Spatial structure and scale-dependent microhabitat use of endemic "tapaculos" (Rhinocryptidae) in a temperate forest of southern South America

GUILLERMO C AMICO [1, ✉], DANIEL GARCÍA [2] & MARIANO A RODRÍGUEZ-CABAL [1]

1. *Laboratorio Ecotono, CRUB, Universidad Nacional del Comahue, Bariloche, RN, Argentina.*
2. *Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo, and ICAB, España.*

ABSTRACT. Endemic tapaculo birds (Rhinocryptidae) are biological indicators of habitat degradation in the temperate forest of southern South America, but little is known about the physiognomical features that determine the use of space in natural habitats. We studied the spatial structure and the microhabitat use at different spatial scales of species of tapaculos in a well-conserved forest of NW Patagonia (Argentina). We recorded the abundance of tapaculos and forest characteristics along a 1500 m transect divided in 75, 20 x 20 m contiguous plots. We evaluated the spatial patchiness in abundance of birds by Moran's *I* correlograms. We disentangled the spatial variability of bird abundance at three different, progressively finer (broad, intermediate, fine), spatial scales by using Principal Coordinates of Neighbour Matrices analysis (PCNM). We assessed the microhabitat use of each bird species with stepwise regression analyses using habitat physiognomical features as independent variables and bird abundance predicted by PCNM at each spatial scale as dependent variables. The clumps of *Scelorchilus rubecula* were smaller and more regularly distributed than those of *Pteroptochos tarnii*. The PCNM analysis detected significant spatial variation at the different scales for both bird species. Microhabitat use was only evident at the broadest spatial scale, but differed between bird species. *Scelorchilus rubecula* used areas with higher tree cover and woody plant volume but lower abundance of fallen branches, whereas *P. tarnii* was found mostly in areas of higher abundance of branches but lower woody plant volume and plant species richness. The differences between bird species in the use of space can also be interpreted in terms of differences in body size, family system and feeding behaviour. The management of this temperate forest needs to consider the scale- and species-specific response of endemic tapaculos to habitat features in order to predict their response to the changes in heterogeneity that operate at different spatial scales and are driven by different degradation processes.

[Keywords: understory birds**,** PCNM, *Pteroptochos tarnii*, *Scelorchilus rubecula*, spatial patchiness, spatial scale]

RESUMEN. Estructura espacial y uso del microhábitat dependiente de la escala de "tapaculos" (Rhinocryptidae) endémicos en un bosque templado de Sudamérica austral: Los tapaculos (Rhinocryptidae) son aves endémicas del bosque templado de Sudamérica austral, que están siendo usadas como especies indicadoras de la degradación de dicho hábitat. Sin embargo, se sabe poco sobre qué características fisionómicas determinan el uso del espacio en los hábitats naturales. Se estudiaron la estructura espacial y el uso del microhábitat a diferentes escalas espaciales de especies de tapaculos en un bosque poco degradado del noroeste de la Patagonia (Argentina). Registramos la abundancia de tapaculos y las características del microhábitat a lo largo de un transecto de 1500 m dividido en 75 parcelas contiguas de 20 x 20 m. La agregabilidad espacial de la abundancia de aves se evaluó a través de correlogramas de *I* de Moran. Utilizando Análisis de Coordenadas Principales de Matrices de Vecinos (ACPMV) se segregó la variabilidad espacial de la abundancia de aves en

---

✉ Laboratorio Ecotono, CRUB, Universidad Nacional del Comahue, Bariloche, RN, Argentina. gamico@crub.uncoma.edu.ar

tres escalas diferentes: amplia, intermedia y fina. Además, se evaluó el uso del microhábitat de cada especie de ave con análisis de regresión múltiple usando las características fisonómicas del hábitat como variables independientes y, como variables dependientes, la abundancia de aves predicha por el ACPMV en cada escala espacial considerada. Los agregados espaciales de *Scelorchilus rubecula* fueron más pequeños y se distribuyeron de forma más regular que los de *Pteroptochos tarnii*. El análisis de ACPMV detectó variación espacial significativa en la abundancia de aves para ambas especies, a todas las escalas. Las relaciones entre las características del microhábitat y la abundancia de aves fueron sólo patentes a la escala espacial más amplia, y difirieron entre especies. *Scelorchilus rubecula* escogió áreas con alta cobertura arbórea y alto volumen de plantas leñosas pero con baja abundancia de ramas caídas, mientras que *P. tarnii* apareció mayoritariamente en áreas de alta abundancia de ramas caídas pero de bajo volumen de plantas leñosas y baja riqueza específica. Las diferencias entre especies en estructura espacial y uso del microhábitat se interpretan también en términos de tamaño corporal, sistema familiar y comportamiento trófico. La gestión y conservación de este bosque templado requiere considerar el grado de especificidad y de dependencia de la escala espacial de la respuesta de los tapaculos a las características del hábitat. De este modo se podrá predecir la respuesta de estas aves a los cambios de heterogeneidad que operen a diferentes escalas espaciales, por ser generados por diferentes procesos de degradación.

