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Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: A multi-scale approach

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ABSTRACT

Habitat-specialists have narrower niches, but achieve higher or similar peak performance (e.g. occurrence probability, ψ) than habitat-generalists along resource gradients that may be selected from the stand- to landscape-levels. Understanding the relationship between niche width and ψ of forest owls will facilitate the development of appropriate management recommendations for their conservation. We assessed ψ of the threatened habitat-specialist rufous-legged owls (*Strix rufipes*) and habitat-generalist austral pygmy-owls (*Glaucidium nana*) across three spatial scales, and tested whether they differed in resource utilization and peak ψ in temperate forests of southern Chile. We conducted 1145 broadcast surveys at 101 sites and used multi-season occupancy models, accounting for imperfect detection, to estimate ψ. For *S. rufipes*, ψ ranged between 0.05 and 1 across sites, and was positively associated with the variability (standard deviation, SD) in diameter at breast height (DBH) of trees and bamboo understory density. For *G. nana*, ψ ranged between 0.67 and 0.98, and was positively associated with forest-patch shape index (irregularity and edge effects) and forest cover at 180 ha, although the parameter estimates were imprecise. Relative to *G. nana*, *S. rufipes* had lower total resource utilization due to lower ψ over gradients of all covariates, but achieved similar peak ψ for resources related with stand-level forest complexity and forest stability at the landscape scale. Occurrence of habitat-specialist owls will be promoted if multi-aged stands with a variety of tree sizes (SD of DBH = 19.9 ± 9 cm), including large old-growth trees, with relatively high bamboo cover (34.2 ± 26.6%), are retained. Landscapes with forest cover >63.5% would also favor occurrence by habitat-specialist owls.

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1. Introduction

Niche theory has a long history in ecology and it is helpful for assessing the condition of ecological communities (Clavel et al., 2011; Hirzel and Le Lay, 2008). In a niche context, specialist species have a narrower width in resource use than generalists (i.e. generalists utilize a greater variety of resources, Fig. 1a). Nevertheless, specialists can reach either a higher or similar level of peak performance (e.g. occurrence, density) than generalists under a subset of relatively stable resources (Fig. 1b and c; Devictor et al., 2010; Peers et al., 2012). Narrower niches render specialists more prone to be negatively affected by habitat degradation and fragmentation, than generalists (Clavel et al., 2011). Therefore, identifying habitat attributes where specialist species have higher peak performance is essential for the development of management guidelines that conserve a diversity of species within a community.

Owls act as apex predators within forest communities, and the implementation of plans for their conservation may deliver enhanced biodiversity benefits (Sergio et al., 2006). To meet their niche requirements, forest owls usually require different habitat patches for breeding and foraging, and thus they select habitat resources from the stand- to the landscape-level (Flesch and Steidl, 2010). Therefore, multi-scale approaches can be useful to identify: (a) relevant scales concerning individual perception of the environment so as to generate habitat suitability models (Martínez et al., 2003; Sergio et al., 2003), and (b) the level of

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sensitivity of species in habitats subject to rapid degradation and fragmentation.

South America hosts the southernmost temperate forests in the world (Armesto et al., 1998). These ecosystems are recognized as a biodiversity "hotspot" because of their high concentration of endemic species, and are subject to conservation concern due to high rates of anthropogenic degradation and fragmentation (Myers et al., 2000). Here, intensive land-use practices have degraded stand-level availability of structural attributes such as the volume of coarse woody debris, large decaying trees and understory vegetation, and thus wildlife populations depending on these niche resources have been negatively affected (Díaz et al., 2005; Reid et al., 2004). At the landscape scale, southern temperate ecosystems have been reduced and fragmented, converting continuous forest into a patchwork of habitat types (Echeverría et al., 2006).

Habitat suitability models offer an operational application of the ecological niche as they presuppose that the observed occurrence of an owl at a site reflects its ecological requirements (Hirzel and Le Lay, 2008). However, the relation between niche requirements and the occurrence patterns of forest owls may sometimes be equivocal as these birds are elusive and mainly nocturnal, and therefore a non-detection of individuals at a site does not mean the species is absent. With the exception of Sberze et al. (2010), most studies on raptor-habitat relations in South America have made the assumption that owl detectability was perfect. This assumption may underestimate the number of sites where owls achieve their niche requirements and miss relevant habitat resources (MacKenzie et al., 2003).

One way to compare niches is to develop habitat models of sympatric species independently and contrast their characteristics (Hirzel and Le Lay, 2008). We studied two sympatric owls that hypothetically differ in site-occurrence patterns and sensitivity to forest degradation and fragmentation: rufous-legged owls (*Strix rufipes*) and austral pygmy-owls (*Glaucidium nana*). Both species occur extensively across South American temperate forests (35–55°S). *S. rufipes* are one of the least known owls in South America with suspected declining populations due to native forest loss (Martínez and Jaksic, 1996). *G. nana* are the most widespread and common owls in Chile (Jiménez and Jaksic, 1989). Previous research suggests that *S. rufipes* inhabit a more specific range of stand-level habitat resources than *G. nana* (Ibarra et al., 2012). *S. rufipes* are considered habitat-specialists because of their affiliation with multi-stratified forest stands >100 years old, whereas *G. nana* are considered habitat-generalists as they utilize a range of environments including forests, forest-steppe ecotones, shrublands and occasionally urban parks (Jiménez and Jaksic, 1989; Martínez and Jaksic, 1996; Trejo et al., 2006). However, whether these species actually differ in either occurrence rates or levels of habitat-specialization have not been tested.

The aims of this study were to (1) examine the association between habitat resources and occurrence patterns for each of these two sympatric forest owls at three spatial scales, and (2) test if habitat-specialist and generalist owls differ in their total resource utilization and peak performance in Andean temperate forests of southern Chile. We predicted that (1) owl occurrence rates are influenced from local within-stand to landscape level habitat resources, and (2) *S. rufipes* have a lower total resource utilization (Fig. 1a) but either a higher (Fig. 1b) or similar (Fig. 1c) level of peak performance for particular niche resources, than *G. nana*. To examine owl occurrence patterns and test our predictions, we used occupancy models that account for the likelihood that owls occurred at some sites without detections (i.e., were present but not detected, Ibarra et al., 2014). Our models allowed us to identify key niche resources to which owls are associated, and thus can provide reliable recommendations for owl conservation.

