

Beyond species richness: an empirical test of top predators as surrogates for functional diversity and endemism

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Abstract. Using surrogate species to monitor the status of target biodiversity in areas undergoing exceptional habitat loss requires extending the traditional assessment of surrogates for taxonomic diversity to validating surrogates for functional diversity. This validation will be critical to inform about broader ecosystem processes and stability. We compared the surrogacy reliability of the habitat-specialist Rufouslegged Owl (Strix rufipes) and the habitat-generalist Austral Pygmy-Owl (Glaucidium nana), and we examined potential underlying mechanisms for surrogacy relationships in Andean temperate forests, a global biodiversity hotspot in southern Chile. During 2011-2013, we conducted 1,145 owl surveys, 505 vegetation surveys, and 505 avian point-transect surveys across 101 sites comprising a range of conditions from degraded forest habitat to structurally complex old-growth forest stands. The habitat-specialist S. rufipes was a reliable surrogate for all avian biodiversity measures, including avian endemism and functional diversity measures (degree of community specialization and density of large-tree users, understory users, and cavity-nesters). On the contrary, the habitat-generalist G. nana did not function as a surrogate. With increasing occurrence of S. rufipes, the density of target specialized biodiversity (species, guilds, and communities) increased nonlinearly and peaked at the least degraded sites. This specialist aggregation might be driven by stand structural complexity available in older, more stable, forests. These results suggest that management actions tailored to promote occurrence of habitat-specialist owls, such as the S. rufipes, may result in enhanced density of endemic species, specialized communities, and likely ecosystem stability.

Key words: Austral Pygmy-Owl; detectability; ecosystem stability; *Glaucidium nana*; indicators; South America; *Strix rufipes*; Rufous-legged Owl; temperate forests.

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INTRODUCTION

The global decline in biodiversity caused by anthropogenic habitat degradation and loss is expected to disrupt important ecological processes and stability in terrestrial ecosystems (Cardinale et al. 2006, Hooper et al. 2012). Direct measurements of the effects of anthropogenic disturbances on biological communities are often complicated, time-consuming, and expensive to assess; therefore, the use of biodiversity surrogates as a shortcut to assess ecological conditions by proxy has been implemented increasingly in both environmental science and biodiversity management (Lindenmayer and Likens 2011). For example, the Fish and Wildlife Service from the United States implemented policy for using biodiversity surrogates as a chief strategy to assess ecological conditions across their national network of Protected Areas (U.S. Fish and Wildlife Service 2012). The criteria for selecting and testing surrogates should be specified explicitly and the species chosen should meet as many of the criteria as possible (Caro 2010). Key criteria to be met by surrogates include that they are (1) sufficiently sensitive to offer a warning of habitat degradation and loss, (2) able to provide an estimate of the status of target biodiversity across wide environmental gradients, (3) easy and cost-effective to survey, (4) distributed over a broad geographical area, and (5) relevant to either ecologically or conservation important phenomena (Noss 1990, Caro 2010).

Studies assessing the impacts of forest degradation and loss often assume that these processes reduce taxonomic diversity or species richness, resulting in similar losses of ecosystem functioning and stability (Milder et al. 2008). This assumption, however, has not been validated either empirically or with theory (Schwartz et al. 2000). Conservation approaches based on functional diversity, as a complement to taxonomic diversity, include the value and range of functional traits (e.g., phenological, behavioral, physiological, or morphological) present in a community, and thus are able to link diversity with ecosystem stability and processes (Julliard et al. 2006, Díaz et al. 2007). For example, higher densities of habitat-specialist species in a community could engender higher complementarity in resource utilization, potentially increasing ecosystem productivity and indicating higher ecosystem stability (Julliard et al. 2006). Further, taxonomic diversity may not be spatially correlated to biodiversity hotspots where exceptional concentrations of endemic species coexist (Kerr 1997). Endemic species commonly have small populations and few areas assigned to conservation; thus, they are intrinsically vulnerable to extinction (Gaston 1998).