[Palabras clave: aves del sotobosque, agregabilidad espacial, escala espacial, ACPMV, *Pteroptochos tarnii*, *Scelorchilus rubecula*]

Introduction

The temperate forest of southern America covers a narrow area on both sides of the Andes range between 36° S and 55° S. This habitat has insular characteristics, with low species richness but high frequency of endemism (Vuilleumier 1985; Armesto et al. 1996; Armesto et al. 1998). In the last decades, this forest has been rapidly disappearing because of reduction and fragmentation of the forest area by human encroachment, fire, agriculture, cattle, logging and pine and eucalyptus plantations (Lara et al. 1996; Estades & Temple 1999; Pauchard & Villarroel 2002; Echeverría et al. 2006). All these forms of degradation alter the habitat heterogeneity with detrimental effects on plant and animal populations (Bustamante & Castor 1998; Vergara & Simonetti 2004a; Díaz et al. 2005). However, the negative effects of these processes depend on the spatial scale considered, since some changes only occur at small scales (e.g., selective species cutting, removal of dead plant material) whereas others can cover larger areas (e.g., forest clearing). The design of conservation and management strategies for this forest must therefore take into account the multi-scaled factors that influence the distribution and abundance of forest species (Lindenmayer et al. 1999; Lindenmayer 2000; Lindenmayer & Franklin 2002; Haythornthwaite & Dickman 2006).

The effect of habitat degradation on this temperate forest is usually assessed by the response of animal species with strict forest requirements, such as the tapaculos, an endemic group of understory bird species (Rhinocryptidae) (Vergara & Simonetti 2004b; Willson 2004). These birds are known to respond negatively to habitat loss, isolation of forest remnants as well as degradation of vegetation structure (Sieving et al. 2000; Vergara & Simonetti 2003; Sieving et al. 2004; Vergara & Simonetti 2004a, 2004b; Willson 2004; Castellón & Sieving 2006; Vergara & Simonetti 2006). Nevertheless, in order to explain the response of tapaculos to habitat and landscape changes, it is necessary to know both the spatial structure of their populations and their habitat requirements in unmodified habitats. In this sense, the habitat use by tapaculos within the forest is expected to be determined by the availability of vegetation structures that provide refuge against predators and safe places for nesting (De Santo et al. 2002; Reid et al. 2004; Vergara & Simonetti 2004b; Willson 2004). However, studies explicitly evaluating habitat use in undisturbed forests are still lacking. Moreover, any study of habitat use should take into account that these birds may respond to different environmental factors and habitat features at different spatial scales (Orians & Wittenberger 1991; Pribil & Pricman 1997; McCollin 1998; Hall & Mannan 1999; Lee et al. 2002). For example, landscape

features, such as the type of forest patch, could control bird presence at large-scale patterns, whereas habitat structural elements, like the number of canopy layers within a forest, could account for small-scale variability of bird presence (Wiens et al. 1987; Jones 2001; Luck 2002; Bakermans & Rodewald 2006; Cueto 2006). Indeed, structurally complex habitats such as the South American temperate forest may provide gradients of internal structure (i.e., microhabitat heterogeneity) wide enough to promote scale-dependent responses of forest birds to habitat features.

In this study we evaluated microhabitat use by two species of endemic tapaculos in an undisturbed mature forest of north-western Patagonia (Argentina) by assessing the relationships between forest characteristics and bird abundance. We used a spatially explicit approach enabling us to i) describe the spatial structure of bird presence; ii) describe the variability in microhabitat characteristics; iii) dissect the spatial variation of bird presence at different spatial scales within the forest; and iv) identify the spatial scale(s) at which tapaculos use microhabitats.

Materials and Methods

Study area

The study was conducted in the Llao-Llao Reserve, 25 km west of San Carlos de Bariloche, Río Negro, Argentina (41°8′ S, 71°19′ W; 800 m.a.s.l.). The reserve covers 1220 ha and has been a protected area since 1958, it never supported cattle and logging was low before the establishment of the reserve. A small forest area (ca. 2 ha) of the reserve was cleared for farming, but then was never farmed and the forest is recovering since 1960. The only human activity allowed at present in the reserve is recreation (i.e., hiking).

This native forest belongs to the Subantarctic biogeographical region (Cabrera & Willink 1980). Dominant canopy trees are the evergreen southern-beech *Nothofagus dombeyi* and the conifer *Austrocedrus chilensis*. The understory presents 15 woody species, but is mainly dominated by the shrub *Aristotelia chi-*

lensis and the bamboo *Chusquea culeou* (about 30% and 25% of total shrub cover, respectively) that has a patchy distribution. These two layers are well differentiated, with the tree canopy reaching up to 40 m and the understory reaching 7 m. The forest has also small canopy gaps of variable size generated by tree falls. The bird community in the area is composed of 24 species representing 17 families; the three tapaculos species (*Pteroptochos tarnii, Scelorchilus rubecula, Scytalopus magellanicus*) are relatively common (Amico & Aizen 2005). The climate in this area is cold temperate, with a dry season in spring-summer and a humid season in autumn-winter. On average, only 12% of the annual precipitation (1800 mm) falls during summer (December–February). Snowfalls are common during winter. Annual average temperature is 9 °C.

Methods

Sampling bird abundance and habitat features was conducted along a 1500 m fixed-distance linear transect that follows a trail seldom visited by people. To assess spatial micro-habitat use patterns of tapaculos, this transect was subdivided in 75 contiguous 20 x 20 m plots. The starting point of each plot was marked with flagging tape and a labelled stake in the ground. Along the transect there were forest gaps, bamboo patches and areas of higher density of understory treelets. Difference in altitude among sampling plots was less than 100 m.

Sampling was carried out during the austral summer (February-March) that is, the post-breeding season of the birds studied. Thus, we considered that summer sampling was representative of both bird presence and habitat use at the peak of seasonal bird abundance, a key moment in the birds' spatio-temporal dynamic (Sieving et al. 1996; Sieving et al. 2000; Reid et al. 2004; Willson 2004; Castellón & Sieving 2006).

Bird surveys

Bird surveys were carried out walking along the transect and registering all birds encountered within 20 m on each side of the transect

line. Every time a bird was seen or heard, we registered the species, the plot where it was present, the distance from the trail, the forest layer occupied (canopy, understory or ground) and its behaviour (feeding, moving or perching). All surveys were carried out by the same observer to minimize sampling errors. A total of 15 surveys were performed from 6:30 to 8:30 am, between February and March 2005, avoiding rainy or windy days. We concentrated our sampling effort in the mornings because these birds show more vocalization activity at this time of day, facilitating detection (Willson et al 1994).