2. Materials and methods

2.1. Study area

The 2585 km^2 study area lies within the Villarrica watershed (39°16′S71°W), located in the Araucarias Biosphere Reserve, southern Chile. We chose this watershed because its rural road and trail system is extensive and accessible, and its landscapes are representative of the Andean portion of Chile's temperate forests (Ibarra et al., 2014). The temperate climate has a short dry season

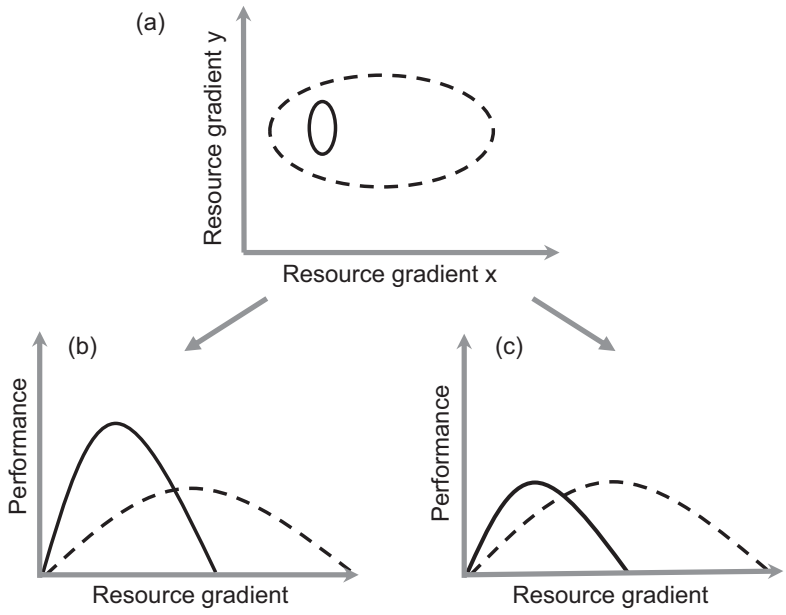

Fig. 1. (a) Specialized species (continuous line) have smaller niche widths than generalized species (dashed line) across resource gradients. Specialists can reach either a (b) higher level of performance (i.e. traditional model of relative niche width between specialists and generalists) or (c) similar level of performance (i.e. alternative model of relative niche width) than generalists, under a subset of resources that are relatively stable.

(<4 months) with a mean annual precipitation of 2500 mm, most falling as snow at higher altitudes (>750 m of altitude). Elevation ranges from 200 to above 2800 m, with forests distributed from 200 to 1500 m of altitude. In lowland areas, the natural vegetation is dominated by deciduous southern beech *Nothofagus* forests. At higher elevations, the vegetation is comprised of mixed deciduous trees with the conifer *Araucaria araucana* (Gajardo, 1993). This area is characterized by steep, rugged topography with valley floors used for agriculture, interspersed with small to medium-sized villages and towns.

2.2. Allocation of survey effort

We defined a "site" as the area within a 500-m detection radius of the sampling point, which corresponded to the area within which an owl could have heard a vocal lure during a survey (Sutherland et al., 2010). To determine the number of sites required to develop robust occurrence models, we simulated different study designs in GENPRES (Bailey et al., 2007). We defined a standard error SE (ψ) = 0.05 as the desired level of precision for the estimated proportion of sites where an owl occurs. Initial estimates of the key population parameters (i.e. occurrence and detectability) were calculated based on published studies of our target owl species (Ibarra et al., 2012; Martínez and Jaksic, 1996). This assessment generated a target of 86 sites. Conservatively, we established 95 sites for 2011–2012 and 101 for 2012–2013 (i.e. six new sites in year two). The term "site" used here is referred to as a "sampling unit" in Ibarra et al. (2014).

We established the 101 sites from 221 to 1361 m of altitude (near the tree-line). This range represented a variety of habitat conditions from degraded and patchy forests to zones comprising continuous undisturbed forests at higher elevations. Using ArcGIS 10.1 we identified all the headwaters of smaller basins that were accessible by rural roads or hiking trails within the Villarrica watershed (N = 19 basins). We randomly selected 13 of these 19 basins and placed the first site for all basins near the headwater (within 1 km of tree-line). We systematically established the remaining sites every 1.5 km descending the drainages (Ibarra et al., 2014).

2.3. Owl data

We surveyed each site over two nesting seasons at intervals of a minimum of 10-days, from mid-October to early February. In 2011–2012, we conducted six repeated surveys at 89 sites, four at four sites and three at two sites ($\bar{x} = 5.85$ surveys per site). In 2012–2013, we conducted six surveys at 93 sites, four at seven sites and three at one site ($\bar{x} = 5.83$ surveys per site; Ibarra et al., 2014).

We used call-broadcast surveys along rural roads and trails, beginning 15 min after sunset until 03:45 h (Trejo et al., 2011; Zuberogoitia and Campos, 1998). Playbacks of calls of both species were played twice and in a different random sequence. We broadcasted owl calls always from the same location at the center of the site. Full details on the nocturnal survey protocol and analyses of factors associated with the detectability of our two owl species are described in Ibarra et al. (2014) (see Table 2 in this study).

2.4. Stand- and landscape-level data

Stand-level niche resources (hereafter covariates) included habitat attributes suggested as important for *S. rufipes* and *G. nana* (Ibarra et al., 2012; Martínez and Jaksic, 1996). At every site, we established an *L-shaped transect* and located five vegetation plots (22.4 m diameter; 0.04 ha; N = 505 plots). The first plot for each site was located 50 m away from the center of the site (where owl calls were broadcasted), at the vertex of the L-shaped transect. The other four plots were established with a distance of 125 m between each along two 250 m lines directed outwards from the vertex (Affleck et al., 2005). For each plot we measured: tree density, tree diameter at breast height (DBH), canopy cover, volume of coarse woody debris, density of bamboo understory and elevation (Table 1). For DBH we calculated the standard deviation (SD) for each plot as it was considered a more reliable indicator than the average of (a) distribution of tree-age classes in a stand, (b) stand structural complexity and (c) the diversity of micro-habitats for owls and their prey (Van Den Meersschaut and Vandekerkhove, 2000). Also, SD of DBH frequently increases with stand age (McElhinny et al., 2005) and it was correlated (Pearson's $r > 0.7$)

Table 1
Stand- and landscape-level resources used to evaluate habitat associations of forest owls in Andean temperate forests.

