

Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales

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Abstract Although it is recognized that anthropogenic forest fragmentation affects habitat use by organisms across multiple spatial scales, there is uncertainty about these effects. We used a hierarchical sampling design spanning three spatial scales of habitat variability (landscape > patch > within-patch) and generalized mixed-effect models to assess the scale-dependent responses of bird species to fragmentation in temperate forests of southern Chile. The abundances of nine of 20 bird species were affected by interactions across spatial scales. These interactions resulted in a limited effect of within-patch habitat structure on the abundance of birds in landscapes with low forest cover, suggesting that suitable local habitats, such as sites with dense understory cover or large trees, are underutilized or remain unused in highly fragmented landscapes. Habitat

specialists and cavity-nesters, such as tree-trunk foragers and tapaculos, were most likely to exhibit interactions across spatial scales. Because providing additional sites with dense understory vegetation or large habitat trees does not compensate the negative effect of the loss of forest area on bird species, conservation strategies should ensure the retention of native forest patches in the mixed-use landscapes.

Keywords Birds · Cross-scale effects · Forest fragmentation · Habitat use · Habitat specialists · Chile

Introduction

Effective species conservation requires determining how habitat quality, distribution and structure change as a result of anthropogenic habitat fragmentation and loss. Such processes result in reduced population size and biodiversity as well as changes in species interactions and ecosystem processes (Lens et al. 2002; Smith and Hellmann 2002). A key issue to develop effective conservation strategies is to assess the relevant spatial scales to examine ecological process (Wiens 1989; Levin 1992; Cooper et al. 1988). Studies considering different spatial scales for a given process provide useful information for conservation in fragmented landscapes (e.g. Donovan et al. 1997; Gehring and Swihart 2003; Cunningham and Johnson 2006; Li et al. 2006).

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Ecological processes at one spatial scale may interact with processes at another scale resulting in threshold responses (Peters et al. 2004; Cash et al. 2006). The interactions among habitat variables across different spatial scales result in nonlinear fragmentation effects on populations (Andr n 1994; Peters et al. 2004; Schooley and Branch 2007). These cross-scale effects are important for conservation because the explanatory power of patch area and habitat features for species richness and abundance may change as a function of landscape configuration, as expected from habitat selection, foraging, and metapopulation theories (Boren et al. 1999; Thompson et al. 2002; Schooley and Branch 2007; Willig et al. 2007).

Birds of Chilean temperate forests, such as cavity nesters, understory dwellers and forest specialists, are especially sensitive to habitat fragmentation as their abundance declines in small, isolated and disturbed forest fragments surrounded by open fields (Willson et al. 1994; D az et al. 2005; Vergara and Marquet 2007). Nevertheless, to date the effect of habitat change across spatial scales on avian assemblages has not been investigated. These cross-scale effects may result in: (1) nonlinear effects of patch size on bird species abundances (or nesting success) as the overall proportion of suitable habitat declines in the landscape (e.g. Andr n 1994; Thompson et al. 2002; Betts et al. 2006); and (2) nonlinear deterioration of habitat quality as forest cover over the landscape and/or patch size decline (Turner 2006, see also Winter et al. 2006).

The purposes of this study were twofold: Firstly, to examine the scale-dependency of bird species responses to forest fragmentation by testing the effects of nested spatial hierarchy of habitat components upon forest birds (e.g. Wu and Li 2006). To assess this effect we used a nested sampling design and modeling framework which provides an estimate the effects of relevant habitat variables at landscape, patch and within-patch scales. We considered forest patches ranging between 0.2 and 70 ha within landscape units of 4 and 36 km², the latter comprising the eight adjacent 4-km² units. Within-forest we measured habitat variables in 0.04 ha plots. Based on the results of the previous analysis, we then assessed the possible association of scale-dependent responses of birds to fragmentation with particular ecological

and life-history traits of birds that may account for their different vulnerability.

Methods

Study area

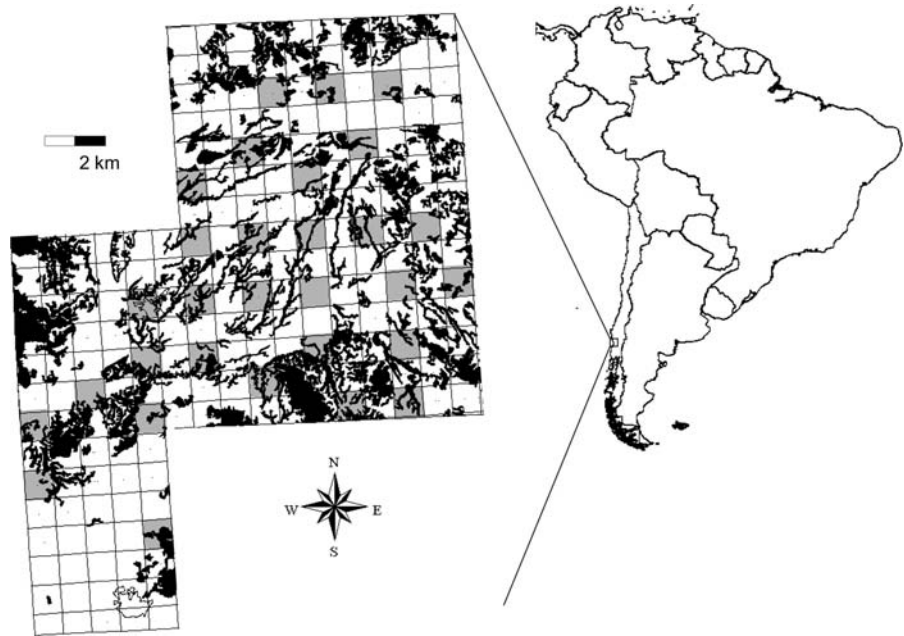
We studied the human-dominated lowland area separating the Andean and Coastal ranges of south-central Chile (39° S, 73° W) or central valley of the Lake District. The topography of rolling hills at this latitude was once covered by continuous lowland forests of two types: mixed deciduous *Nothofagus obliqua*-dominated forest (hereafter referred as *Nothofagus* forest) with an evergreen understory and broad-leaved evergreen forests (Donoso 1993). Both of these lowland forest types have been largely cleared by humans for agriculture and livestock grazing, using fire and logging, resulting in landscapes with scattered, small remnant forest patches surrounded by extensive areas of farmland and pastures (e.g. Echeverr a et al. 2006).