The species of tapaculos considered in this study were: black-throated huet-huet (*Pteroptochos tarnii*), chucao tapaculo (*Scelorchilus rubecula*) and the Andean tapaculo (*Scytalopus magellanicus*). The abundance of tapaculos was estimated as the cumulative number of bird records per plot across all surveys. Although this parameter did not distinguish between successive records belonging to the same or different individuals or family groups of birds, it was considered to be a fair estimate of the frequency of use of a particular plot along time, and thus, a suitable variable for representing the probability of occurrence of a given species in a given sampling location.

Microhabitat characteristics

Habitat sampling was carried out by subdividing each 20 x 20 m plot in eight subplots (5 x 10 m) covering the whole area (four at each side of the trail). In four non-adjacent subplots (alternating sequentially left and right of the trail) we measured the following six microhabitat structural variables that could affect the presence of tapaculo species: 1) tree canopy cover (%); 2) total understory cover (%); 3) understory bamboo (*Chusquea culeou*) cover (%); 4) understory volume; 5) abundance of fallen branches and 6) richness of woody plant species. We estimated the abundance of dead stems and fallen branches and the woody plant volume by means of a semi-quantitative scale from 0 (none) to 5 (maximum). All these variables were calculated on a per plot basis, by averaging values from the four subplots. The richness of woody plant species was calculated as the total number of woody species recorded

per plot. Bamboo cover is considered to be relevant for the presence of tapaculos (Ridgely & Tudor 1994; Reid et al. 2004), whereas the abundance of fallen branches as well as woody plant volume may represent the availability of feeding, refuge and nesting microhabitats (De Santo et al. 2002; Reid et al. 2004).

Data analysis

The first analytical goal was to describe the spatial aggregation (patchiness) in the abundance of each bird species by means of Moran's *I* correlograms. A correlogram is a graph in which spatial autocorrelation values of a given parameter are plotted, on the ordinate, against distance classes among sampling points (Legendre & Fortin 1989; Legendre & Legendre 1998). The spatial autocorrelation value at a given distance class *x* indicates how predictable, positive or negatively, is the abundance of birds in a given point of the sampling framework, as a function of the abundance of birds in a sampling point located at the distance *x*. Autocorrelation Moran's index typically varies between -1 (repulsion) and +1 (contagion), with non-significant values close to zero. A positive significant Moran's *I* value indicates the existence of a patch (or a peak of a patch) at a given distance class, and a negative significant value indicates the existence of a "valley" between patches at two distance classes. The difference in distance classes between positive significant values in the correlogram indicates the distance between the peaks of successive aggregation patches in the transect. The same is applied for negative values, but representing the valleys between aggregation patches (the areas with no presence of birds). Taking into account our sampling design, we considered 30 distance classes of 50 m interval, using the starting point of each sampling station as an unidimensional coordinate. We chose this number arbitrarily, in order to provide a high level of spatial resolution for interpreting the spatial structures of bird abundance and, at the same time, to enable us to estimate most autocorrelation indices with reasonable power (i.e., all autocorrelation indices, except those corresponding to the distance classes of 1450 and 1500 m, were calculated from more than 20 pairs of distances between points). In addi-

tion, we tested for the relationship between the abundance of different tapaculo species with partial Mantel tests (Legendre & Fortin 1989). A partial Mantel statistic is similar to a partial correlation coefficient (with a value from -1 to +1) and can account for the spatial position of sampling points. This test will allow us to evaluate if the distribution of one species along the transect is independent of the presence of the other. The significance level for the partial Mantel test was determined by a permutation procedure (from 1000 permutations). Both spatial correlograms and partial Mantel test were performed with R 4.0 statistical software (Autocorrelation and Mantel programs, respectively; Casgrain et al. 1997).

As a second analytical goal, we dissected the spatial variability of the abundance per plot of each bird species at different spatial scales, by using Principal Coordinates of Neighbour Matrices analysis (PCNM) (Borcard & Legendre 2002; Borcard et al. 2004). The PCNM belongs to the family of spatial models designed to cope with spatially-structured data, taking explicitly into account the presence of large-scale spatial structures and/or fine-scale spatially autocorrelated structures, and relating the form of these spatial structures with environmental factors (Borcard et al. 2004; Dray et al. 2006). As a first step, the PCNM achieves a spectral decomposition of the spatial relationships among all the sites in a given sampling framework, creating new variables (spatial predictors called vectors of principal coordinates) that correspond to all the spatial scales that can be perceived in the sampled dataset. In our case, we used SpaceMaker 2 (Borcard & Legendre 2004) to generate 50 PCNM vectors from the 75 sampling points along the transect. These vectors were then used as explanatory variables in a multiple regression model against the bird abundance per plot (response variable) in order to identify the spatial templates accounting for some spatial variability in bird presence (those predictors significantly correlated after fitting). All significant spatial predictors were then partitioned into three additive spatial submodels corresponding to three progressively finer scales: broad (including those significant predictors among the 14 first PCNM vectors, which would represent progressively smaller patches from about 750

to nearly 180 m in diameter), intermediate (significant predictors among PCNM15 and PCNM34, which would represent patches from ca. 170 to nearly 80 m in diameter) and fine scale (predictors among PCNM35 and PCNM50, which would represent patches from about 70 to nearly 65 m in diameter). The coefficient of determination of each spatial submodel represents the proportion of predictable spatial variability accounted for by each scale. Before fitting to PCNM spatial submodels, the bird abundance of each species was log-transformed and detrended from significant linear trends (residuals of fitting to the unidimensional coordinate; Borcard & Legendre 2002).