Resource	Abbreviation for models	Description
Stand-level		
Tree density (trees/ha)	Tre	Density of all trees with DBH > 12.5 cm
Standard deviation of tree diameter at breast height (DBH, cm)[a]	Dbh	SD of tree DBH measures the variability in tree size, and was considered indicative of the diversity of micro-habitats within a stand for both owl and potential prey (Van Den Meersschaut and Vandekerkhove, 2000)
Canopy cover (%)[a]	Can	Proportion of sky covered by canopy estimated from the center of the plot
Volume of coarse woody debris (VCWD)[a]	Cwd	Calculated based on the length and diameter of each piece with diameter > 7.5 cm crossing a transect of 22.4 m length (oriented N–S)
Bamboo understory density (NC)[a]	Und	Density of bamboo vegetation up to 3 m high, expressed as the number of contacts (NC) using the method described in Díaz et al. (2006), quantified at five points of a transect of 22.4 m length (oriented N–S)
Elevation (m.a.s.l)	Ele	Meters above sea level measured at the center of the plot
Landscape-level		
Forest areas (180 ha[a]/1206 ha)	For180/ For1206	% Extent of forested area
Shrubland areas (180 ha[a]/1206 ha)	Shr180/ Shr1206	% Extent of shrubland
Core habitat (180 ha/1206 ha)	Cor180/ Cor1206	Mean size of interior core habitat ($\geqslant$100 m from polygon edge) of all forest patches in plot
Forest-patch shape index (Si) (180 ha[a]/ 1206 ha[a])	Si180/ Si1206	$Si = 0.25 \times p/\sqrt{A}$, where p = forest-patch perimeter and A = forest-patch area. Si is an estimator of forest-patch shape irregularity and edge effects, describing the extent to which patches depart from a geometrically simple compact configuration of the same area (for raster maps, square: Si = 1)
Relative habitat diversity (180 ha[a]/ 1206 ha)	Hd180/ Hd1206	Relative habitat diversity within a circular plot measured as Shannon's diversity index, which equals zero when there is only one patch and increases as the # of patch types or the proportional distribution of patch types increases

[a] Covariates retained for tests of habitat associations of forest owls after reducing collinearity.

with mean DBH in our system. Values of each habitat covariate for the five plots were averaged and thus a single value was obtained for each site.

We evaluated landscape-level covariates tested in other occurrence studies of forest raptors (Finn et al., 2002; Henneman and Andersen, 2009). These covariates included: forest extent, shrubland extent, core habitat, forest-patch shape index and relative habitat diversity (Table 1). Landscape covariates were measured within 180 and 1206 ha circular areas around each site. These areas corresponded to the minimum (1.8 km^2) and maximum (12.8 km^2) home-ranges reported for *S. rufipes* (Martínez, 2005). As no information exists on home-range sizes for *G. nana*, we used the home range size considered appropriate for *S. rufipes* for evaluating habitat associations in an area larger than a nest or roost site for *G. nana*, which allowed us to formally compare results between the two species. Spatial covariates were obtained from a composition of three Landsat (Landsat Enhanced Thematic Mapper Plus ETM+) scenes: one from January 2012 and two from January 2013. To obtain a land-use model for the study area, these scenes were corrected in a mixed-thematic classification process using the program IDRISI Selva (Eastman, 2012), into the following habitats: forest, shrubland, open area (including water bodies) and snow or glaciers. From this model, the two circular areas for each site were extracted using ArcGIS 10.1. Finally, forest patch and landscape metrics were quantified using Fragstat 4.1 (Table 1, McGarigal et al., 2002). Here we use the terms "degradation" for stand-level and "fragmentation and reduction" for landscape-level covariates indicating anthropogenic alteration of forest attributes (Newton, 2007; Wiens, 1994).

2.5. Modeling occurrence probabilities

Presence/absence data were analyzed using multi-season occupancy models (MacKenzie et al., 2003). We used the program R-Unmarked (Fiske and Chandler, 2011), which uses maximum-likelihood methods to estimate probabilities of occurrence and detection. Probability of occurrence (ψ) was defined as the probability that at least one individual owl occurred at a site.

To evaluate ψ, we assessed collinearity to reduce the number of covariates presented in Table 1. With strongly correlated covariates (Pearson's $r > 0.7$), we retained for analysis only the one considered to be most biologically meaningful for the study species (Sergio et al., 2003). In total, nine covariates were used in the final ψ modeling: four at the stand-level (SD of tree DBH, canopy cover, volume of coarse woody debris and bamboo density), four at the 180 ha landscape-level (forest extent, shrubland extent, shape index and relative habitat diversity) and one at the 1206 ha landscape-level (shape index).

We used multi-model inference and Akaike's Information Criterion (AIC; Burnham and Anderson, 2002) to identify the "best" model(s) representing arrangements of the covariates that we defined a priori. All models contained the sources of variation in detection probabilities previously identified as important for our target species using the same dataset (Ibarra et al., 2014; Table 2). To obtain the best ψ model for each owl, we first fit models using each covariate singly to predict ψ and also fitted a model with ψ constant (i.e. null model) across sites. More complex models were then built by combining stand- and landscape-level covariates among the best-supported covariates, on the basis of model weights and the precision of the estimated beta coefficients. We added covariates until all supported covariates not in the initial model had been considered. We evaluated 16 models for *S. rufipes* and 20 for *G. nana*. Model weights, referring to the relative weight of evidence for model *i*, were computed and the best model was the one that ranked with the highest weight (Burnham and Anderson, 2002). Models with $\Delta AIC \leqslant 2$, representing a measure of each model AIC value relative to the best model in the set, were considered the models best supported by the data. We addressed model selection uncertainty by averaging models with $\Delta AIC \leqslant 4$ in the final confidence set for each owl, which also accounted for 95% Akaike weight (Burnham and Anderson, 2002). The model-averaged predictions were used to project the distribution of owls in the study area using the spatial interpolation toolbar Kriging (Oliver and Webster, 1990), implemented in ArcGIS 10.1.

Residual analyses were used to test for spatial autocorrelation across a set of distance classes using the Moran's Index method (Moran, 1950). We based residuals on model-averaged estimates for each owl and calculated them as the observed values at site *i* (detection = 1, non-detection = 0) minus the predicted probabilities of detecting the species at least once. We selected distance classes of 3 km (0–3, 3–6, ..., 27–30 km) because this was twice the distance between nearest sites. Only *G. nana* showed positively correlated residuals, thus we calculated an autocovariate (Aut) term for this species following Moore and Swihart (2005). The inclusion of an autocovariate term resulted in additional six models ($N = 26$) for *G. nana*.