Study design

We selected ca. 900 km² for analysis of the landscape mosaic (see below, Fig. 1), using ortho-photos taken in 1999 (scale 1:10,000). This area was subdivided into a grid of about 217 cells of 2 × 2 km. For subsequent sampling and analyses, each cell in the grid was considered a landscape subunit varying in heterogeneity and containing different habitat patches. The extension of these landscape subunits (4 km²) was suitable for measuring landscape and patch variables relevant to its use by forest birds (Drapeau et al. 2000). In each cell of the grid, we measured habitat variables in a nested design (see the next section).

Since the absence of cross-correlations among habitat variables is an important requirement to assess their effects across spatial scales (e.g. Kristan and Scott 2006), we used stratified-random sampling, selecting 30 2 × 2 km cells from the 217-cell grid. Stratified sampling ensured that all possible combinations of patch size, forest cover remaining per grid cell, and forest types were represented in the selected cells. This sampling also reduced the expected positive correlation between forest cover per cell

Fig. 1 Map of South America showing the location of the study area in the Lake District of southern Chile (right). The area on the left is the sampling grid, made up of 217 2 × 2 km cells where landscape, patch and within-patch variables were measured. Selected cells using a stratified-random sampling ($n = 30$) are shown by black squares and dark shading within cells represents cover of evergreen or *Nothofagus* forest



and mean patch size (Trzcinski et al. 1999; Fahrig 2003; Betts et al. 2006; Table 1). Accordingly, we selected cells including: (1) various categories of percent forest cover remaining in the cell, resulting in 10 grid cells for each of the three forest cover ranges: 5–15%, 16–30% and 30–60%; (2) various types of forest composition, resulting in 30 cells with both broad-leaved evergreen and *Nothofagus*-dominated deciduous forest; and (3) a range of forest patch sizes within the grid cells, resulting in 30 cells containing simultaneously a number of patches of the following size categories: <1 ha, 1–5 ha and 5–70 ha. This sampling procedure required searching for landscapes with specific combinations of forest cover and patch sizes that minimized correlations between variables across spatial scales ($r < 0.33$ and $p > 0.8$, for all variable combinations, see Table 1). We sampled a similar type of matrix habitat (i.e. pasture) and a similar gentle slope (<10%) in all cells. Cells covered by exotic plantations (*Pinus radiata* and *Eucalyptus* sp.) were not sampled because they were located mostly on steeper slopes (>10%) and represented <5% of the entire mapped area. Because of their restricted presence in this landscape, it is unlikely that the distant presence of exotic plantations would have influenced bird abundances in the sampled cells. The minimum distance between the edges of selected cells was about 2 km (Fig. 1).

Landscape, patch and habitat variables

We used a nested hierarchical sampling scheme to characterize landscapes, patches and habitat structure within patches: first, we measured landscape attributes (i.e., the proportion of forest cover by type vs. matrix habitat) in all grid cells ($n = 217$) in the mapped area; then, we measured forest patch attributes (size and isolation) within the stratified sample of cells ($n = 30$); and finally, we measured habitat variables within the forest patches of each of the 30 selected grid cells. To characterize each sampled cell we used an existing GIS database (CONAF-CONAMA-BIRF 1999), derived from aerial and satellite photos taken between 1994 and 1997. This database provides estimates of the area (ha) covered by native forest types and other land uses within each grid cell at scale 1:50,000. The database distinguished: (1) broad-leaved evergreen forest without *Nothofagus* species (hereafter called as evergreen forest); and (2) *Nothofagus* forest, composed by the deciduous *N. obliqua* often mixed with the evergreen *N. dombeyi*. Furthermore, using this database we were able to categorize *Nothofagus* forest stands in two subgroups: (1) naturally regenerating second-growth stands, characterized by small diameter trees, usually <30 cm diameter at breast height and <60 year old (hereafter called second-growth

Table 1 Summary, mean and standard deviations (SD), of habitat variables measured at three spatial scales

Variables	Mean	SD
<i>Within-patch habitat variables (n = 510 plots)</i>		
Total understory cover (%)	62.0	1399.5
Canopy cover (%)	52.4	1182.9
Cover of understory bamboo (<i>Chusquea quila</i>) (%)	44.9	1014.0
Tree density (number of trees/ha)	490.7	11082.5
Mean diameter at breast height (cm)	37.1	836.9
Canopy height (m)	13.5	304.2
Forest type ^a	0.61	0.23
<i>Patch variables (n = 238 patches)</i>		
Patch size (ha)	13.7	211.5
Patch isolation (m)	86.1	1327.7
<i>Landscape variables (n = 30 grid cells)</i>		
Total forest cover (4 km ²) (%)	22.5	123.0
Mature forest cover (4 km ²) (%)	1.1	6.2
Second-growth <i>Nothofagus</i> forest cover (4 km ²) (%)	16.1	88.0
Evergreen forest cover (4 km ²) (%)	5.3	28.8
Total forest cover (36 km ²) (%)	20.6	113.1
Mature forest cover (36 km ²) (%)	0.1	0.8
Second-growth <i>Nothofagus</i> forest cover (36 km ²) (%)	13.8	75.7
Evergreen forest cover (36 km ²) (%)	6.6	36.1