Once the spatial variability of the bird abundance per plot at three different spatial scales was assessed, we evaluated scale-dependent microhabitat use by relating this scale-dependent variability to the characteristics of the habitat. For that, we calculated the predicted values of bird abundance provided by each of the aforementioned spatial submodels. Then, we used these predicted values as response variables in multiple regression models considering the six microhabitat variables as explanatory variables. We performed backward elimination of explanatory variables based on significance value and checked visually the linearity of the relationship between the dependent and each (untransformed) explanatory variable. Prior to the use of the microhabitat tests, and in order to avoid the inclusion in the regression models of highly correlated explanatory variables, we checked for the correlation among microhabitat variables by means of Pearson's coefficient.

RESULTS

We registered 229 tapaculos, from which 162 observations belonged to *Scelorchilus rubecula*, 56 to *Pteroptochos tarnii*, and 11 to *Scytalopus magellanicus*. Most tapaculos were observed on the ground or perching at the lowest understory level. Because of the small sample size, no further analyses were performed for *S. magellanicus*. We observed, on average, 10 individuals (range 3-16) per census for *S. rubecula,* and four individuals (range 1-12)

for *P tarnii*. The average number of observations of *S. rubecula* per plot was 2.1 (CV=70), while for *P. tarnii* was 0.7 (CV=168). Most *P. tarnii* were recorded in small groups, usually of two individuals, occurring in the same or in neighbouring plots. In three opportunities we registered a family of four individuals, two adults and two juveniles. Conversely, *S. rubecula* individuals usually were alone, some of them being juveniles.

Spatial patchiness of bird presence

Moran's *I* correlograms revealed significant spatial autocorrelation in bird abundance, with different spatial structures between species (Figures 1). *Scelorchilus rubecula* correlogram, with five successive and regularly distributed changes from positive to negative significant Moran's *I* values (Figure 1b), suggested the occurrence of patches of similar

size (about 150 radius), separated regularly (peaks nearly every 300 m) along the transect (Figure 1a). *Pteroptochos tarnii* presence was also patchy, but with a less regular spatial structure: three large patches of variable size (100 to 250 m radius), separated by variable distances (300 to 800 m, Figure 1d). On the other hand, *S. rubecula* distribution along the transect was independent of the presence of *P. tarnii* (partial Mantel test: r=-0.066, P=0.123).

Variability in microhabitat features

All the microhabitat characteristics showed strong variation along the transect (Table 1). Measurements of most variables were found to cover the whole range of potential values in their respective gradients. The coefficients of variation suggested highly aggregated spatial distribution for all variables (Table 1). Microhabitat features showed some correlations
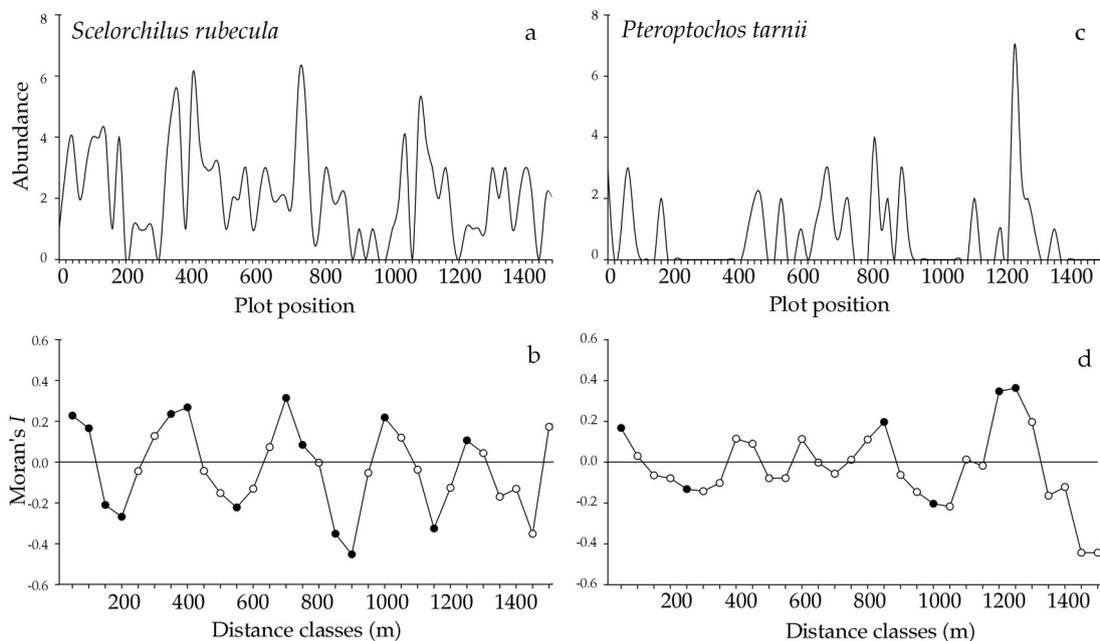
Figure 1. Abundance (cumulative number of records) of *Scelorchilus rubecula* and *Pteroptochos tarnii* in different sampling plots along the 1500 m transect (a, c) and spatial correlogram (b, d). Solid symbols indicate significant Moran's *I* values ($P \leq 0.05$), for globally significant correlogram after sequential Bonferroni adjustment.

