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Habitat substitution by pine plantations alters foraging niche attributes of temperate forest birds in Chile

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ABSTRACT

The replacement of native temperate forests by exotic tree plantations is widespread in southern South America, yet its functional consequences for forest birds remain insufficiently understood. Because population density alone may not reliably indicate habitat quality, we evaluated whether substitution by mature *Pinus radiata* plantations alters foraging niche attributes of forest birds in south-central Chile. We compared bird densities, microhabitat use, foraging manoeuvres, and multidimensional niche overlap between native forest fragments and adjacent pine plantations during breeding and non-breeding seasons. Bird densities were generally lower in pine plantations, and several forest specialists were absent from this habitat. Mean foraging height showed no consistent habitat effect once species identity and temporal variation were accounted for. However, plantations were characterised by reduced foliage volume in lower strata, and foraging observations were disproportionately associated with native understory vegetation within plantations. For focal species with sufficient observations, multidimensional niche analyses revealed habitat-specific shifts in microhabitat use and, for one species pair, greater convergence in niche space in plantations relative to native forests. These patterns were accompanied by changes in the frequency of certain foraging manoeuvres. Our results indicate that habitat substitution by pine plantations modifies microhabitat use and niche relationships among forest birds, consistent with reduced structural complexity relative to native forests. Although some species exhibited behavioural flexibility, plantations did not support the full assemblage of forest specialists. Integrating behavioural niche attributes with density measures provides an informative assessment of habitat substitution effects in temperate Neotropical forest landscapes.

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Distance sampling; niche overlap; microhabitat partitioning; behavioural flexibility; forest fragmentation; plantation forestry

Introduction

The expansion of exotic tree plantations has profoundly transformed forest landscapes worldwide. Globally, planted forests exceed 290 million hectares (FAO 2020), and in Chile, more than two million hectares of native temperate forest have been replaced over the last six decades, largely by Pinus radiata plantations (Lara and Veblen 1993; Kanowski *et al.* 2005; Uribe *et al.* 2020). In south-central Chile, these plantations now dominate the landscape matrix, leaving remnant fragments of native forest embedded within commercial stands (Estades and Temple 1999). Although mature pine plantations may retain closed-canopy structure and can function as semi-permeable matrix habitats for some species (Tomasevic and Estades 2008; Villard and Haché 2012), they differ substantially from native forests in vegetation composition and vertical complexity, particularly in understory development (Nájera and Simonetti 2010; Simonetti *et al.* 2013). These structural differences are known to influence bird assemblages in fragmented landscapes (Fischer and Lindenmayer 2007; Lindenmayer and Fischer 2013).

Studies in Chile and elsewhere indicate that some forest birds persist in exotic plantations, while others – particularly habitat specialists – decline or disappear (Estades and Temple 1999; Vergara and Simonetti 2004; Julliard *et al.* 2004; Brockerhoff *et al.* 2008; Clavel *et al.* 2010). However, presence or density alone may not adequately reflect habitat quality. Density has long been used as a proxy for habitat suitability (Van Horne 1983), yet in modified landscapes it can be misleading due to source – sink dynamics (Pulliam 1988) or mass effects (Shmida and Wilson 1985), whereby immigration from higher-quality habitats sustains local populations despite reduced demographic performance.

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Consequently, additional functional indicators are needed to assess how habitat substitution influences ecological processes.

Foraging behaviour provides a functional lens through which habitat quality can be evaluated. In forest bird assemblages, species often partition resources through differences in vertical strata, substrate use, and foraging manoeuvres (Robinson and Holmes 1982; Cody 1985; Remsen and Robinson 1990; Kent and Sherry 2020). Such partitioning is central to niche theory (Vandermeer 1972; Pianka 1981), where niche breadth describes the range of resources or microhabitats used by a species, and niche overlap reflects the extent to which species share those resources. Structural complexity is positively associated with avian diversity and functional differentiation (Karr and Roth 1971; Horváth *et al.* 2005), whereas structural simplification may constrain available microhabitats and potentially modify patterns of niche dispersion and overlap (Luiselli 2006). In addition to altering physical structure, plantation forestry can modify arthropod community composition and biomass, thereby influencing the trophic resources available to insectivorous birds (Beltrán and Wunderle 2013; Nell *et al.* 2023). Such changes may not only affect species presence or abundance but also the behavioural strategies through which birds exploit available substrates.

In plantation landscapes, changes in tree architecture and understory structure alter the distribution of substrates and vertical foraging space (Peck 1989; Ulyshen 2011). In Chile, native understory vegetation within pine stands has been shown to influence bird abundance and diversity (Nájera and Simonetti 2010; Poch and Simonetti 2013), suggesting that microhabitat structure may be critical for maintaining functional aspects of bird communities. Behavioural plasticity – the capacity of individuals to adjust foraging tactics under differing structural conditions (Tuomainen and Candolin 2011; Ducatez *et al.* 2020) – may enable some species to persist in plantations despite altered habitat conditions.

Here, we evaluate how the replacement of temperate native forest by mature *Pinus radiata* plantations influences foraging niche attributes of forest birds in south-central Chile. We define foraging niche attributes as the multidimensional use of vertical strata, substrates, and foraging manoeuvres within each habitat. Niche breadth refers to the dispersion of observations within this multidimensional space, whereas niche overlap represents the probabilistic extent to which individuals of one species occur within the niche region of another.