Landscape, patch and within-patch habitat variables were measured in 30 grid cells of 2 × 2 km, selected from 217 cells using a stratified random sampling (Fig. 1)

^a Dummy variable: *Nothofagus* forest (1) and evergreen forest (0)

Nothofagus); and (2) old-growth *Nothofagus* forest including large emergent trees, >100 years old (hereafter called mature *Nothofagus*; see Table 1 and Aravena et al. 2002 for discussion forest succession). We measured all landscape variables at two spatial scales, 4 km² (i.e. the area of one grid cell) and 36 km² (combining eight grid cells adjacent to the selected central cell; Table 1). The broader spatial scale was used to account for population abundance and behavior of the larger bird species (e.g. Chimango Caracaras or Black-throated Huet-huets) that have large habitat requirements.

Each forest patch within the 30 selected 2 × 2 km cells was mapped and digitized on screen from 1:10,000 aerial photos, with a resolution for a patch polygon of 0.1 ha. This resolution was larger than that obtained from CONAF-CONAMA-BIRF (1999), which mapped only patches larger than 6.25 ha. We estimated patch area and isolation (i.e. the minimum center-to-center distance between patches) from digitized aerial photos (Table 1). We also measured compositional and structural variables of vegetation within forest patches that are commonly associated with the density and species composition of forest birds (e.g. Vergara and Simonetti 2004; Vergara and

Schlatter 2006; Díaz et al. 2005). Following James and Shugart (1970), in each random point used for bird surveys (see Bird survey section), we set up a 0.04-ha circular plot where the following habitat variables were recorded: (1) total understory cover ($n = 4$ 1-m² plots); (2) percent cover of understory bamboo, i.e. Chilean weeping bamboo (*Chusquea quila*); (3) percent canopy cover (%), estimated with a densitometer pointed in each cardinal direction; (4) tree density (number of trees/ha) in the plot; (5) mean diameter at breast height of all trees in the plot (dbh in cm), measured using a wooden caliper; (6) canopy height (m), measured from the ground using a clinometer; and (7) dominant forest type (evergreen or *Nothofagus*), included as a dummy variable (Table 1).

Bird surveys

We estimated bird abundances during the 2006-breeding season (September–November) using 50 m fixed-radius point counts (Ralph et al. 1995; Jiménez 2000). Once during the breeding season, we recorded the number and identity of birds seen or heard between 05:30 and 11:00 (local time) on clear days

with little or no wind. The same two equally trained observers conducted all avian surveys in the different forest sites and habitat assessments were made on subsequent days. From previous studies of Chilean forest birds (e.g. Jiménez 2000; Díaz et al. 2005; Cofré et al. 2007) and our experience, we were certain that the duration, fixed radius and number of counts used in this study are reasonable to detect most bird species in Chilean temperate rain forests and yield reliable estimates of relative abundance (Fig. 2). Nevertheless, Chilean bird species differ in their detectability, which may bias abundance estimates from point count data, especially for high-mobility birds such as the Green-backed firecrown and the Chilean swallow (e.g. Jiménez 2000; Estades et al. 2006). Consequently, some of our abundance estimates should be taken with caution, and confirmed by abundance data based on detectability curves.

Inside remnant forest patches in each 2×2 km cell, we established point counts >250-m apart at random locations. We sampled proportional to forest area (15–25 points per grid cell and 1–7 points per forest patch). In total over the breeding season, we sampled 510 points in 238 different forest patches. This sampling effort is suitable to estimate the abundance of most species of Chilean birds in most forest fragments, as the number of species and individuals leveled off at 8 points sampled (Fig. 2; see also Jiménez 2000).

Statistical models

To assess scale-dependent effects of fragmentation on forest bird abundance we used generalized linear mixed-effect models using Penalized Quasi-Likelihood inference, whose error structure, that includes fixed and random effects, is suitable to analyze hierarchically nested data such as those in this study (see Study design section; Breslow and Clayton 1993; Venables and Ripley 2002). We tested for the effect of habitat variables measured at the landscape (grid cells), forest patch and within patch scales and the interactions between these scales. For 20 forest bird species detected in at least 50% of the grid cells and in more than 10% of the forest patches (Table 2), regression models could be fitted (i.e. the quasi-maximum likelihood functions of these models did converge). Species also present in the area that had