2.6. Comparing owl niches

To fully understand differences between specialists and generalists, a broad spectrum of niche resources should be tested simultaneously (Peers et al., 2012). We compared total resource utilization and peak performance between *S. rufipes* and *G. nana* by exploring their ψ according to each of the 16 covariates singly (Table 1). We considered each covariate both as a linear and a non-linear quadratic relationship. The response curves showed the degree of variation in habitat suitability for each covariate. We integrated across the range of *x* and *y* values for all response curves to obtain the total area under each response curve (i.e. index of total resource utilization; Peers et al., 2012). We divided each area calculation by the range across the x axis for each covariate to obtain a range from 0 to 1, with values closer to 1 representing a higher utilization of that specific resource (Peers et al., 2012). We estimated the peak ψ value for each covariate and compared the responses between owls using Student's *t*-tests. Data were normally distributed based on Kolmorogov–Smirnov test ($P < 0.05$).

3. Results

We had 292 and 334 detections to model occurrence patterns of *S. rufipes* and *G. nana*, respectively. The proportion of sites at which *S. rufipes* were detected ranged from 0.62 (59 sites out of 95 total sites) in 2011–2012, to 0.55 (56 out of 101 total sites) in 2012–2013. The proportion of sites at which *G. nana* were detected ranged from 0.72 (68 out of 95 total sites) in 2011–2012, to 0.77 (78 out of 101 total sites) in 2012–2013 (Ibarra et al., 2014).

3.1. Habitat suitability for owls

For *S. rufipes*, predicted ψ (mean ± standard error) ranged between 0.05 ± 0.04 and 1.00 ± 0.00 across sites. The models with highest support ($\Delta AIC \leqslant 2$) for *S. rufipes* contained two to four covariates for ψ (Table 2a). Model selection results indicated that ψ for *S. rufipes* was positively associated with the variability (SD) in the DBH distribution of trees, bamboo density and canopy cover; however, the 95% confidence interval for the beta coefficient of canopy cover overlapped with zero and thus this covariate was considered non-informative. Best models also supported a positive association between forest extent at 180 ha and *S. rufipes* ψ (Table 2a); however, beta coefficient for this covariate also overlapped with zero (Table 2a). The averaged predictions of ψ for

Table 2
Model selection statistics based on Akaike's Information Criterion (AIC) for estimating probability of occurrence (ψ) and detection (p) of two owl species (a) *Strix rufipes* and (b) *Glaucidium nana* in Andean temperate forests. Only the top model set with ΔAIC values <4 are shown. Parameter estimates are listed in the order of variable under Model structure column, and beta estimates in bold font have 95% confidence intervals that do not overlap 0.

Species	Model structure	K[c]	AIC	ΔAIC[d]	Wi[e]	Parameter estimates	Estimated 95% CI
(a) *Strix rufipes*	ψ(Dbh + Und + Can), p[a]	10	1070.16	0.00	0.27	**2.59**, **0.98**, 2.07	0.39, 4.79 0.02, 1.94 −0.85, 5.00
	ψ(Dbh + Und), p[a]	9	1070.17	0.02	0.27	**3.28**, **1.03**	1.27, 5.29 0.09, 1.97
	ψ(Dbh + Und + For180), p[a]	10	1070.81	0.65	0.20	**2.82**, 0.95, 1.55	0.68, 4.97 −0.02, 1.93 −1.08, 4.17
	ψ(Dbh + Und + For180 + Can), p[a]	11	1071.32	1.17	0.15	2.29, 0.90, 1.25, 1.82	−0.01, 4.58 −0.10, 1.90 −1.94, 3.94 −1.15, 4.79
	ψ(Dbh + For180), p[a]	9	1073.17	3.01	0.06	**3.07**, 2.43	1.05, 5.10 −0.15, 5.01
(b) *Glaucidium nana*	ψ(Si1206 + For180 + Aut), p[b]	12	1258.64	0.00	0.38	0.72, 0.17, 1.84	−2.43, 3.87 −2.63, 2.96 −2.00, 3.89
	ψ(Si1206 + For180), p[b]	11	1259.16	0.52	0.29	2.74, 0.44	−4.31, 9.78 −2.37, 3.25
	ψ(Shr180 + For180 + Aut), p[b]	12	1259.92	1.28	0.20	−0.57, 0.51, 1.94	−5.81, 4.67 −2.63, 3.64 −0.41, 4.30
	ψ(Shr180 + For180), p[b]	11	1260.80	2.16	0.13	−1.84, 0.79	−6.61, 2.94 −2.19, 3.77

[a] p(Ml + No + Ow).
[b] p(Wi + Ml + No + Da^2 + Ow). Important detection covariates were identified previously by Ibarra et al. (2014) using the same data set, and consisted of moonlight (Ml), environmental noise (No), whether the other owl species was detected at the unit for the specific survey (Ow), wind speed (W_i) and number of days since start of surveys (Da).
[c] Number of parameters estimated.
[d] ΔAIC is the difference in AIC values between each model and the lowest AIC model.
[e] AIC model weight.

S. rufipes revealed a zone of high habitat suitability to the east of the study area, associated with forests located close to the Andes Range (Fig. 2a). Areas of high habitat suitability occurred to the south and southeast of the study area as well, where a diagonal chain of volcanoes oriented south to south-east encompasses relatively continuous and old-growth forests between 700 and 1500 m of elevation. Zones of high suitability were mostly located inside or surrounding protected areas to the east, south and southeast of the study area (Fig. 2a). For easier implementation in forest management and planning programs, we calculated the values of covariates associated with predicted low (0–0.33), moderate (0.34–0.66) and high (0.67–1) values of ψ for *S. rufipes* in Andean forests based on averaged model predictions (Table 3).