Specifically, we compare bird densities, vertical foraging patterns, substrate use, foraging manoeuvres, and multidimensional niche overlap between native forest fragments and adjacent pine plantations during breeding and non-breeding seasons.

We tested the following predictions:

If pine plantations exhibit lower structural complexity than native forests, birds will show reduced vertical dispersion of foraging observations and increased niche overlap among species in plantations relative to native forests.

Birds will shift their use of vertical strata and substrates, with increased reliance on native understory elements in plantations.

Species will exhibit shifts in the relative frequency of foraging manoeuvres between habitat types, reflecting behavioural adjustments to differing structural conditions.

By integrating density estimates with behavioural niche attributes, this study provides a functional assessment of habitat substitution effects in temperate Neotropical forest landscapes.

Methods

Study area

We studied the bird community of the temperate forest of south-central Chile, focusing on 7500 km^2 of the Roble-Hualo forest type distributed across the coastal range (Figure 1). The topography is characterised by rolling hills and steep slopes, with elevation ranging from 100 to 800 metres above sea level. The region experiences a Mediterranean climate, with mean annual temperatures around 13°C and average annual precipitation between 800 and 1200 mm, concentrated between May and August. This deciduous forest is dominated by the Hualo tree *Lophozonia glauca* (Nothofagaceae) and has experienced extensive alteration, leaving small forest fragments embedded within a matrix of Monterey Pine (*Pinus radiata*) plantations (Estades and Temple 1999).

To encompass the breeding home range of most species of forest-dwelling passerines, landscape units of 4 km^2 were defined (McGarigal and McComb 1995, Villard *et al.* 1999). The selection process prioritised continuous forest habitat, choosing only landscapes with at least 85% forest cover, to minimise edge effects and eliminate potential confounding influences from recently harvested or young stands. A total of 22 such landscape units were selected across the region. Within these, we selected ten native forest fragments (minimum size: 3 ha) surrounded by mature Monterey Pine plantations to study the foraging behaviour of forest bird species. These fragments were chosen to represent the remaining native forest patches in the region.

The landscape unit (4 km^2) constituted the primary sampling unit for inference, whereas individual forest fragments and pine stands within each landscape served as

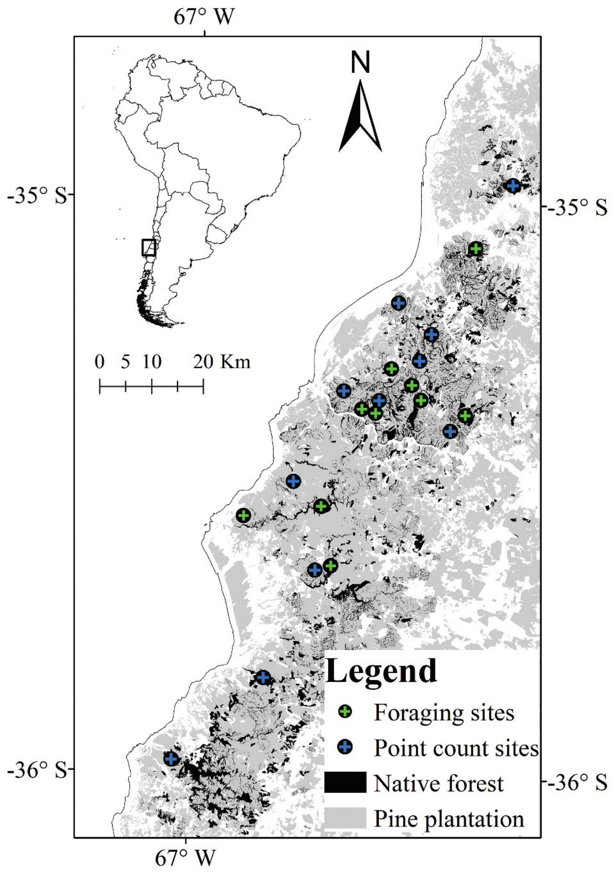

Figure 1. Geographic location of the study area in the coastal range of south-central Chile.

habitat-level sampling units. Point counts represented observational units nested within habitats and landscapes. Because continuous native forest was largely absent in the study region, comparisons reflect differences between remnant native forest fragments and adjacent mature pine plantations within the same landscape context.

Field methods

Sampling design and bird counts

To estimate bird density in native forest fragments and pine plantations, we conducted 12 counts per site using the variable circular-plot method (Buckland 1987). Counts involved repeated 5-minute observations with a 50 m maximum radius. All surveys were performed during the first 5 hours after dawn by a single experienced observer (RT) to ensure consistency. All birds seen or heard within the radius were recorded, and their distances were estimated in 10 m increments. With the exception of hummingbirds and swallows, birds flying over plots were not counted. While we acknowledge that density estimates might be influenced by edge effects (Thomson 2015), the selected methodology captures a realistic snapshot of bird communities in this mosaic landscape. Points were separated by at least 300 m to ensure spatial independence. In native forest plots, stations were set at least 25 m from habitat edges; in pine plantations, the minimum distance to other forest types was 100 m. Sampling effort was deemed sufficient to estimate species richness and density for most Chilean forest bird species, as species accumulation curves plateaued after sampling eight points (Jiménez 2000). Each point was surveyed twice during the breeding season (January 2014) and surveyed again during the 'non-breeding' season (July 2014).

Repeated visits were conducted within a short seasonal window to minimise phenological effects and to improve detection probability estimates under distance sampling assumptions.