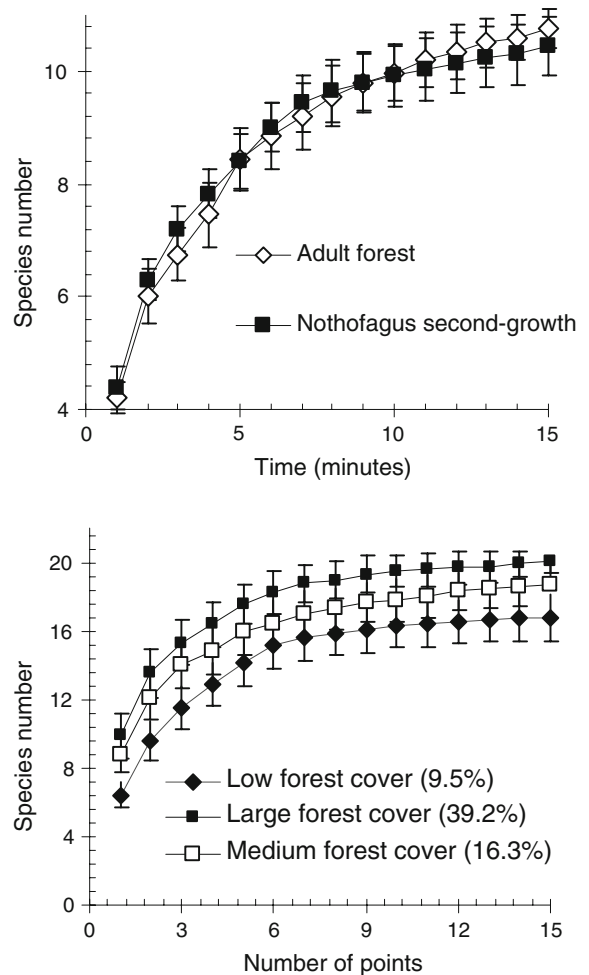


Fig. 2 Above: Changes in the number of bird species recorded (bars are 95% CI) over time at each 50-m fixed radius point from a total of 13 points established per forest type. Point counts were conducted in forest patches within the study area (see Fig. 1). According to this analysis >90% of the species were detected during the first 8-min count period (from Vergara and Schlatter, unpublished). Although we could not fit a species curve for evergreen forest, similar results are expected for that forest type. Below: Mean number of species (bars are 95% CI) recorded for a cumulative number of 50-m fixed radius points sampled in three units of landscape with different percentages of forest cover. Each mean was generated by bootstrapping the data set 1000 times. Data indicate that 90% of the species were accumulated after eight plots were sampled

insufficient sample sizes are listed in the footnote to Table 2.

Because bird abundance data are counts, we used a Poisson error model for this response variable. The random errors associated with landscape, patch and within-patch scales were included in the models as

Table 2 Ecological and life-history traits of the 20 forest bird species recorded in the study area

Species	Habitat specificity ^a	Diet ^b	Nest type ^c	Feeding substrate ^d	Migratory status ^e	Clutch size ^f	Body mass (g)	n	SE	CO	PO
Chimango Caracara (<i>Mivago chimango</i>)	G	O	O	SG	R	3	300	1.46	0.02	0.93	0.3
Chilean Pigeon (<i>Columba araucana</i>)	G	H	O	SG	m	1	200	1.75	0.04	0.93	0.36
Green-backed Firecrown (<i>Sephanoides galericus</i>)	G	O	O	SG	M	2	5.6	1.43	0.02	1	0.45
Des Murs's Wiretail (<i>Sylviorthorhynchus desmursii</i>)	G	I	O	SS	R	3	10.5	1.65	0.04	1	0.52
Thorn-tailed Rayadito (<i>Aphrastura spinicauda</i>)	S	I	C	SS	m	4	10.6	1.87	0.04	0.93	0.33
White-throated Treerunner (<i>Pygarrhichas albogularis</i>)	S	I	C	SS	R	3	13.0	1.35	0.02	0.57	0.11
Black-throated Huet-huet (<i>Pterotochos tarnii</i>)	S	O	C	SS	R	2	144.3	1.31	0.01	0.7	0.11
Ochre-flanked Tapaculo (<i>Eugralla paradoxo</i>)	S	O	O	SS	R	2.5	34.5	1.63	0.03	0.97	0.43
Chucoa Tapaculo (<i>Scelorchilus rubecula</i>)	S	O	C	SS	R	2	40.4	1.54	0.03	0.8	0.31
Andean Tapaculo (<i>Scytalopus magellanicus</i>)	G	I	C	SS	R	3	11.9	1.52	0.03	1	0.45
Fire-eyed Diucon (<i>Xolmis pyrope</i>)	G	O	O	SG	m	2.5	30.5	3.36	0.06	1	0.95
White-crested Elaenia (<i>Elaenia albiceps</i>)	G	O	O	SG	M	3	15.6	1.43	0.02	0.8	0.19
Tufted Tit-Tyrant (<i>Anairetes palurus</i>)	G	I	O	SG	R	3	7.2	1.64	0.03	1	0.58
Chilean Swallow (<i>Tachycineta meyeni</i>)	G	I	C	SS	M	5	15.4	1.59	0.03	0.97	0.32
House wren (<i>Troglodytes aedon</i>)	G	I	C	SG	M	5.5	9.5	1.95	0.04	1	0.79
Austral Thrush (<i>Turdus falklandii</i>)	G	O	O	SG	R	2.5	86.3	2.26	0.06	1	0.78
Rufous-collared Sparrow (<i>Zonotrichia capensis</i>)	G	H	O	SG	M	3.5	20.8	1.35	0.02	0.93	0.27
Austral Blackbird (<i>Curaeus curaeus</i>)	G	H	O	SG	R	4.5	90.0	1.96	0.05	0.97	0.57
Patagonian Sierra-Finch (<i>Phrygilus patagonicus</i>)	G	H	O	SG	M	3	20.1	1.54	0.03	0.9	0.26
Black-chinned Siskin (<i>Carduelis barbata</i>)	G	H	O	SG	M	4.5	22.3	2.05	0.06	1	0.47

We also showed: (1) the mean zero truncated abundance (n, individuals/ha); (2) Standard errors (SE) of the mean abundance; (3) frequency of these species in landscape or grid cell occupancy (CO, n = 30 landscapes); and (4) forest patch occupancy (PO, n = 238 patches) within grid cells

^a G = generalist, S = specialist; ^b O = omnivore, H = herbivorous, I = insectivorous; ^c O = open nester; ^d SG = Substrate generalist, SS = substrate specialist; ^e R = resident; m = short-distance migrant, M = long-distance migrant; ^f Median clutch size. Source: Schlatter et al. (1997); Vergara and Schlatter (2006) and Cofré et al. (2007)