For *G. nana*, predicted ψ ranged between 0.67 ± 0.18 and 0.98 ± 0.04 across sites. The models with highest support (ΔAIC ⩽ 2) for *G. nana* contained two or three covariates for ψ, although two of the best models included the autocovariate term (Aut, Table 2b). The spatial auto-covariate term effectively controlled for intra-landscape data dependence; it improved the AIC weight of two of the best models as those with the auto-covariate were 0.09 and 0.07 units higher than models without this term (compare Table 2b). Model selection results indicated that ψ for *G. nana* was positively associated with the forest-patch shape index at 1206 ha and forest cover extent at 180 ha. The third best model had a negative association between *G. nana* ψ and shrubland extent at 1206 ha (Table 2b). However, beta coefficient for all covariates overlapped with zero in all models. The averaged predictions of ψ for *G. nana* showed chiefly uniform mid- to high-levels of habitat suitability across much of the study area, with zones of slightly higher suitability either inside or close to protected areas (Fig. 2b).

3.2. Resource utilization and peak performance by owls

The predicted ψ for our two owl species varied in habitat suitability according to each environmental covariate (Fig. 3). Total resource utilization was lower for *S. rufipes* (mean ± standard error: 0.625 ± 0.080) and higher for *G. nana* (0.804 ± 0.020; t_{30}: −27.569, $P < 0.001$) in all 16 covariates (Fig. 4a), indicating a lower ψ for *S. rufipes* over the range of all covariate values. Averaged results of peak performance (i.e. peak ψ) for all 16 covariates together did not differ between *S. rufipes* (0.913 ± 0.045) and *G. nana* (0.894 ± 0.029; t_{30}: 0.736, $P = 0.467$; Fig. 4b). Considering each covariate separately, *S. rufipes* had higher peak ψ for elevation, tree density, SD of DBH, bamboo density, volume of coarse woody debris, canopy cover, forest extent at 180 and 1206 ha, and core habitat at 180 and 1206 ha than *G. nana*. *G. nana* had higher peak performance for forest-patch shape index at 180 and 1206 ha, shrubland extent at 180 and 1206 ha, and habitat diversity at 180 and 1206 ha than *S. rufipes*.

4. Discussion

Multi-scale approaches, accounting for detection probability, improve understanding of species habitat suitability and thus perceptions of ecological pressures under which habitat selection and niche requirements have evolved (Martínez et al., 2003). Our forest owls responded to habitat resources at several spatial scales. *S. rufipes* responded more strongly to stand-level whereas *G. nana* to landscape-level resources; however, the parameter estimates for the latter owl were imprecise (i.e. 95% CI overlapped zero). Furthermore, the comparison of niche widths suggested that habitat-specialist *S. rufipes* had a lower total resource utilization of the 16 resources under consideration while achieving a similar peak performance than the generalist *G. nana*. These results on niche relationships indicate that specialist owls use smaller portions of the potentially available habitat, and may require specific management considerations in an area subject to rapid forest degradation (at the stand-level) and fragmentation (at the landscape-level) such as is happening in South American temperate ecosystems.

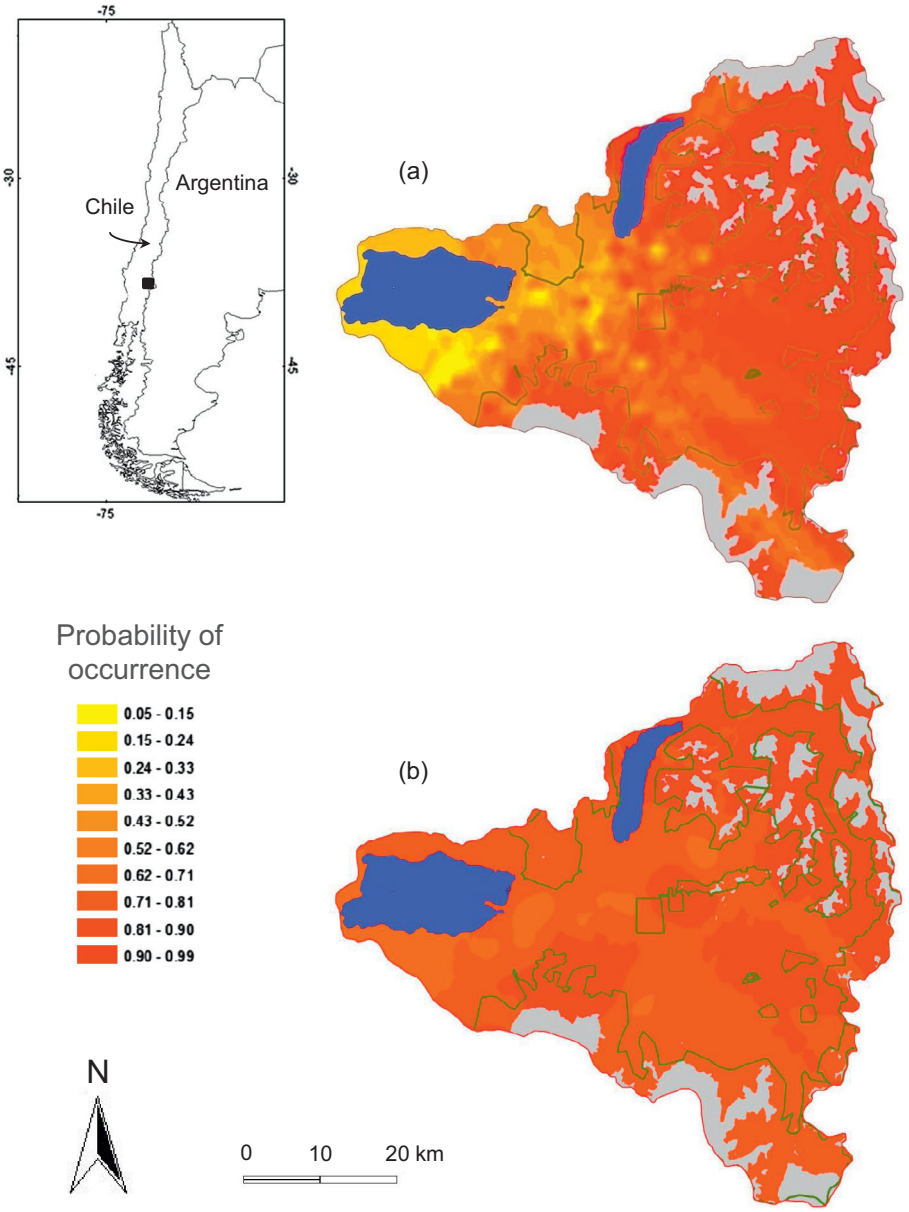

Fig. 2. Averaged predictions of occurrence for (a) *Strix rufipes* and (b) *Glaucidium nana* in the Villarrica watershed, Andean zone (black square) of the Araucanía Region, Chile. Red depicts areas of higher habitat suitability whereas yellow represents areas of lower habitat suitability or probability of occurrence. Alpine areas (gray), large lakes (blue) and boundaries of public protected areas (green), are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4.1. Habitat suitability across spatial scales