At each point-count location, vegetation structure was characterised following Estades and Temple (1999). The total foliage volume and foliage height diversity were estimated visually using five vertical strata: 0–0.3 m, 0.3–2 m, 2–5 m, 5–10 m and >10 m, within a 5 m radius. For each stratum, observers recorded the estimated percentage of space occupied by vegetation, ranging from 0% to 100%. These estimates of understory foliage volume (UFV) were used as a covariate in both bird detectability and foraging models. UFV was selected as a structural proxy because previous studies in Chile have demonstrated its importance in structuring bird assemblages within pine plantations (Nájera and Simonetti 2010; Poch and Simonetti 2013).

Detectability curves for individual species in each vegetation type were fitted using hazard-rate or half-normal models (Buckland *et al.* 1993), with understory foliage volume as a covariate, using Distance 6.0 software (Thomas *et al.* 2010). Species with insufficient detections to fit reliable detection functions were excluded from quantitative density comparisons and retained only for presence – absence reporting. This approach avoids imposing arbitrary detection probabilities and ensures comparability among species with adequate sample sizes. Bird densities between native forest fragments and pine stands were compared using the Mann-Whitney U rank-sum test.

Foraging niches

During January and July 2014, three trained observers (M.A. Vukasovic, J. Bustos-Weisser, and RT) visited each site twice per season to record bird foraging behaviour. Under similar weather conditions across all sites and time periods, avoiding mist, rain, or strong winds, observers conducted ad-libitum searches for any foraging birds within each 3-ha site. Although *ad-libitum* sampling may introduce bias towards conspicuous behaviours, observer training, standardised effort across habitats, and repeated

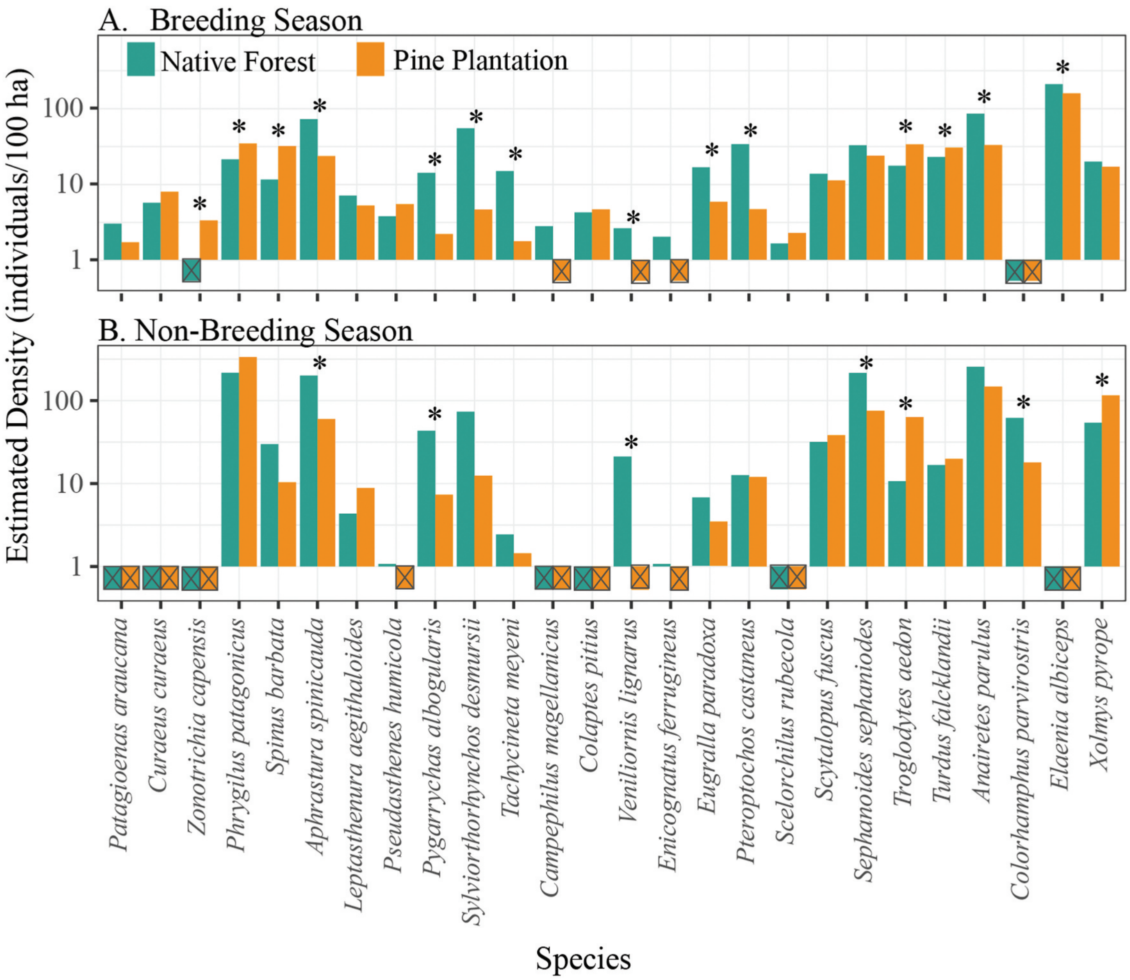

Figure 2. Estimated density (mean individuals/100 ha) of 26 species in native forests and pine plantations during breeding season (A) and non-breeding (B) season in the coastal range of south-central Chile.