Species whose abundance was insufficient to fit Poisson models were: the California Quail (*Callipepla californica*), the Chilean Flicker (*Colaptes pitius*), the Austral Parakeet (*Enicognathus ferrugineus*), the Plain-mantled Tit-spinetail (*Leptasthenura aegithaloides*), the Chilean tinamou (*Nothoprocta perdicaria*), the Harris's Hawk (*Parabuteo unicinctus*), the Striped Woodpecker (*Picoides lignarius*), the Grassland Yellow-Finch (*Sicalis luteola*), the Black-faced Ibis (*Theristicus melanopus*), the Eared dove (*Zenaida auriculata*), the Crested Caracara (*Polyborus plancus*), the Long-tailed Meadowlark (*Sturnella loyca*), the Dark-bellied Cinclodes (*Cinclodes patagonicus*), the Picui Dove (*Columbina picui*), the Spectacled Tyrant (*Hymenops perspicillata*), the Chilean Mockingbird (*Mimus thenca*) and the Common Diuca-finch (*Diuca diuca*)

nested random intercepts (i.e. points nested within patches, and patches nested within grid cells). In addition, we included a random intercept to control for over dispersion of abundance data.

To test for interactions across spatial scales, our model selection “rules” were as follows. In step 1, we developed and evaluated separately single scale (without interaction terms) and cross-scale models. To do this, we defined cross-scale effects as the product between: (1) landscape and patch variables; (2) patch and within-patch habitat variables; (3) landscape and within-patch habitat variables (Table 1). In step 2, we developed “mixed” models, which included both single and cross-scale effects. In mixed models, we included only landscape, patch or within-patch variables that were included as explanatory variables in the best models selected in step 1. We selected candidate models tested in steps 1 and 2 using the AICc (Akaike’s information criterion, corrected for small sample sizes; Burnham and Anderson 2002). Finally, in step 3, we applied the same selection procedure to rank the subset of models selected previously (in steps 1 and 2).

We did not include highly correlated variables ($r > 0.6$) as predictors in the same models (Table 1) and variables that departed from normality were log-transformed. We checked for spatial autocorrelation in the Pearson’s residuals of regression models by developing Moran’s spatial autocorrelograms, running 10,000 Monte Carlo permutations and applying Bonferroni’s correction (Legendre and Legendre 1998). These spatial analyses revealed no evidence of spatial autocorrelation in the residuals for any final model. We developed all generalized linear mixed-effect models using R statistical software (<http://www.R-project.org>).

Effects of life-history and ecological traits

A posteriori, we assessed whether birds’ life histories and ecological traits affected species-specific responses to forest fragmentation. We used a binomial logistic regression with taxonomic order and family as random effects to correct for potential phylogenetic constraints on shared traits (Felsenstein 1985; Blackburn and Duncan 2001). For the logistic regression analysis we created two dummy dependent variables: (1) whether the abundance of a bird species was explained only by single scale models (yes = 1

and no = 0); and (2) whether the abundance of a bird species was explained by a cross-scale model and/or a mixed model (yes = 1 and no = 0). We obtained from the literature seven life history and ecological traits previously associated with the abundance and distribution of Chilean forest birds (Table 2).

Results

Interactions across spatial scales

Cross-scale effects were supported for five of the 20 bird species studied: the green-backed firecrown, black-throated huet-huet, ochre-flanked tapaculo, Andean tapaculo and the Chilean swallow (Tables 3, 4). For firecrowns and ochre-flanked tapaculos, interaction effects across spatial scales imply that as total forest cover in the landscape increases, so does the positive relationship between canopy height or understory bamboo and their abundances (Fig. 3; Table 4). The positive relationship of understory bamboo on the abundance of huet-huets increased in landscapes with a larger proportion of mixed *Nothofagus* forest cover (Table 4). In large patches, the positive correlation of understory cover and the abundance of Andean tapaculos increases (Fig. 3; Table 4). In landscapes with a high proportion of mature *Nothofagus* forest, the correlation of patch area and the abundance of swallows increases.

We found no support for the hypothesis of cross-scale habitat effects in 13 bird species (65% of species, Tables 3, 5). For the Chimango caracara there were two equally parsimonious models without cross-scale interaction effects (Table 3). Of these species, the abundance of the fruit eating Chilean pigeon, white-crested elaenia and the tufted tit-tyrant was positively correlated only with patch characteristics and within-patch habitat variables (forest type, mean dbh of trees, canopy height and understory cover, Table 5). On the other hand, the abundance of firecrowns, austral blackbird and Patagonian sierrafinch was correlated only with landscape-level variables (including total forest cover in 4 km² grid cells and cover of *Nothofagus* forest at the scale of 36 km², Table 5). The house wren was the only species significantly correlated with patch scale variables exclusively (its abundance decreased in larger patch sizes, Table 5). The abundance of the open field