We identified a set of environmental resources which could drive habitat selection for *S. rufipes*. Habitat selection is considered a hierarchical decision-making process occurring from large to small spatial scales (Hutto, 1985). However, resources at the stand-level were more influential than landscape-level resources on occurrence rates for *S. rufipes* in our study such that habitat selection for this owl species could involve "bottom-up" choices (sensu Flesch and Steidl, 2010). *S. rufipes* were more likely to occur in structurally complex multi-aged forest-stands (i.e. higher values of SD of DBH), characterized by the presence of large trees and relatively high availability of bamboo understory. Our results support the findings of the two previous studies of *S. rufipes* habitat use in temperate forests (Ibarra et al., 2012; Martínez and Jaksic, 1996). *S. rufipes* are secondary cavity nesters that build nests in cavities generated by tree-decay processes or excavated by Magellanic woodpeckers (*Campephilus magellanicus*). The reported dimensions of nesting trees (mean DBH ± SD = 122.8 ± 36.2 cm) in Andean temperate forests suggest that trees greater than 100 years old are necessary to support suitable-sized cavities for this owl (Beaudoin and Ojeda, 2011). For its part, the bamboo understory provides habitat for several endemic arboreal and scansorial small mammals which constitute the main prey of *S. rufipes* in temperate forests (Figueroa et al., 2006). Dense understory of native bamboos is frequent under: (a) large canopy gaps generated by natural tree falls, (b) high-elevation (>900 m altitude) old-growth stands with relatively open canopies (54–81% canopy cover) and (c) logged forests where the canopy has been opened (Ibarra et al., 2012; Veblen, 1982).

The presence of large trees (likely related to breeding and roosting requirements) and dense bamboo understory (likely related to

Table 3
Mean (SD) values of habitat resources associated with probabilities of occurrence categorized as low (0–0.33), moderate (0.34–0.66) and high (0.67–1) for *Strix rufipes* in Andean temperate forests, based on model-averaged predictions.

Habitat resource	Predicted probability of occurrence		
	0–0.33	0.34–0.66	0.67–1
Stand-level			
Tree density (#/ha)	225.4 (223.2)	435.7 (300.0)	487.4 (244.7)
SD of diameter at breast height (cm)	5.4 (2.4)	11.2 (2.0)	19.9 (9.0)
Bamboo understory density (NC)[a]	0.1 (0.1)	0.2 (0.3)	2.8 (2.7)
Volume of coarse woody debris (m^3)	0 (0.0)	0.2 (0.7)	0.4 (0.4)
Canopy cover (%)	29.9 (22.4)	50.3 (18.8)	65.5 (17.8)
Landscape-level			
Forest extent 180 ha (%)	26.4 (20)	49.9 (23.1)	63.5 (23.5)
Forest extent 1206 ha (%)	35.3 (17.4)	53.2 (19.5)	66.5 (20.0)
Forest shape index 180 ha	1.2 (0.2)	1.3 (0.3)	1.4 (0.3)
Forest shape index 1206 ha	1.4 (0.1)	1.4 (0.1)	1.6 (0.5)
Shrubland extent 180 ha (%)	27.2 (15.7)	22.9 (14.4)	17.2 (13.4)
Shrubland extent 1206 ha (%)	24.8 (8.8)	22.2 (9.7)	16.8 (10.4)
Habitat diversity 180 ha (Shannon index)	0.9 (0.4)	1 (0.4)	0.7 (0.4)
Habitat diversity 1206 ha (Shannon index)	1.1 (0.2)	1.1 (0.2)	0.8 (0.4)
Core habitat 180 ha (# of ha)	5.4 (10.0)	19.1 (26.5)	40.8 (41.6)
Core habitat 1206 ha (# of ha)	107.9 (105.3)	223.4 (192.2)	389 (271.3)

[a] For easier implementation in forest management, the values of this resource in percentage of coverage approximate 1.6 ± 3% (low), 3.4 ± 5.4% (moderate) and 34.2 ± 26.6% (high probability of occurrence).

food supply), constitute key structural resources at the stand-level for *S. rufipes*. However, our results and previous descriptions of *S. rufipes* habitat (e.g. multi-storied forest sites >100 years old, dominant trees with DBH > 28 cm, more than 5 snags/ha and presence of large decaying trees; Martínez and Jaksic, 1996), emphasize the importance of several resources that generate the structural complexity suitable for these owls. Other *Strix* species in temperate forests from the northern hemisphere select similar habitat resources (Lõhmus, 2003; Seamans and Gutiérrez, 2007; Singleton et al., 2010), offering similarities between congeneric habitat-specialist owls in ecologically comparable environments. Across the study area, stand structural complexity increased from lowland unprotected areas to higher elevations (>700 m) comprising protected areas and their adjacent zones (Ibarra et al., 2012). These changes generated heterogeneous distributions of resources important for the predicted distribution of *S. rufipes*.

Incorporating landscape-level habitat data into the analyses did not substantially improve our ability to predict *S. rufipes* occurrence in Andean temperate forests as the estimated beta coefficients were imprecise. However, the best supported models included forest cover at 180 ha, and indicated a positive relation with *S. rufipes* occurrence. We therefore stress the importance of including this spatial structural resource in further studies of *S. rufipes*. The central depression of Chile and coastal range zones are highly deforested and lack protected areas (Echeverría et al., 2006; Smith-Ramírez, 2004). The long-term survival of *S. rufipes* is jeopardized in these areas of its range (Martínez, 2005); thus, including forest cover measures at the territory scale will be an important first step in refining landscape-level assessments for habitat use of *S. rufipes*. However, although occurrence patterns are directly associated with overall habitat quality and population performance (Sergio and Newton, 2003), we recommend that future studies should account directly for the influence of habitat quality on owl fitness because forest degradation and fragmentation are known to negatively affect habitat quality and reduce the long-term suitability for raptor populations (Hinam and St. Clair, 2008; Newton, 1998).