visits were used to ensure comparability between forest types. Upon detecting a bird, we recorded its foraging height from the ground (m), canopy height (m), foraging position in the tree (branch, cone, deadwood, foliage, ground, soil, trunk, and twig), foraging substrate (litter, air, tree species, snag) and foraging manoeuvres (chisel, glean, hover, lunge, peck, picking, and sally) (Remsen and Robinson 1990). Foraging events were only recorded for individuals actively feeding or searching for food, with a maximum wait time of 15 seconds for feeding behaviour to occur before resuming the search. To reduce pseudoreplication, repeated observations of the same individual were avoided. Observers moved continuously within each site and did not record multiple sequential events from the same individual unless clear spatial displacement occurred. Territorial spacing and movement direction were used as cues to distinguish individuals. Birds in mixed-species flocks were excluded to minimise potential non-independence of foraging events. We also visually estimated the foliage volume as percentage in five vertical strata (0–0.3 m, 0.3–2 m, 2–5 m, 5–10 m, and >10 m). Sampling effort was balanced across habitat types to obtain comparable numbers of foraging observations per species whenever possible. We categorised foraging manoeuvres following Remsen and Robinson (1990):

Chisel: Bird removes substantial substrate portions to extract prey.

Glean: Perched bird captures prey from nearby substrate.

Hover: Bird flies out and hovers momentarily to capture prey from a nearby substrate.

Lunge: Bird runs to capture prey.

Peck: Bird strikes and removes small substrate portions to obtain prey.

Picking: Bird captures prey from the substrate it is perched on.

Sally: Bird flies out to catch prey in the air.

Statistical analysis

Foraging niche analysis

Species with ≥10 foraging observations were included in descriptive behavioural analyses. A minimum of 10 observations was required to ensure adequate representation of categorical variables, whereas at least 20 observations per habitat were required for Bayesian niche estimation to obtain reliable posterior distributions. Using four continuous variables (canopy height, foraging height, foliage volume in 0–0.3 m and 0.3–2 m vertical strata), we estimated species niche regions and pairwise niche overlap in native forest and pine plantations using the R package *nicheROVER* (Swanson et al. 2015). In this framework, a species' niche region is defined as the multivariate space containing 95% of the posterior probability of occurrence for that species (García-Vernet et al. 2021). Niche regions were estimated using 10,000 iterations at a 0.95 probability level.

Pairwise niche overlap was estimated using 2000 iterations. Overlap is directional and represents the probability that individuals of species A occur within the niche region of species B. Differences in niche overlap between habitats were evaluated by comparing posterior means and their 95% credible intervals.

All continuous variables were inspected for normality; foraging height was log-transformed prior to analysis to meet model assumptions.

Associations between bird species and (1) habitat type, (2) foraging position, (3) substrate, and (4) foraging manoeuvre were evaluated using chi-square tests of independence with Bonferroni-adjusted post-hoc comparisons. Pearson's standardised residuals were used to identify positive and negative associations (Agresti 2013; Deshwal *et al*. 2022). Mosaic plots were generated using the R package graphics (Friendly 1994). All analyses were conducted in R 4.3.2 (R Core Team 2023).

We assessed associations between species and categorical foraging variables (habitat type, foraging position, substrate – including tree species – and foraging manoeuvre) using chi-square tests of independence with Bonferroni-adjusted post-hoc comparisons. Pearson's standardised residuals were used to identify cells driving significant associations, and results were visualised with mosaic plots. For multivariate niche analyses, we used nicheROVER to estimate species-specific 95% niche regions and directional pairwise niche overlap in native forest and pine plantations, based on four continuous variables (canopy height, log-transformed foraging height, and foliage volume in the 0–0.3 m and 0.3–2 m strata). Niche regions were estimated with 10,000 iterations and overlap with 2000 iterations, summarising posterior means and 95% credible intervals. All analyses were performed in R 4.3.2.

Foraging height analysis

To evaluate how foraging height varied across habitat types and time of day, we used generalised linear mixed models (GLMMs) fitted with the lmer function in the lmerTest package (Kuznetsova *et al*. 2017). Foraging height (log-transformed) was the response variable. Habitat type and time after sunrise were included as fixed effects. Bird species and sampling site were included as random intercept effects to account for interspecific variability and non-independence of observations within sites. Model residuals were inspected for normality and homoscedasticity, and model fit was evaluated using diagnostic plots.

Results

In total, 26 forest bird species were recorded in 1025 5-min counts across the surveyed landscapes (Figure 1, Table 1). The density of 11 out of 26 species was significantly higher in native forests than in pine plantations (Figure 2). Three species – Magellanic Woodpecker (*Campephilus magellanicus*), Austral Parakeet (*Enicognathus ferrugineus*), and Striped Woodpecker (*Veniliornis lignarius*) – were only detected in native forests. Six species were more abundant in pine plantations, and only one, the Rufous-collared Sparrow (*Zonotrichia capensis*), was detected exclusively in pine stands. The White-crested Elaenia (*Elaenia albiceps*), the only breeding migrant species in the area, was the most abundant forest bird during the breeding season.

We observed foraging events for 19 species, but analysis was restricted to the 10 species with ≥10 records, yielding 629 foraging observations (Table 2). The number of observations per habitat type was similar for most species, though some clearly preferred or avoided one habitat. For example, the House Wren (*Troglodytes aedon*) was more common in pine plantations despite foraging in the understory, whereas the Striped Woodpecker (*Veniliornis lignarius*) was never recorded foraging in pine stands.