Figura 1. Abundancia (número acumulado de registros) de *Scelorchilus rubecula* y *Pteroptochos tarnii* en diferentes parcelas de muestreo a lo largo de la transecta de 1500 m (a, c) y correlograma espacial (b, d). Los círculos llenos indican valores significativos de *I* de Moran ($P \leq 0.05$), para correlograma globalmente significativo después del ajuste secuencial de Bonferroni.

among them. The understory cover showed a positive and significant relationship with the abundance of branches, woody plant volume and bamboo cover (Table 2). Bamboo cover was positively correlated to woody plant volume but negatively correlated to the number of plant species.

PCNM analysis and variation of bird presence at different spatial scales

Five out of the 50 PCNM variables were significant for *S. rubecula* abundance (Table 3), distributing equitably among the three spatial submodels (two on broad, two on intermediate and one on fine scale), the whole spatial model explaining ca. 32% of the spatial variability. In the case of *P. tarnii*, three out of the 50 PCNM variables were significant, two of them cor-

responding to the broad scale and one to the fine scale (Table 3). The whole spatial model explained nearly 28% of the spatial variability. The broad-scale spatial submodel accounted for most of the predictable spatial variability in the abundance of both bird species (Table 3), spatial randomness increasing with decreasing scale. The periodic bumps depicted by predicted values of broad spatial models (Figures 2) fitted well with the large-scale patches suggested by correlograms (Figures 1).

Scale-dependent microhabitat use

The relationship between the predicted values of bird abundance at different spatial scales and microhabitat characteristics was only significant at the broad scale. The coefficient of determination was not significant

Table 1. Microhabitat characteristics of the temperate forest. Coefficient of variation (CV), maximum (Max) and minimum (Min) values for each of the six variables measured. Abundance of fallen branches and understory volume: 0=none, 5=maximum.

Tabla 1. Características del microhábitat del bosque templado. Coeficiente de variación (CV), valores máximo (Max) y mínimo (Min) para cada una de las seis variables relevadas. Abundancia de ramas caídas y volumen del sotobosque: 0=ninguno, 5=máximo.

Variable	Mean	Median	CV	Max	Min
Tree cover (%)	71.8	82.5	40	100	0
Understory cover (%)	73.0	80.0	34	100	10
Branches	1.6	1.5	45	3.3	0
Volume	2.6	2.7	44	5	0
Bamboo cover (%)	31.3	17.5	104	97.5	0
Num. of species	7.3	7.0	32	13	2

Table 2. Spearman correlation between microhabitat characteristics (upper hemi matrix: coefficients of correlation; lower hemi matrix: significance level, *P*).

Tabla 2. Correlaciones de Spearman entre las características del microhábitat (hemimatriz superior: coeficientes de correlación; hemimatriz inferior: niveles de significancia, *P*).

	Tree cover	Understory cover	Branches	Volume	Bamboo cover	Num. of species
Tree cover	1	0.098	0.359	0.021	0.030	-0.043
Understory cover	0.402	1	0.589	0.879	0.500	0.079
Branches	0.002	<0.001	1	0.545	0.107	0.034
Volume	0.861	<0.001	<0.001	1	0.616	0.054
Bamboo cover	0.801	<0.001	0.362	<0.001	1	-0.293
Num. of species	0.712	0.498	0.771	0.642	0.011	1

Table 3. Summary of multiple regression models fitting the abundance of each tapaculo species to PCNM vectors. Also shown are: the significant PCNM vectors for each spatial submodel representing three progressively finer scales, the coefficient of determination (R^2) for the total spatial model and the coefficient of significance p value.

Tabla 3. Resumen de los modelos de regresión múltiple ajustando la abundancia de cada especie de tapaculo a los vectores de ACPMV. Se indican los vectores de ACPMV significativos para cada submodelo espacial (amplio, intermedio, fino), el coeficiente de determinación (R^2) para todo el modelo espacial y el valor de significancia.

Scale	*Scelorchilus rubecula* abundance	*Pteroptochos tarnii* abundance
Broad		
PCNM vectors	3, 12	7, 14
R^2	0.15	0.23
P	0.011	
Intermediate		
PCNM vectors	30, 31	
R^2	0.08	
P	0.049	
Fine		
PCNM vectors	39	40
R^2	0.09	0.05
P	0.043	0.007
R^2 Total	0.32	0.28

Table 4. Summary of stepwise regression models fitting microhabitat characteristics to the values of abundance of the two tapaculo species, predicted by the broad spatial submodel from previous PCNM (see Table 3). Also shown are: the coefficient of determination (R^2) for the whole model, the standardized regression partial coefficient and the level of significance p value.

Tabla 4. Resumen de los modelos de regresión múltiple ajustando los valores predichos de la abundancia de tapaculos del submodelo a macroescala (generado previamente por el ACPMV a las características del microhábitat (ver Tabla 3). Se indican, para cada especie de ave, el coeficiente de determinación (R^2), los coeficientes parciales de regresión y los valores de significancia cuando $P \leq 0.1$.

	Scelorchilus rubecula	*Pteroptochos tarnii*
R^2	0.270	0.162
Tree cover	4.58 ($p<0.001$)	
Branches	-1.93 ($p=0.057$)	2.57 ($p=0.012$)
Volume	2.11 ($p=0.038$)	-1.84 ($p=0.068$)
Num. of species		-2.60 ($p=0.011$)

DISCUSSION

Our study suggests that *Scelorchilus rubecula* and *Pteroptochos tarnii*, two species of tapaculos co-occurring in the same areas of well-conserved temperate forests of northern Patagonia, showed different population spatial structures and forest habitat use patterns. Moreover, each species is distributed within the forest independently of the presence of the other; our data suggest lack of competition or facilitation between species.