Table 3 The best Poisson's regression models for bird species abundance

Bird common names	Models											
	No cross-scale interaction				Cross-scale interaction				Mixed			
	k	AICc	Δ AIC	w	k	AICc	Δ AIC	w	k	AICc	Δ AIC	w
Chimango Caracara	2	1304	0	0.64	2	1309	5.8	0.04	2	1707	403	0.00
Chimango Caracara	2	1305	1.4	0.32								
Chilean Pigeon	3	1585	0	1.00	3	1640	54	0.00	2	1695	109	0.00
Green-backed Firecrown	2	679	1.4	0.33	2	677	0	0.67	3	1651	974	0.00
Des Murs's Wiretail	2	767	0	0.75	3	1143	376	0.00	2	769	2.2	0.25
Thorn-tailed Rayadito	6	1396	17	0.00	4	1612	1612	0.00	4	1379	0	1.00
White-throated Treerunner	2	2054	1412	0.00	2	2055	1412	0.00	3	642	0	1.00
Black-throated Huet-huet	3	2050	1981	0.00	4	69	0	1.00	3	2147	2078	0.00
Ochre-flanked Tapaculo	2	802	86	0.00	2	716	0	1.00	3	1364	648	0.00
Chucao Tapaculo	4	1544	91	0.00	3	1459	5	0.06	4	1453	0	0.94
Andean Tapaculo	2	801	6	0.06	2	795	0	0.94	2	1292	497	0.00
White-crested Elaenia	2	420	0	1.00	4	488	68	0.00	4	473	53	0.00
Fire-eyed Diucon	3	832	0	1.00	3	2229	1398	0.00	5	2131	1299	0.00
Tufted Tit-Tyrant	2	766	0	1.00	4	855	89	0.00	4	1379	612	0.00
Chilean Swallow	4	1550	283	0.00	3	1267	0	1.00	3	1557	290	0.00
House wren	1	930	0	1.00	3	1062	132	0.00	2	1141	212	0.00
Austral Thrush	3	868	0	0.93	1	938	70	0.00	4	873	5.1	0.07
Rufous-collared Sparrow	4	1330	0	1.00	2	1478	148	0.00	3	1510	180	0.00
Austral Blackbird	2	1294	0	0.97	2	1300	6.8	0.03	2	1378	84	0.00
Patagonian Sierra-Finch	2	1233	0	1.00	3	1498	264	0.00	3	1280	46	0.00
Black-chinned Siskin	2	1402	0	1.00	2	1608	206	0.00	3	1427	24	0.00

Results are shown for models without cross-scale interactions; models supporting the existence of interactions across spatial scales; and mixed models, supporting the importance of both single-scale variables and cross-scale interactions. The total number of estimated parameters (k), the change in AICc (Δ AICc) and the Akaike weights (w) are specified for each model. The best models (Δ AICc <4) are given in bold. For the Chimango caracara there were two equally parsimonious models without cross-scale effects. Variables included and their estimated coefficients are presented in Tables 4–6

Table 4 Regression coefficients (β), standard errors (SE) and p -values of the best models supporting the existence of interactions of habitat variables across spatial scales in fragmented forests

Species/Variables	β^a	SE	p
1) Green-backed Firecrown			
Total forest cover (4 km ²) \times canopy height	0.160	0.071	0.029
2) Black-throated Huet-huet			
Patch size \times understory bamboo cover	0.010	0.002	<0.001
<i>Nothofagus</i> forest (36 km ²) \times understory bamboo cover	0.002	0.0006	<0.001
<i>Nothofagus</i> forest cover (36 km ²) \times patch size	0.006	0.002	0.002
3) Ochre-flanked Tapaculo			
Total forest cover(4 km ²) \times understory bamboo cover	0.025	0.003	<0.001
4) Andean Tapaculo			
Patch size \times understory cover	0.081	0.003	0.005
5) Chilean Swallow			
Mature forest cover (36 km ²) \times patch size	0.379	0.104	<0.001

^a Intercepts not shown

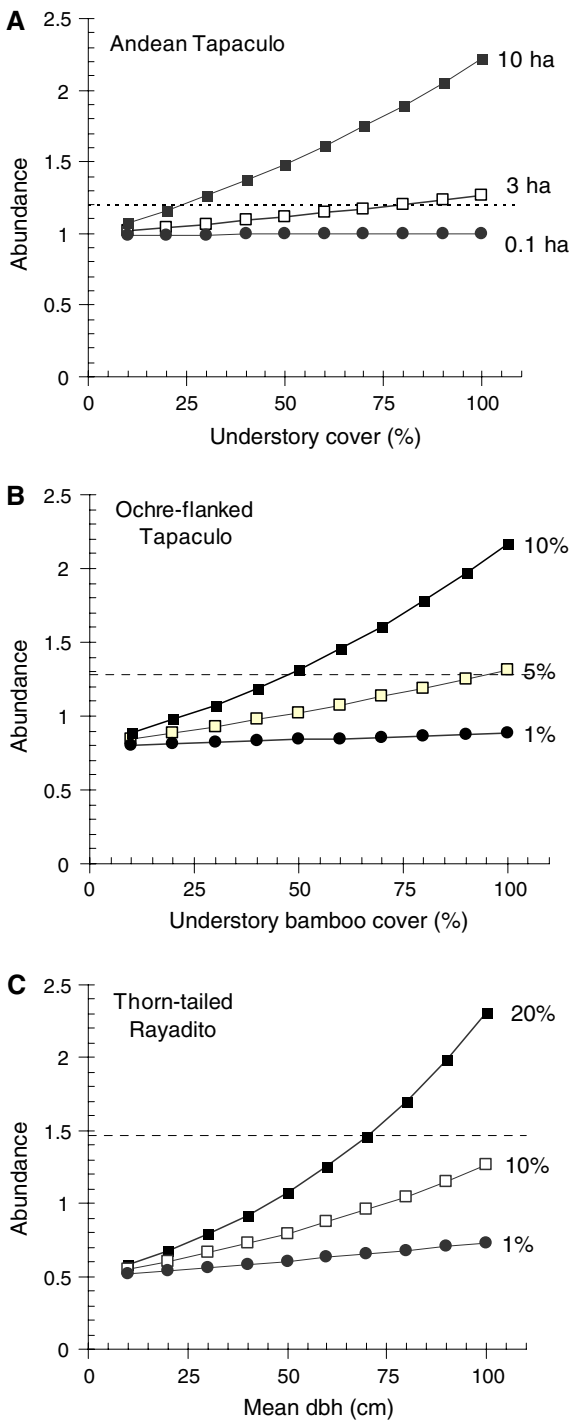


Fig. 3 Graphical representation of habitat effects across spatial scales for three forest bird species. Predicted values were derived at arbitrary intervals for each independent habitat variable using generalized linear mixed-effects models. **a** Effect of understory cover with changing patch size (0.1, 3 and 10 ha). **b** Effect of understory bamboo cover with changing total forest cover (4 km²) (10, 5 and 1%). **c** Effect of mean dbh with changing total forest cover (36 km²) (20, 10 and 1%). Dashed lines represent the zero-truncated mean species abundance in the landscape (see Table 2)