Species also differed in their canopy use across habitats. The small Black-chinned Siskin (*Spinus barbata*) foraged up to 15 m in native forests, but over 20 m in pine stands. Conversely, the larger Austral Thrush (*Turdus falklandii*) never foraged above 1 m in pine stands despite singing from tall pines.

Table 1. Estimated densities for species from forested landscapes in south-central Chile during the 2012–2013 breeding season, showing *U* test for estimated densities between native forest and pine plantations.† species with records for only one landscape.

		Breeding season					Non breeding season				
Species	Categorization	Estimated density (Mean Ind/100 Ha)		Mann-Whitney-Wilcoxon U test			Estimated density (Mean Ind/100 Ha)		Mann-Whitney-Wilcoxon U test		
Scientific name	Forest Specialist	Native fragment	Pine plantation	U	*Z*	*p*value	Native fragment	Pine plantation	U	*Z*	*p*value
COLUMBIDAE											
Patagioenas araucana		2.99	1.70	8579	1.43	–	0	0	–		-
PSITTACIDAE											
Enicognatus ferrugineus†	FS	2.01	0	8256	1.43	–	1.07	0	1980	1.05	–
TROCHILIDAE											
Sephanoides sephaniodes		32.33	23.50	9219	1.94	.	215.82	75.54	3019	5.45	0
PICIDAE											
Campephilus magellanicus	FS	2.76	0	8320	1.75	.	0.53	0	1980	1.05	–
Colaptes pitius		4.20	4.62	8307	0.59	–	0.53	0	1980	1.05	–
Veniliornis lignarius		2.60	0.18	9689	4.74	0	21.14	0	2277	3.46	0
EMBERIZIDAE											
Curaeus curaeus		5.64	7.89	7647	−1.02	–	0	0	–		-
Zonotrichia capensis		0.53	3.31	6683	−4.20	0	0	0	–		-
FRINGILIDAE											
Spinus barbata		11.44	31.45	5582	−4.70	0	29.91	10.38	2064	1.09	–
Phrygilus patagonicus		21.04	34.04	5532	−4.60	0	216.90	334.93	1394	−3.27	**
FURNARIIDAE											
Aphrastura spinicauda	FS	71.3	23.3	11,669	6.24	0	200.93	60.16	2996	5.29	0
Leptasthenura aegithaloides		7.03	5.18	7573	−1.50	–	4.34	8.87	1788	−1.53	–
Pygarrychas albogularis	FS	13.99	2.19	12,065	7.73	0	43.36	7.34	2667	4.69	0
Pseudasthenes humicola		3.74	5.39	8195	0.28	–	1.07	0	1980	1.05	–
Sylviorthorhynchos desmursii		53.96	4.59	11,521	7.03	0	73.48	12.43	2192	1.79	.
HYRUNDINIDAE											
Tachycineta meyeni		14.72	1.76	10,165	4.88	0	2.43	1.44	1987	0.58	–
RHINOCRYPTIDAE											
Eugralla paradoxa	FS	16.57	5.81	9981	3.70	0	7.55	5.78	2025	0.70	–
Pteroptochos castaneus	FS	33.38	4.65	11,737	7.13	0	12.62	12.05	2080	1.77	.
Scelorchilus rubecola†	FS	1.64	2.26	8194	0.60	–	0	0	–		-
Scytalopus fuscus		13.57	11.14	8586	0.81	–	31.74	38.28	1852	−0.65	–
TROGLODITIDAE											
Troglodytes aedon		17.35	33.14	4879	−5.67	0	10.67	63.35	1125	−4.88	0
TURDIDAE											
Turdus falklandii		22.65	30.07	6711	−2.43	*	16.73	19.84	2014	0.39	–
TYRANNIDAE											
Anairetes parulus		84.03	32.44	12,065	6.76	0	256.42	148.32	2237	1.44	–
Colorhamphus parvirostris		0	0	–		-	61.99	18.01	2662	3.96	0
Elaenia albiceps		205.97	155.99	10,498	4.02	0	0	0	–		-
Xolmys pyrope		19.62	16.85	8160	0.05	–	54.13	116.14	1084	−4.39	0
Total Number of Species		9.64	8.44	10,608	4.24	0	6.32	5.54	2226	1.40	–

*Signif. codes: 0; '***' 0.001; '**' 0.01; '*' 0.05; '.' 0.1; '– ' 1.*

Table 2. Number of foraging observations from 10 species of birds in two habitat types observed in south-central Chile.

Common Name	Scientific Name	Species code	Native	Pine
Tufted-tit Tyrant	*Anairetes parulus*	Anapar	42	64
Thorn-tailed Rayadito	*Aphrastura spinicauda*	Aphspi	100	94
White-crested Elaenia	*Elaenia albiceps*	Elaalb	58	9
Patagonian Sierra-Finch	*Phrygilus patagonicus*	Phrpat	50	31
White-throated Treerunner	*Pygarrhichas albogularis*	Pygalb	37	34
Black-chinned Siskin	*Spinus barbata*	Spibar	10	32
Southern House Wren	*Troglodytes* aedon	Troaed	2	15
Austral Thrush	*Turdus falklandii*	Turfal	18	6
Striped Woodpecker	*Veniliornis lignarius*	Venlig	12	0
Fire-eyed Diucon	*Xolmis pyrope*	Xolpyr	11	4

Foraging height (GLMM)

After accounting for species identity, site and sampling date as random effects, mean foraging height was not significantly influenced by habitat type ($\beta = 0.24 \pm 0.27$ SE, $p = 0.37$) or time of day ($\beta = -0.04 \pm 0.08$ SE, $p = 0.67$). Including Season or a Cover × Season interaction did not substantially improve model fit ($\Delta AIC < 2$), and interaction terms were not statistically supported. Variation in foraging height was therefore largely structured by species identity and sampling date rather than by a consistent habitat effect.

