patch density during the breeding season. Bottom row: Functional dispersion (FDis) is not significantly related to landscape metrics in either season. Lines show GLMM predictions (Table 2) with 95 % confidence intervals (shaded areas); points are observed values for individual count points.

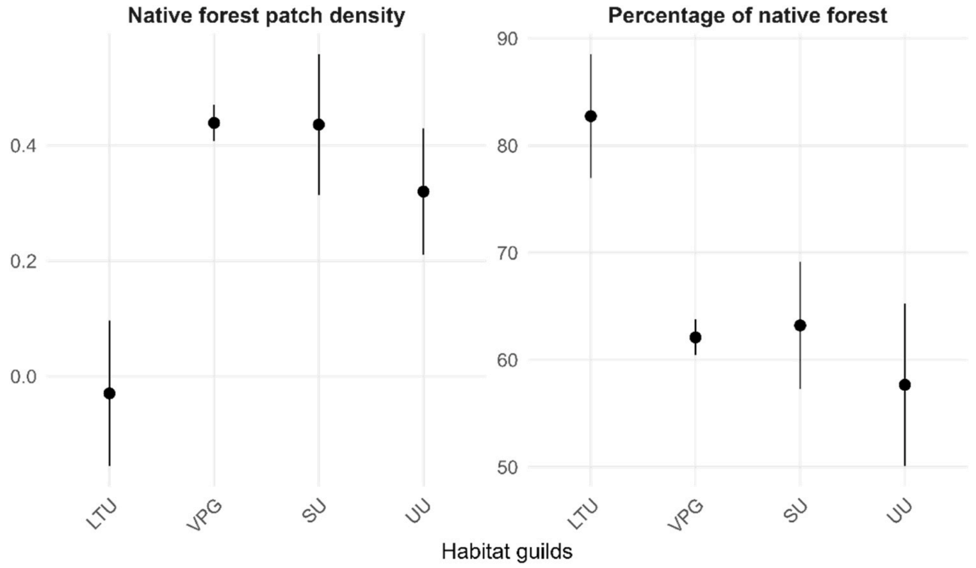

Fig. 4. Variation in the relative abundance of the Large Tree Users (LTU) functional guild across gradients of native forest cover and patch density. Left panel: LTU dominance is significantly higher in landscapes with greater native forest cover ($F_{3,251} = 3.148$, $p = 0.025$). Right panel: LTU dominance is higher in landscapes with lower patch density of native forest ($F_{3,251} = 4.512$, $p = 0.004$). Bars represent mean ± SE, and different letters indicate significant differences among categories (Tukey post hoc test).

loss has led to reductions in functional diversity despite relatively stable species richness, indicating that ecosystem processes can be compromised even before major taxonomic losses occur (Mariano-Neto and Santos, 2023). In the Coastal Range of central Chile, pine plantations established directly over former native forest tend to maintain more forest specialists and fewer generalists than those established over agricultural land, suggesting that land-use history can modulate the degree of biotic homogenization (Uribe et al., 2021). Together, these findings indicate that both the amount of native forest and its historical continuity are crucial for preserving functionally diverse bird communities.

The interaction between native forest cover, fragmentation, and structural complexity reveals mechanisms through which landscape configuration influences avian functional diversity. Although small patches can contribute to species persistence, their ability to maintain functionally diverse communities, particularly those containing specialists like LTU, appears limited. Global syntheses indicate that conservation effectiveness increases with fragment size, with strict protection (>50 ha) being especially important for maintaining bird communities, and moderate protection requiring even larger fragments (>175 ha) to be effective (Timmers et al., 2022). Given the dramatic reduction of continuous Maulino forest (Echeverría et al., 2006), conservation strategies should prioritize retaining large tracts of native forest, limiting further fragmentation, and enhancing connectivity to safeguard both taxonomic and functional diversity.

Our findings emphasize the need for integrated forest management approaches that reconcile production forestry with biodiversity conservation, explicitly incorporating seasonal dynamics, functional trait composition, and the legacy of past land use into planning. Future research should assess whether the patterns observed here are consistent across other forest ecosystems and evaluate the long-term resilience of functional guilds under different management and restoration scenarios.

CRediT authorship contribution statement

Roberto F. Thomson: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andrew G. Gosler:** Writing – review & editing, Supervision.

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

During the preparation of this work, R. Thomson used OpenAI's ChatGPT to assist with language editing and clarity improvements in English. After using this tool, the authors thoroughly reviewed and revised the content as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123201.

Data availability

Data will be made available on request.

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