We identified spatial autocorrelation of initial-model residuals for *G. nana*, revealing that sites closer together resembled each other more than sites that are further apart. Although controlling for such spatial dependence allowed improvement of model fit, the model selection statistics showed moderate uncertainty about the most plausible model for occurrence of *G. nana*. As reported for other *Glaucidium* species (Campioni et al., 2013), the weak association between resources and *G. nana* occurrence could indicate a continuum of good habitat conditions across Andean temperate forests. This hypothesis is supported by the fairly uniform level of habitat suitability for *G. nana* across much of the Villarrica watershed. Forest fragment shape irregularity at 1206 ha, forest extent at 180 ha and shrubland extent at 180 ha (the latter with a negative association), were the resources present in the best-supported models. A previous study suggested a positive association between forest fragment irregularity and *G. nana* occupancy (Farias and Jaksic, 2011). As reported for *Glaucidium gnoma* and *Glaucidium brasilianum*, this higher irregularity, as generated by riparian zones and linear human structures (e.g. roads and fences), may provide these owls with different resources and hunting perches with extensive views (Campioni et al., 2013; Piorecky and Prescott, 2006).

4.2. Niche width of forest owls

Our species distribution models for the study area and analyses of resource utilization and peak performances for forest owls, indicate that *S. rufipes* use a narrower width of environments than *G. nana*. Similar to an evaluation of habitat-specialization on other top-predators (e.g. *Lynx canadensis* and *Lynx rufus*), our results of niche width for forest owls best fit the similar level of peak performance "alternative model of niche width" (Fig. 1; Peers et al., 2012).

The ability of species to exploit a range of resources and their performance using each one have usually been approached using the trade-off model that some species are the "jack of all trades" (i.e. species that use a greater diversity of resources perform less well on average) and either the "master of none" (Caley and Munday, 2003), "master of some" (Richards et al., 2006) or "master of all" (Barkae et al., 2012). For example, Caley and Munday (2003) reported that specialist coral reef fishes grew faster than generalists in one or two habitats, but the growth rate of generalists was more consistent between habitats. In a small-mammal assemblage, the habitat-specialist *Ochrotomys nuttali* showed stronger selection of one micro-habitat whereas generalists *Tamia striatus* and *Peromyscus leucopus* were able to exploit a range of micro-habitat types; however, *Ochrotomys* outperformed the generalist rodents

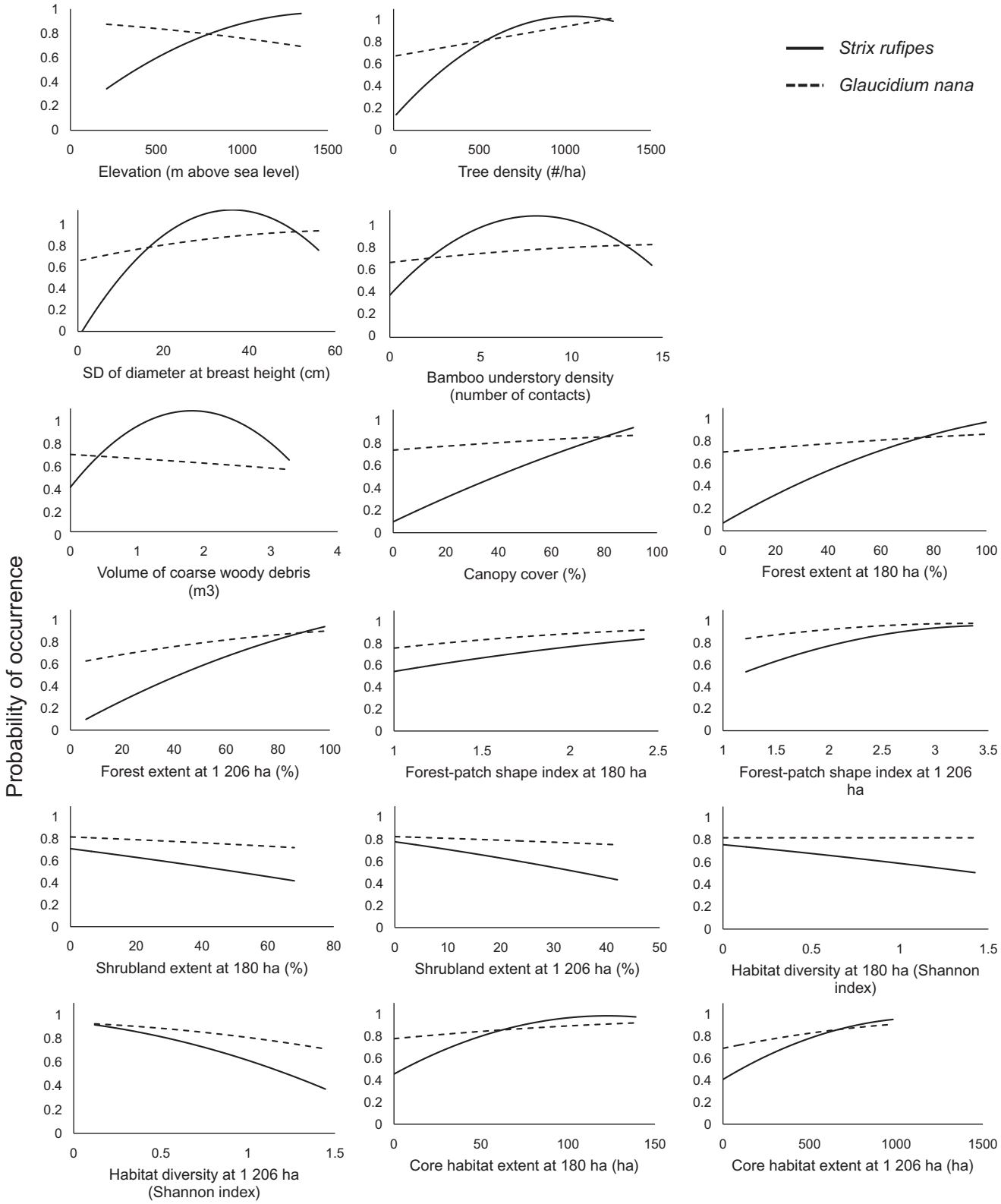

Fig. 3. Predicted probabilities of occurrence of *Strix rufipes* and *Glaucidium nana* in Andean temperate forests (2011–2013), in relation to environmental resources. The curves are representative of models developed for each owl using only the corresponding resource.