Multivariate niche structure

The structure of the trophic niche of four focal species revealed variation in behavioural strategies between forest types (Figure 3). The Thorn-tailed Rayadito (*Aphrastura spinicauda*) foraged higher in pine plantations, while the Patagonian Sierra-Finch (*Phrygilus patagonicus*) and White-throated Treerunner (*Pygarrhichas albogularis*) foraged lower in plantations than in native forests. No consistent height shift was observed for the Tufted Tit-Tyrant (*Anairetes parulus*). Foraging sites in pine plantations had higher canopy height but lower foliage volume in the lower vertical

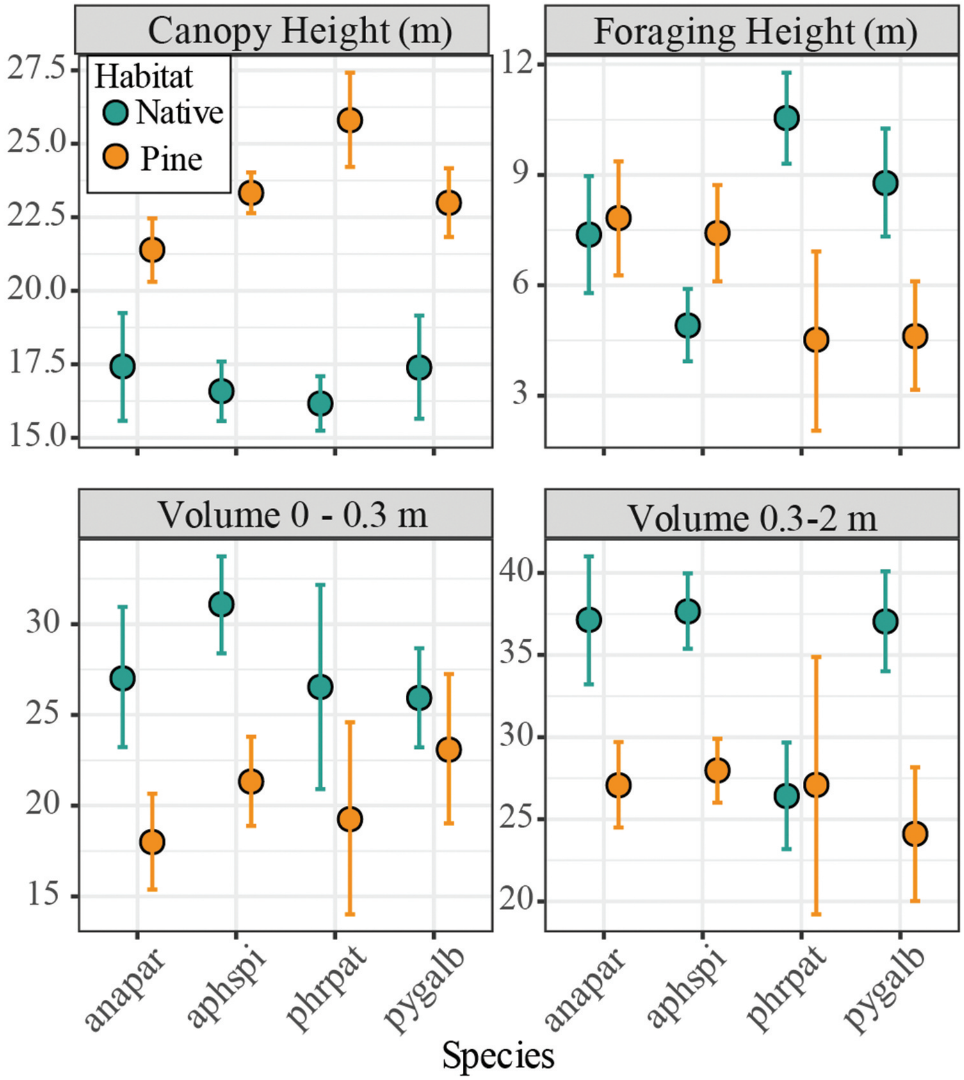

Figure 3. The mean and 95% credible interval for four variables characterising foraging niche region of species in native forest (green) and pine plantations (orange) on the coastal range of south-central Chile. The units of variables are indicated in panel headings. The four species are Tufted-tit Tyrant (anapar), Thorn-tailed Rayadito (aphspi), Patagonian Sierra-Finch (phrpat), and White-throated Treerunner (pygalb).

strata (0–0.3 m and 0.3–2 m), indicating vertical simplification.

Niche overlap among species pairs shifted across habitats (Figure 4). The overlap between *A. spinicauda* and *P. patagonicus* increased in pine plantations, suggesting greater convergence in multivariate niche space under simplified structural conditions. Overlap was directional, with *P. patagonicus* more frequently occurring within the niche region of *A. spinicauda* than vice versa. This asymmetry was more pronounced in pine plantations for three focal species pairs.