Spatial autocorrelation and PCNM analyses evidenced a patchy distribution in bird records, meaning that some plots in the transect were significantly more used by tapaculos than others. Moreover, patchiness differed between tapaculos species, with *S. rubecula* showing smaller and more regularly distributed patches than *P. tarnii*. Besides the potential effect of habitat features on the bird population spatial structure (see below), differences in patchiness may be explained in terms of differences between species in terri-

for *S. rubecula* at the intermediate and fine scales ($R^2=0.12$, $P=0.234$; $R^2=0.03$, $P=0.95$, respectively) and for *P. tarnii* only at a fine scale ($R^2=0.06$, $P=0.745$). Multiple regression models at broad-scale with microhabitat features accounted for ca. 27% of the variance for *S. rubecula* and nearly 17% for *P. tarnii* (Table 4). Nevertheless, the models incorporated different microhabitat characteristics with different signs for each bird species. *Scelorchilus rubecula* showed positive relationships with tree cover and woody plant volume and a negative relationship with abundance of branches (Table 4, Figure 2). On the other hand, *P. tarnii* presence at the broad scale related positively to the abundance of branches, and negatively to woody plant volume and the number of plant species (Table 4, Figure 2).

toriality, body size and family structure. In the first place, as *S. rubecula* has a strong territorial behaviour (Sieving et al. 1996) we hypothesize that the sampled individuals showed a greater regularity in territory distribution, because they moved and/or were established in new areas at the end of the reproduction season. On the other hand, differences in average patch size seem to correspond to differences in body size, as *S. rubecula* weighs on average 40 g, whereas *P. tarnii* weighs 150 g (Sieving et al. 2000). Therefore the former requires smaller average home ranges, that may affect the size of bird clusters. In addition, the number of individuals observed for each species in one plot or in the neighbouring plots differed as well. In fact, *P. tarnii* was found more often in groups (more than one individual per plot) than *S. rubecula*. This pattern can be related to the family system of the former species, adults moving with juveniles at the time of sampling, resulting in the need for a bigger feeding area for the group. It might be that when the juveniles abandon the adults, the

spatial patchiness of this species changes. If this is the case, the area required by *P. tarnii* will probably vary depending on the time of year, increasing after the chicks' hutch.

Our spatially-explicit analysis allowed to identify the most significant scales for variation in bird abundance within the spatial extent of the sampling transect, as a previous step to assess microhabitat use. In both species, spatial predictability was higher at the broader scale, the spatial patchiness depicted by the predicted values of abundance at this scale being concordant with the aggregation patterns depicted by correlograms. More importantly, the dissection of spatial variance by means of the PCNM enabled us to identify what habitat features contribute the most to the major trends of spatial patchiness of each bird species. In fact, habitat variables affected each bird species differently (Sieving & Karr 1997; Parker et al. 2005; Peh et al. 2005). Forest cover, a major structural feature assumed to be decisive for the persistence of most forest bird species was only positively significant
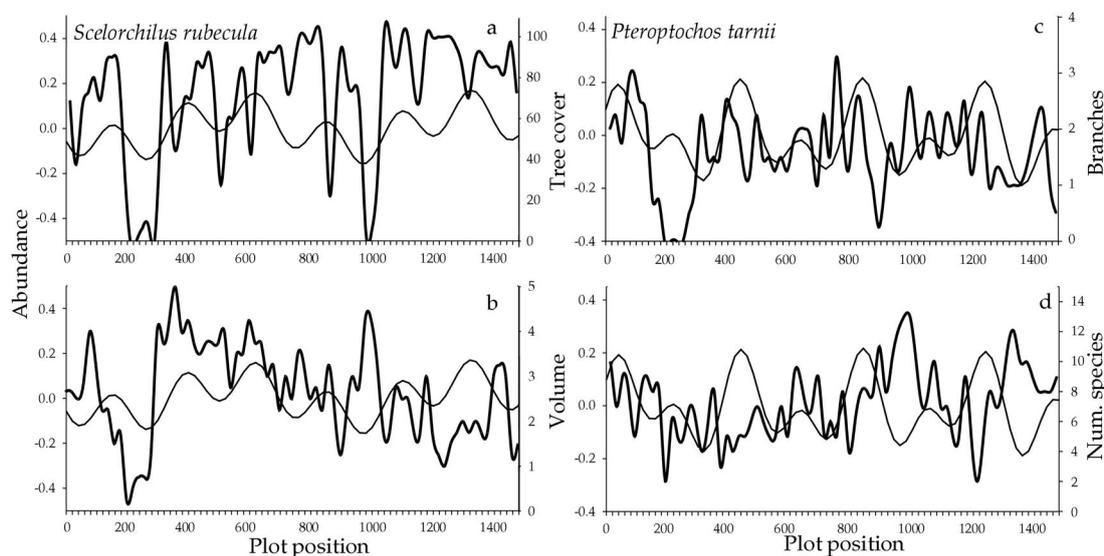
Figure 2. Abundance of birds (cumulative number of records) predicted by the broad spatial submodel of PCNM (thin line) and in thick line for *Scelorchilus rubecula* the percentage of tree cover (a) and volume of woody plants (b); and for *Pteroptochos tarnii* the abundance of branches (c) and number of woody species (d) in different sampling plots along the 1500 m transect.

Figura 2. Abundancia de aves (número acumulado de registros) predicho por el ACPMV a escala espacial amplia (línea fina) y en línea gruesa para *Scelorchilus rubecula* el porcentaje de cobertura arbórea (a) y volumen de plantas leñosas (b); para *Pteroptochos tarnii* la abundancia de ramas caídas (c) y número de especies leñosas (d), en las diferentes parcelas de muestreo a lo largo de la transecta de 1500 m.

for *S. rubecula*. On the other hand, the effect of the abundance of branches was positive for *P. tarnii* but negative for *S. rubecula*. The tendency was reversed for the volume of understory woody plants, *S. rubecula* preferring plots with high volume whereas *P. tarnii* occupying low understory volume areas. Similar relationships with woody plant volume had been found for these birds in Chile (Reid et al. 2004; Díaz et al. 2005). Conversely, we did not detect any effect of bamboo cover, as had been previously suggested for *S. rubecula* (Reid et al. 2004). However, in that study the bamboo species was *Chusquea quila* and not *C. culeou*, and the cover was very different in both studies: 75% in Reid et al. (2004), while in our study it was less than 40%, thus this may explain why there was no effect in our study.