in the habitat where they were specialized (Dueser and Hallett, 1980). Studying top-predator felids, Peers et al. (2012) found that the specialist *L. canadensis* did not have a narrower width for each resource gradient compared to the generalist *L. rufus*, but rather had a wider width and higher performance within a subset of resources. Our results were a mixture of these scenarios as we found peak performance estimates for *S. rufipes* were slightly higher over a select number of resources associated with stand-

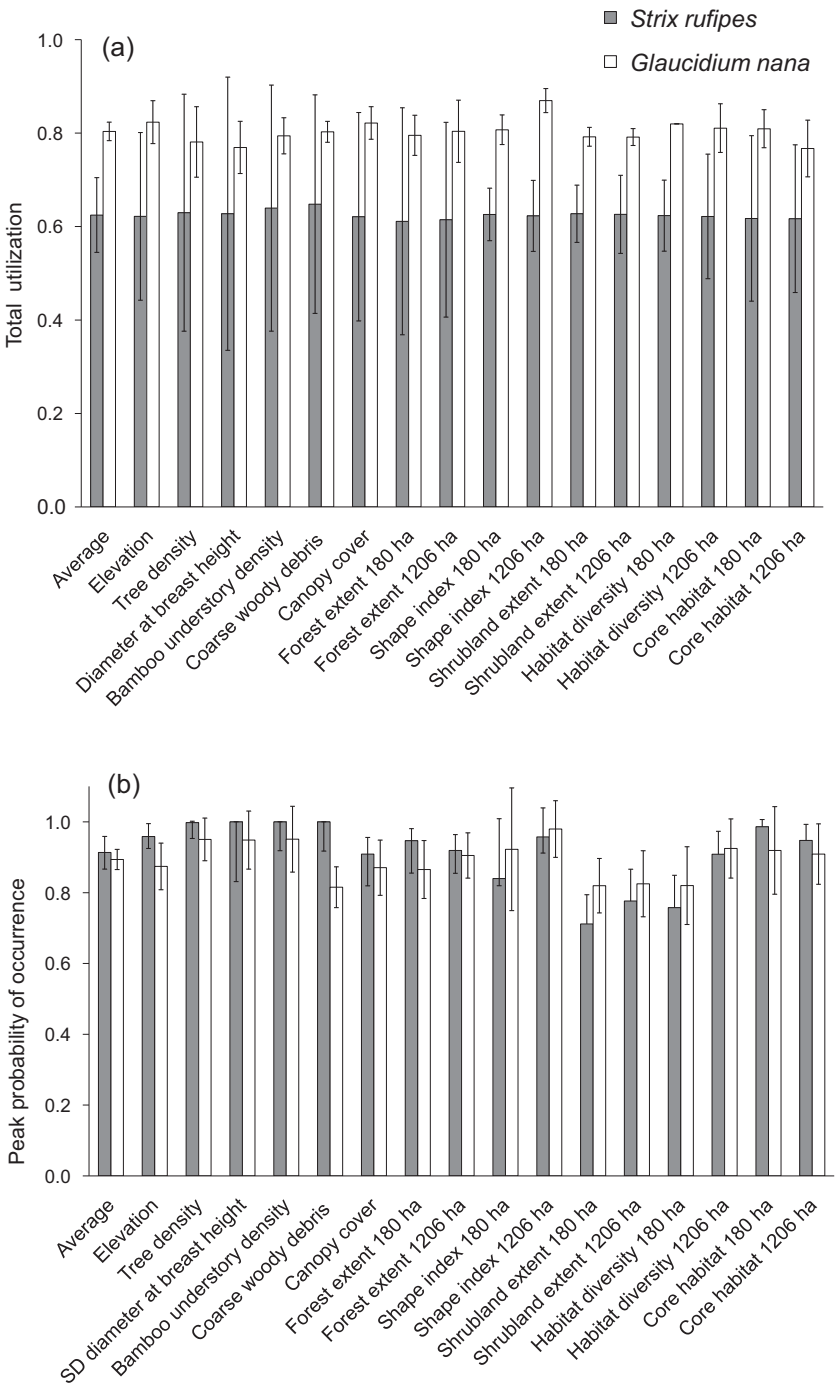

Fig. 4. (a) Total resource utilization (i.e. average area under the curve ± SE) and (b) predicted peak performance ± SE, for *Strix rufipes* (gray bars) and *Glaucidium nana* (white bars) in relation to habitat niche resources.

level forest complexity (sensu McElhinny et al., 2005) and forest stability at the landscape scale. For their part, *G. nana* had higher estimates of peak performance for resources related to human-induced forest degradation and landscape fragmentation. Because occurrence of habitat-specialists is associated with a subset of niche resources, these species usually have lower occurrence rates across the landscape as there are a smaller number of habitats in which they perform highly (Devictor et al., 2010; Peers et al., 2012). Our projected distribution of both owls goes in this direction as areas of high habitat suitability for the habitat-specialist owl were mostly associated with higher elevation forests close to the Andes Range and located inside or surrounding protected areas.

4.3. Recommendations for management

The worldwide decline of habitat-specialist species is a symptom of current global processes of "biotic homogenization" (Olden et al., 2004). In Chile, conservation practices to secure long term survival of the habitat-specialist *S. rufipes*, that extend beyond protected areas, are urgently needed for sites where forestry and agricultural activities take place (Ibarra et al., 2012; Martínez and Jaksic, 1996). Our results suggest that these owls may benefit if management actions are tailored at the stand-level, but that landscape context also needs to be considered.

Forest management that maintains multi-aged stands with a variety of tree sizes (SD of DBH = 19.9 ± 9 cm), including large

old-growth trees, with relatively high bamboo understory cover (34.2 ± 26.6%), will promote high occurrence of *S. rufipes*. Furthermore, landscapes that contain forest cover >63.5% would also promote occurrence by these habitat-specialists. These desired habitat attributes might be reached by either dispersed or aggregated retention of large and small trees (the latter for a continuous supply of large trees over forest generations), together with a dense bamboo understory maintained by gap release (Gustafsson et al., 2012). By incorporating these recommendations, forest and wildlife managers will be better able to meet the requirements of habitat-specialist owls and will likely provide for the generalist *G. nana* as well, and will also benefit other avian habitat-specialists of conservation concern in South American temperate forests (Díaz et al., 2005; Reid et al., 2004).

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