Categorical niche components

Species were not randomly associated with habitat type (χ^2 (9, $N = 629$) = 84.3, $p < 0.01$, Cramer's V = 0.366), indicating a moderate association. Some species, including *A. parulus*, *S. barbata*, and *T. aedon*, were more frequently recorded in pine plantations, whereas others such as *E. albiceps* and *V. lignarius* were more frequent in native forests (Supplementary Figure S1; Tables S2–S3).

Species also differed in their use of microhabitats such as vertical foraging strata and substrates. In native forests (χ^2 (54, $N = 340$) = 399.6, $p < 0.01$, Cramer's V = 0.437) and pine plantations (χ^2 (56, $N = 289$) = 341.0, $p < 0.01$, Cramer's V = 0.411), species exhibited distinct preferences for vertical strata (Supplementary Figure S2; Tables S4–S5).

Tree species and substrate use varied across forest types (χ^2 (225, $N = 629$) = 941.1, $p < 0.01$, Cramer's V = 0.392). In native forests, birds used a wide array of native tree species (e.g. *Gevuina avellana*, *Aextoxicum punctatum*, *Aristotelia chilensis*, *Cryptocarya alba*) and multiple substrates, whereas in pine plantations foraging was largely restricted to *Pinus radiata* (Supplementary Figure S3). Generalist species such as *S. barbata* and *T. falklandii* made greater use of ground and litter substrates in plantations.

Foraging manoeuvres also differed between forest types. In native forests, 7 of 10 species showed clear manoeuvre preferences (χ^2 (54, $N = 340$) = 612.7, $p < 0.01$, Cramer's V = 0.548), whereas in pine plantations only 5 species did so (χ^2 (40, $N = 289$) = 391.6, $p < 0.01$, Cramer's V = 0.521) (Supplementary Figure S4; Tables S8–S9). For example, *T. falklandii* used 'lunge' and 'pick' manoeuvres in native forests but showed no strong manoeuvre preference in plantations. *Elaenia albiceps* favoured 'hover' and 'sally' in native forests but exhibited weaker manoeuvre differentiation in plantations.

For forest specialists, shifts in manoeuvre use were subtle rather than categorical. *Aphrastura spinicauda* avoided 'sally' in native forests but not in plantations, *P. albogularis* reduced 'chisel' use in plantations, and *A. parulus* avoided 'pick' in plantations. In contrast, generalist species such as *T. aedon* and *S. barbata* showed greater behavioural flexibility in simplified habitats.

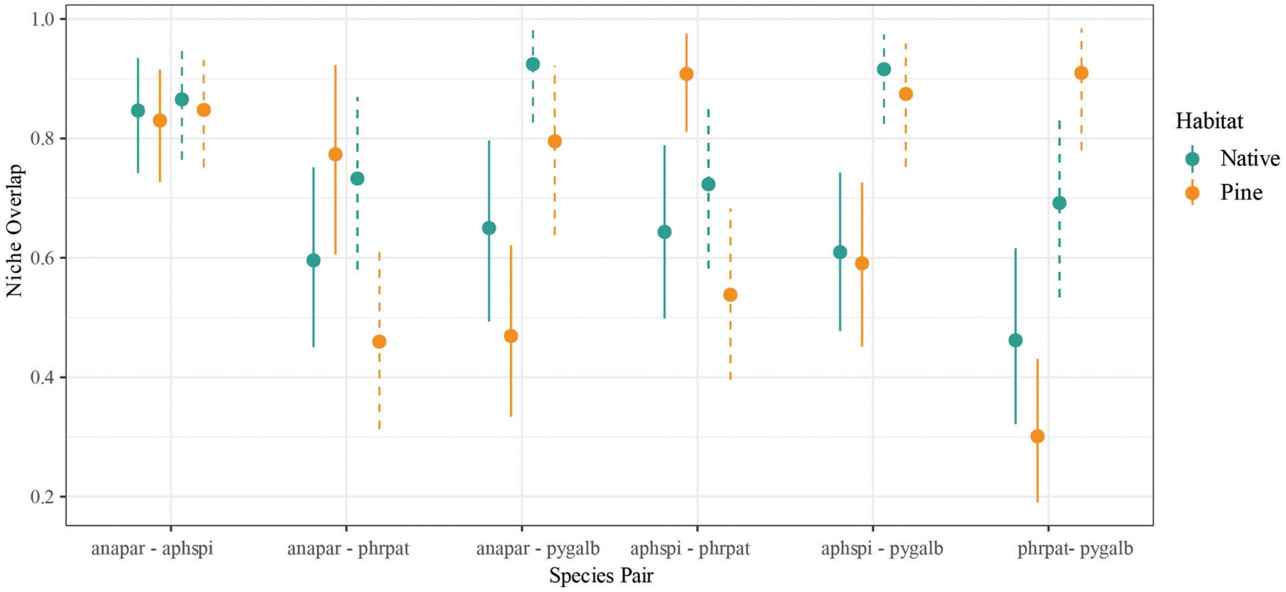

Figure 4. Foraging niche overlap (mean ±95% credible interval) between pairs of bird species in native forest (indicated in green) and pine plantations (indicated in orange). Solid lines represent the overlap of species a in niche region of species B, species A and B being the pair of species labelled on x-axis and dashed lines represent individuals of species B in niche regions of species A. The four species in the pairwise comparisons are Tufted-tit Tyrant ('anapar '), Thorn-tailed Rayadito ('aphspi '), Patagonian Sierra-Finch ('phrpat '), and White-throated Treerunner ('pygalb').