Microhabitat use differences between species reported here could also be associated to differences in feeding behaviour and diet. In this sense, *S. rubecula* has been reported to be an omnivore, mostly feeding on insects but also on fleshy fruits or seeds (Correa et al. 1990). The diet of *P. tarnii* is unknown, but it is considered to be mainly an insectivore. Regarding their feeding behaviour, *P. tarnii* searches for food principally on the ground and outside dense bamboo patches (authors' unpublished observation), removing ground litter (debris, soil, leaves, etc.) with its legs. On the other hand, *S. rubecula* never uses its legs to search for food and most of the observations were in dense patches. This species takes insects from the ground or from low levels of the understory but without removing any material. This behaviour will promote the preference for areas of high vegetation volume where above-ground food is more abundant, as corroborated by our data. Conversely, in areas with low vegetation volume it would be easier for *P. tarnii* to remove ground material to find food.

Conservation and management implications

Endemic tapaculos have been identified as species highly susceptible to forest habitat loss and therefore, they have been used as indicators of degradation of temperate forest in southern South America (Sieving et al. 1996; Sieving et al. 2000; Castellón & Sieving 2006). Moreover, species such as *S. rubecula*

are known to use degraded forest areas depending on understory vegetation structure (Castellón & Sieving 2006). Despite of previous findings evidencing habitat-bird relationships at the large scale in fragmented landscapes, conservation plans based on relationships between tapaculos abundance and microhabitat features within unmanaged forest is absent. We present here two findings to be considered as management guidelines for these birds and their natural habitats. First, microhabitat priorities are species-specific, with no common multi-specific response to a single habitat feature, and thus different forms of habitat degradation or even management may affect different species diversely. For example, *S. rubecula* would be affected by forest cover losses, whereas *P. tarnii* would be even affected by the removal of dead branches (a common practice in forest fire prevention even in protected areas). Second, bird population patchiness and microhabitat use is scale-dependent, most of habitat-bird relationships emerging at particular scales within the extent of forest stands. In this sense, the size of patches of birds may be used as a threshold grain size above which the different forms of habitat modification should be avoided. Thus, taking into account the differences in patch size between bird species, the management recommendation is that forest canopy removal would be only acceptable in small patches, even smaller than the removal of fallen branches within the forest. Clearly, the management of this South American temperate forest requires a multi-scale approach that considers the specific response of forest birds to the changes in forest heterogeneity at different spatial scales.

Acknowledgements

REFERENCES

AMICO, GC & MA AIZEN. 2005. Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién? *Ecol. Aust.* **15**:89-100.

ARMESTO, JJ; P LEÓN-LOBOS & MTK ARROYO. 1996. Los bosques templados del sur de Chile: una isla biogeográfica. Pp 23-28 in: Armesto, JJ; C Villagran & MTK Arroyo (Eds.) *Ecología de los bosques nativos de Chile.* Editorial Universitaria, Santiago, Chile.

ARMESTO, JJ; R ROZII; C SMITH-RAMÍREZ & MTK ARROYO. 1998. Ecology - Conservation targets in South American temperate forests. *Science* **282**:1271-1272.

BAKERMANS, MH & AD RODEWALD. 2006. Scale-dependent habitat use of acadian flycatcher (*Empidonax virescens*) in central Ohio. *Auk* **123**:368-382.

BORCARD, D & P LEGENDRE. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Mod.* **153**:51-68.

BORCARD, D & P LEGENDRE. 2004. SpaceMaker2 – User's guide. Département de sciences biologiques, Université de Montréal, Montréal, Canada.

BORCARD, D; P LEGENDRE; C AVOIS-JACQUET & H TUOMISTO. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* **85**:1826-1832.

BUSTAMANTE, RO & C CASTRO. 1998. The decline of an endangered temperate ecosystem: the ruil (*Nothofagus alessandrii*) forest in central Chile. *Biodivers. Conserv.* **7**:1607-1626.

CABRERA, AL & A WILLINK. 1980. *Biogeografía de América Latina*, Washington, District of Columbia.

CASGRAIN, P; P LEGENDRE & A VADOUR. 1997. The R Package for Multidimensional and Spatial Analysis. Département de sciences biologiques, Université de Montréal, Montréal, Canada.

CASTELLÓN, TD & KE SIEVING. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conserv. Biol.* **20**:135-145.

CORREA, A; JJ ARMESTO; RP SCHLATTER; R ROZZI R & JC TORRES-MURA. 1990. La dieta del chucao (*Scelorchilus rubecula*), un Passeriforme terrícola endémico del bosque templado húmedo de Sudamérica austral. *Rev. Chil. Hist. Nat.* **63**:197-202.

CUETO, VR. 2006. Escalas en ecología: su importancia para el estudio de la selección de hábitat en aves. *Hornero* **21**:1-13.

DE SANTO, TL; MF WILLSON; KE SIEVING & JJ ARMESTO. 2002. Nesting biology of tapaculos (Rhinocryptidae) in fragmented south-temperate rain forests of Chile. *Condor* **104**:482-495.

DÍAZ, IA; JJ ARMESTO; S REID; KE SIEVING & MF WILLSON. 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloe' Island, Chile. *Biol. Conserv.* **123**:91-101.