while that of fire-eyed diucon and black-chinned siskin was correlated with both patch and landscape variables (including negative effects of both *Nothofagus* forest in 36 km² and patch size, and the positive effect of total forest in 4 km² cells, Table 5). Both patch and within-patch habitat variables explained the abundance of wiretails (patch area and understory bamboo cover) and the abundance of austral thrush was not significantly correlated with within-patch habitat, patch and landscape variables (Table 5).

Models including at least one cross-scale interaction explained the abundance of nine bird species (45%). Mixed models (with single-scale and cross-scale effects) were supported for four species: Des Murs’s wiretail, thorn-tailed rayadito, white-throated tree runner and chucao tapaculo (Tables 3, 6). Additionally, a mixed model and a model without cross-scale effects accounted for the abundance of firecrowns, and models with and without interactions across spatial scales explained the abundance of wiretails (Tables 3–6). For wiretails, rayaditos, and chucao tapaculos cross-scale interactions imply that the positive correlation of structural, within-patch habitat variables, such as understory cover, understory bamboo cover or mean tree dbh on species abundances, increases in landscape units with high forest cover (Table 6; Fig. 3). In addition, for rayaditos and chucao tapaculos, the positive correlation of mean tree dbh and understory bamboo cover with bird abundance increases in larger forest patches, respectively (Table 6). The positive correlation of patch area with the abundance of treerunners increased in landscape units with a larger fraction of mature forest cover (Table 6).

raptor chimango caracara and of the rufous-collared sparrow was correlated with both within-patch and landscape habitat variables (including positive effects of understory cover and mature forest cover in 4 km² cells and the negative effect of mean dbh of trees),

Effects of life-history and ecological traits

The response of bird species to habitat fragmentation at different spatial scales was generally associated with their ecological and life-history traits (Table 7).

Table 5 Regression coefficients (β), standard errors (SE) and p -values for the best models assuming no effects across spatial scales for habitat variables relevant to forest bird species

Species/Variables	β^a	SE	p
1) Chimango Caracara ^b			
Understorey cover	-0.011	0.003	<0.001
Mature forest cover (4 km ²)	3.716	1.168	0.004
2) Chilean Pigeon			
Forest type	0.486	0.179	0.007
Mean dbh	0.008	0.003	0.003
3) Green-backed Firecrown			
Total forest cover (4 km ²)	0.654	0.282	0.029
4) Des Murs's Wiretail			
Patch size	0.213	0.202	0.294
Understorey bamboo cover	0.008	0.001	<0.001
5) White-crested Elaenia			
Canopy height	0.042	0.004	<0.001
6) Fire-eyed Diucon			
Total forest cover (4 km ²)	0.864	0.270	0.004
Patch size	-0.373	0.215	0.086
7) Tufted Tit-Tyrant			
Understorey cover	0.007	0.001	<0.001
8) House wren			
Patch size	-0.657	0.229	0.005
9) Austral Thrush			
<i>Nothofagus</i> forest cover (4 km ²)	0.010	0.430	0.381
Patch isolation	0.022	0.059	0.087
Understorey cover	0.002	0.001	0.172
10) Rufous-collared Sparrow			
Mature forest (4 km ²)	2.588	1.228	0.045
Mean dbh	-0.001	0.003	0.781
Tree density	0.000	0.001	0.464
11) Austral Blackbird			
<i>Nothofagus</i> forest cover (36 km ²)	2.021	0.731	0.011
12) Patagonian Sierra-Finch			
Total forest cover (4 Km ²)	-0.314	0.429	0.471
13) Black-chinned Siskin			
Patch size	-0.764	0.433	0.080
<i>Nothofagus</i> forest cover (36 km ²)	-1.991	0.564	0.002

^a Intercepts not shown

^b Coefficients of two equally parsimonious models were pooled

The best logistic model that estimated the probability that bird abundance was explained only by a single scale model (AICc = 24.5) includes the effect of bird's habitat specificity and nest type (Table 7). According to this logistic model, habitat generalists

and open nesters were unaffected by interactions across spatial scales. The effects of body mass and habitat specificity were included in the best logistic model (AICc = 5.8) that estimated the probability that the abundance of a bird species was explained by a model with interactions across spatial scales and/or a mixed model (Table 7). According to this logistic model, habitat specialists and small-sized bird species were particularly affected by cross-scale effects (Table 7).

Discussion

We found that landscape and patch effects may deter birds from using potentially suitable habitat in small forest patches within landscape units with reduced forest cover. Although previous studies of Chilean forest birds revealed that their abundance and nesting success respond additively to within-patch, patch-scale and landscape-scale features (e.g. Estades and Temple 1999; Vergara and Marquet 2007), the interactions among spatial scales have not been assessed (Estades and Temple 1999, Reid et al. 2004, Díaz et al. 2005, Castellón and Sieving 2006). We suggest that fragmentation effects at different spatial scales commonly have non-additive effects on south temperate forest bird species, and hence such effects should be further explored to develop useful conservation guidelines. However, because our study is based on observations and abundance records during one year, it is necessary to assess the consequences of inter-annual (and seasonal) environmental variability on habitat-scale, patch-scale and landscape scale-variables. Moreover, at longer time scales, bird species that were negatively affected by the reduction in forest cover, and its interaction with habitat variables, such as rayaditos and treerunners, could be declining in the landscape due to increased forest fragmentation in the central valley of southern Chile. Therefore, long-term studies are necessary to validate our conclusions.