Discussion

Our findings reinforce the contention that local densities alone provide a limited measure of habitat quality. Although several species were more abundant in pine plantations, density differences did not consistently translate into uniform shifts in vertical foraging height once species identity, site, and sampling date were accounted for. This suggests that responses to habitat substitution operate through changes in behavioural composition and niche configuration rather than through simple vertical displacement. The absence of hole-creating species such as the Striped Woodpecker in pine plantations may further influence community structure in ways not directly captured by density or height metrics, underscoring the importance of integrating multiple functional parameters when evaluating habitat quality.

The conversion of native forests into pine plantations alters vegetation structure and substrate diversity, reshaping how species exploit food resources. Insectivorous birds are known to adjust their foraging strategies in response to prey distribution and structural constraints (Powell *et al.* 2015). Similarly, birds in pine plantations must operate within a vegetation structure characterised by reduced native plant diversity and simplified vertical layering, rather than exhibiting a consistent shift in mean foraging height, species showed habitat-specific adjustments in microhabitat use, substrate selection, and manoeuvre frequency. Such species-specific responses are consistent with behavioural plasticity as a mechanism mediating ecological change (Tuomainen and Candolin 2011).

Behavioural flexibility may buffer some species from habitat alterations. White-crested Elaenia, for example, exhibits interannual shifts in foraging microhabitat and substrate use in response to variation in fruit and arthropod availability (Cueto *et al.* 2016). Similar flexibility was observed here, particularly among generalist species that exploited multiple substrates in plantations. However, behavioural adjustments do not necessarily imply equivalent habitat quality. Plastic responses may allow persistence under suboptimal conditions, potentially incurring energetic or demographic costs (Guillaumet and Russell 2022).

Although we did not detect a consistent difference in average foraging height between habitats after accounting for hierarchical structure in the data, plantation stands were characterised by higher canopy height but reduced foliage volume in lower strata. Foraging observations indicated that birds concentrated activity within the native understory vegetation embedded in plantations, supporting previous findings that native understory structure strongly influences bird abundance and community composition (Poch and Simonetti 2013; Dagan and Izhaki 2019). These substrates provided diverse foraging positions, whereas pine canopies offered comparatively limited structural heterogeneity. While some authors have suggested that exotic plantations may function as complementary foraging habitats (Tubelis *et al.* 2004; Mortelliti and Lindenmayer 2015), our observations indicate that birds relied disproportionately on native vegetation components within plantations. This pattern is consistent with documented differences in arthropod communities between native trees and exotic pines (Escobar 2008; Ulyshen 2016).

Multivariate niche analyses revealed increased niche convergence among some focal species in plantations. Rather than interpreting this pattern strictly as intensified competition, it may reflect reduced structural and substrate diversity, constraining the range of available foraging options. Directional overlap patterns suggest asymmetric use of niche space, indicating that some species expand into the functional space of others under simplified conditions. Similar reductions in multidimensional niche segregation have been documented in structurally simplified tropical montane forests (Yepes-Arcila *et al.* 2025). These results emphasise that structural complexity and microhabitat diversity are key determinants of functional organisation in bird assemblages.

Differences in foraging behaviour across habitats often reflect vegetation structure (Whelan 2001) and prey availability (Hološková *et al.* 2023). In our study, changes in manoeuvre frequencies between forest types suggest behavioural adjustment rather than wholesale displacement. For instance, some Furnariids increased aerial behaviours in plantations, whereas flycatchers reduced their reliance on such manoeuvres. These shifts may represent context-dependent optimisation strategies rather than maladaptive departures from 'normal' behaviour. Habitat-driven changes in manoeuvre composition could nevertheless influence energetic efficiency or prey capture success (Tuomainen and Candolin 2011), with potential demographic consequences that warrant further study.

While exotic pine plantations present ecological constraints, most species in this study foraged at least occasionally on pine substrates, highlighting dietary and behavioural flexibility (Simeone *et al.* 1997; Estades 2001). Generalist or euryphagous species are typically better equipped to exploit novel environments (Rotenberry and Wiens 1980; Sol *et al.* 2002; Ducatez *et al.* 2020). However, specialist taxa may be more sensitive to reductions in structural and botanical diversity. The absence of certain forest specialists from plantations underscores these limits.

Reduced ecological diversity in pine plantations likely constrains niche occupancy through diminished substrate heterogeneity and prey diversity (Newton 1998; Twining *et al.* 2016; Hallmann *et al.* 2017). Three limitations of our study should be acknowledged. First, while niche occupancy provides functional insight, demographic parameters such as reproductive success and survival are necessary to assess habitat quality directly. Second, prey availability was not quantified and should be incorporated into future work. Third, predation risk – which can influence foraging decisions – was not examined.

Although exotic pine plantations contribute to regional tree cover, they do not replicate the structural or functional properties of mature native forests (Osuri *et al.* 2020). Our results indicate that habitat substitution alters the functional organisation of forest bird assemblages, even when the average vertical foraging height remains similar. Protecting remnant native forests and enhancing native understory complexity within plantation landscapes appear to be critical for maintaining trophic and behavioural diversity in temperate South American bird communities.

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Author contributions

CRediT: **Roberto F. Thomson:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing; **Anant Deshwal:** Formal analysis, Writing – review & editing; **Pooja Panwar:** Formal analysis, Visualization, Writing – review & editing; **Andrew G. Gosler:** Investigation, Supervision, Writing – review & editing.

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Data availability statement

Data will be made available upon acceptance in ORA (Oxford).

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