DRAY, S; P LEGENDRE & PR PERES-NETO. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM) *Ecol. Mod.* **196**: 483-493.

ECHEVERRÍA, C; D COOMES; J SALAS; JM REY-BENAYAS, A LARA ET AL. 2006. Rapid deforestation and fragmentation of Chilean Temperate Forests. *Biol. Conserv.* **130**:481-494.

ESTADES, CF & SA TEMPLE. 1999. Deciduous-forest bird communities in a fragmented landscape dominated by exotic pine plantations. *Ecol. App.* **9**:573-585.

HALL, LS & RW MANNAN. 1999. Multiscaled habitat selection by elegant trogons in southeastern Arizona. *J. Wildlife Manage.* **63**:451-461.

HAYTHORNTHWAITE, AS & CR DICKMAN. 2006. Distribution, abundance, and individual strategies: a multi-scale analysis of dasyurid marsupials in arid central Australia. *Ecography* **29**:285-300.

JONES, JW. 2001. Habitat selection studies in avian ecology: A critical review. *Auk* **118**:557-562.

KOTLIAR, NB & JA WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**:253-260.

LARA, A; C DONOSO & JC ARAVENA. 1996. La conservación del bosque nativo en Chile: Problemas y desafíos. Pp. 23-28 in: Armesto, JJ; C Villagran & MTK Arroyo (Eds.) *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago.

LEE, M; L FAHRIG, K FREEMARK & DJ CURRIE. 2002. Importance of patch scale vs landscape scale on selected forest birds. *Oikos* **96**:110-118.

LEGENDRE, P & MJ FORTIN. 1989. Spatial pattern and ecological analysis. *Vegetatio* **80**:107-138.

LEGENDRE, P & L LEGENDRE. 1998. *Numerical Ecology*, 2nd ed. Elsevier, Amsterdam.

LINDENMAYER, DB & JF FRANKLIN. 2002. Conserving forest biodiversity: a comprehensive multiscaled approach. Island Press, Washington.

LINDENMAYER, DB. 2000. Factors at multiple scales affecting distribution patterns and their implications for animal conservation - Leadbeater's Possum as a case study. *Biodivers. Conserv.* **9**:15-35.

Lindenmayer, DB; MA McCarthy & ML Pope. 1999. Arboreal marsupial incidence in eucalypt patches in south-eastern Australia: a test of Hanski's incidence function metapopulation model for patch occupancy. *Oikos* **84**:99-109.

Luck, GW. 2002. The habitat requirements of the rufous treecreeper (*Climacteris rufa*). I. Preferential habitat use demonstrated at multiple spatial scales. *Biol. Conserv.* **105**:383-394.

McCollin, D. 1998. Forest edges and habitat selection in birds: a functional approach. *Ecography* **21**:247-260.

Orians, GH & JF Wittenberger. 1991. Spatial and Temporal Scales in Habitat Selection. *Am. Nat.* **137**:S29-S49.

Parker, TH; BM Stansberry, CD Becker & PS Gipson. 2005. Edge and area effects on the occurrence of migrant forest songbirds. *Conserv. Biol.* **19**:1157-1167.

Pauchard, A & P Villarroel. 2002. Protected areas in Chile: History, current status, and challenges. *Nat. Area J.* **22**:318-330.

Peh, KSH; J De Jong; NS Sodhi; SLH Lim & CAM Yap. 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biol. Conserv.* **123**:489-505.

Pribil, S & J Pricman. 1997. The importance of using the proper methodology and spatial scale in the study of habitat selection by birds. *Can. J. Zoolog.* **75**:1835-1844.

Reid, S; IA Díaz, JJ Armesto & MF Willson. 2004. Importance of native bamboo for understory birds in Chilean temperate forests. *Auk* **121**:515-525.

Ridgely, RS & G Tudor. 1994. *The Birds of South America: Vol. II, The Suboscine Passerines*. University of Texas press, Austin, TX.

Sieving, KE; MF Willson & TL De Santo. 1996. Habitat barriers to movement of understory birds in fragmented south-temperate rainforest. *Auk* **113**:944-949.

Sieving, KE & JR Karr. 1997. Avian extinction and persistence mechanisms in lowland Panama. Pp. 156-170 in: Laurance, WF & RO Bierregaard Jr. (Eds.). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.

Sieving, KE; MF Willson & TL De Santo. 2000. Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conserv. Biol.* **14**:1120-1132.

Sieving, KE; TA Contreras & KL Maute. 2004. Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in North-Central Florida. *Auk* **121**:738-751.

Vergara, PM & JA Simonetti. 2003. Forest fragmentation and rhinocryptid nest predation in central Chile. *Acta Oecol.* **24**:285-288.

Vergara, PM & JA Simonetti. 2004a. Avian responses to fragmentation of the Maulino Forest in central Chile. *Oryx* **38**:383-388.

Vergara, PM & JA Simonetti. 2004b. Does nest-site cover reduce nest predation for rhinocryptids? *J. Field Ornithol.* **75**:188-191.

Vuilleumier, F. 1985. Forest birds of Patagonia. *Ornithol. Monogr.* **36**:255-304.

Wiens, JA; JT Rotenberry & B Van Horne. 1987. Habitat occupancy patterns of North American shrub steppe birds: the effects of spatial scale. *Oikos* **48**:132-147.

Willson, MF; TI Desanto; C Sabag & JJ Armesto. 1994. Avian Communities of Fragmented South-Temperate Rain-Forests in Chile. *Conserv. Biol.* **8**:508-520.

Willson, MF. 2004. Loss of habitat connectivity hinders pair formation and juvenile dispersal of Chucao Tapaculos in Chilean rainforest. *Condor* **106**:166-171.