Several studies outside of South America have focused on the interaction between landscape forest and patch size or isolation (e.g. Trzcinski et al. 1999; Fahrig 2003; Betts et al. 2006). These cross-scale effects motivated ecologist to propose the so called "nonlinear fragmentation hypothesis" for habitat loss (sensu Andrén 1994). Alternatively, the

Table 6 Regression coefficients (β), standard errors (SE) and p -values of the best mixed models, which suggest that both single-scale and cross-scale effects are important for predicting bird abundance in a fragmented forest landscape

Species/Variables	β^a	SE	p
1) Des Murs's Wiretail			
Understory bamboo cover	0.765	0.133	<0.001
Total forest cover (4 km ²) \times understory cover	0.001	0.001	0.473
2) Thorn-tailed Rayadito			
Canopy cover	2.428	0.297	<0.001
Total forest cover (36 km ²) \times mean dbh	0.151	0.002	<0.001
Patch size \times mean dbh	0.234	0.038	<0.001
3) White-throated Treerunner			
Canopy height	0.039	0.006	<0.001
Mature forest cover (36 km ²) \times patch size	0.167	0.036	<0.001
4) Chucao Tapaculo			
Understory bamboo cover	1.118	0.373	0.002
Patch size \times understory bamboo cover	0.321	0.008	0.000
Total forest cover (4 km ²) \times understory bamboo cover	1.551	0.025	<0.001

^a Intercepts are not shown

Table 7 Regression coefficients, standard errors (SE) and p -values of the best (Δ AICc < 4) logistic models testing for the effect of ecological and life-history traits on scale-dependent responses of birds to fragmentation

Model/Variables	Parameter	SE	p
Single scale models			
Intercept	-0.21	1.80	0.906
Habitat specificity ^a	-46.28	0.15	<0.001
Nest type ^a	29.19	0.15	<0.001
Cross-scale or mixed models			
Intercept	-2.60	3.21	0.440
Body mass	-0.06	0.00	<0.001
Habitat specificity ^a	22.69	0.001	<0.001

Response variables of logistic regressions were: (1) the probability that the abundance of a bird species is explained only by single scale model; and (2) the probability that the abundance of a bird species is explained by a model with interactions across spatial scales and/or a mixed model (see Table 4)

^a Parameter values of habitat generalist species, substrate specialist species and cavity nesters were set equal to zero

“random-sample hypothesis” states that small patches acting as random samples from large ones (Haila 1983) and the “landscape fragmentation hypothesis” proposes that habitat loss and patch attributes have additive (independent) effects on species abundance (e.g. Villard et al. 1995; Betts et al. 2006). Theoretical studies have shown that the effects of patch size become apparent when 20–30%

of the original habitat has been lost from the landscape (Flather and Bevers 2002; Fahrig 2003). Our findings suggest that interactions across spatial scales in fragmented landscapes go further than the simple interaction between forest cover and patch size, since different habitat structures within forest stands (e.g. canopy height, tree dbh, understory cover, etc.) can interact with landscape configuration or patch size significantly affecting bird abundance.

Our results indicate that bird species which are sensitive to effects across spatial scales share similar ecological and life-history traits. Models showed that habitat and foraging specialists, cavity nesters and relatively small birds (Table 2) were often affected across spatial scales. Habitat specialists were mostly understory, trunk-branch and aerial insectivorous birds, which are often strongly affected by forest fragmentation or stand degradation (Díaz et al. 2005; Vergara and Schlatter 2006; Vergara and Simonetti 2006). In addition, most of these bird species nest in soil and trunk cavities, which make them particularly sensitive to forest fragmentation. Particularly, trunk-branch foragers such as treerunners and rayaditos depended on within-patch structural attributes, such as canopy cover, tree height and density of large trees which provide food or nesting sites (e.g. Vergara and Marquet 2007). Similarly, understory bird species, such as tapaculos, responded positively to understory cover depending on forest patch area and percent forest cover in the landscape. In contrast, bird species whose abundance was unaffected by interactions

across spatial scales were mostly generalist species that respond to habitat features proportionally to their availability in the landscape or patch, and hence scale-dependent effects are fairly additive. For example, it is likely that the generalist chimango, whose abundance was negatively affected by understorey cover, prefers open sites to search for prey, usually bird nests (Willson et al. 2001).

Interactions across spatial scales imply that the negative impact of forest cover loss on bird species cannot always be compensated by specific measures improving local habitat quality, such as maintaining large habitat trees, dense understorey, or patch area. Conservation measures at the landscape scale are also necessary to ensure the regional persistence of bird species sensitive to forest fragmentation. We suggest that conservation strategies for the Chilean Lake District should focus primarily on specialist birds such as rayaditos, hueta-hueta and treerunners which need extensive areas of mature forest cover and larger patch sizes than other species affected by cross-scale interactions. Management guidelines, however, could be difficult to implement in lowland forests of the study area because the overall proportion of mature forest remaining in the rural landscape is currently about 1% (Table 1) and remnant native forests are being massively converted into large-scale eucalyptus plantations or pasture. For this reason, it becomes imperative to protect landscapes with a large percentage of forest cover and large forest patches (see above) and to maintain their connectivity in order to provide habitat corridors for birds across the central depression of southern Chile.

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