A suite of studies conducted in the northern hemisphere has shown that top predators are spatially correlated with high biodiversity and may thus act as reliable surrogates (Sergio et al. 2006, Burgas et al. 2014). Top predators represent the apex of food webs with effects that can cascade through the ecosystem, require large areas that cover populations of other less areademanding species, often select areas with high structural complexity, and if they are sensitive (respond negatively) to habitat disturbance may provide early indications of habitat degradation and loss (Sergio et al. 2008). However, few studies have attempted to elucidate the ecological mechanisms behind a spatial correlation between top predators and enhanced biodiversity (Lindenmayer and Likens 2011). Some forest structural attributes increase stand-level complexity (McElhinny et al. 2005), providing the necessary conditions for wildlife in general. Therefore, stand-level structural complexity may be the driver of a positive association between the surrogate candidate and target biodiversity (Drever et al. 2008, Lindenmayer et al. 2014a). Furthermore, it can expected that not all members of the top predator guild will be reliable surrogates because those that are habitatgeneralists may be able to adapt to degraded habitats (Ozaki et al. 2006, Rodríguez-Estrella et al. 2008). Studies identifying the potentially contrasting role of specialist and generalist predators as surrogates for functional diversity and endemism will contribute significantly to applied ecology (Martin et al. 2015).

The biodiversity hotspot Winter Rainfall-Valdivian Forest of South America is a globally exceptional ecoregion given its high concentration of endemic species. This ecoregion is also one of the most endangered on Earth for its high rates of anthropogenic habitat degradation and loss (Myers et al. 2000). Earlier, we assessed the detectability and occurrence rates for two owls across a gradient from degraded forest sites to zones comprising old-growth forests within protected areas in this ecoregion (Ibarra et al. 2014*a*, *b*).

Having thus set the stage in terms of detectability (Fig. 1a) and habitat occurrence (Fig. 1b), in this paper we (1) compare the surrogacy reliability of two forest owl species (a habitatspecialist and a habitat-generalist) for taxonomic diversity, endemism, and functional diversity (Fig. 1c), and (2) test whether and which surrogate candidate and target biodiversity



Fig. 1. Approach for testing a surrogacy relationship. Before testing for surrogacy reliability, (a) factors associated with the detectability (p) of two sympatric forest owls were identified (Ibarra et al. 2014a). After accounting for the estimated variation in detectability, (b) Ibarra et al. (2014b) assessed the occurrence rates (ψ) from the stand to the landscape-level for these owls. In this paper, (c) the predicted occurrence (ψ) for specialist and generalist owls were tested as predictors of avian taxonomic diversity, endemism, and functional diversity. We also examined (d) whether and which surrogate candidate and target biodiversity measures have similar habitat correlates (exploring underlying mechanisms that may drive surrogacy relationships) across forest conditions ranging from highly degraded to old growth stands in Andean temperate ecosystems.

measures have similar habitat correlates and responses to anthropogenic habitat degradation (exploring underlying mechanisms that may drive surrogacy relationships; Fig. 1b, d). We predict (1) the habitat-specialist owl will outperform the generalist as a surrogate for all target biodiversity measures and (2) forest stand-level complexity may be the underlying mechanism driving a positive surrogacy relationship. To test these predictions, our study design was set up to explicitly validate surrogacy relationships in a poorly studied biodiversity hotspot in southern South America.

Methods

Study area, model species, and field surveys

We conducted our study in an area of 2,585 km² in the Villarrica watershed, Andean zone of the La Araucanía Region (39°15′ S 71° W), Chile. Forests in the area range from 200 m to 1,500 m above sea level and are dominated by deciduous *Nothofagus* species at lower elevations and mixed deciduous species with the coniferous *Araucaria araucana* at higher elevations (Ibarra et al. 2012).

We evaluated the reliability as biodiversity surrogates of two forest owls: Rufous-legged Owls (*Srix rufipes*) and Austral Pygmy-Owls (*Glaucidium nana*). *Strix rufipes* are strictly nocturnal habitat-specialists that hunt and nest only within forests, whereas *G. nana* are nocturnal and diurnal habitat-generalists that can hunt and/or nest within forests and more open habitats (Ibarra et al. 2014*b*). These two owls are upper trophic level consumers and are free from predation themselves in temperate forests (Figueroa et al. 2014); thus, they were considered top predators (sensu Sergio et al. 2014). Both species occur extensively across South American temperate forests (35–55° S).

Owl and target biodiversity surveys

We located 101 sites at a minimum distance of 1.5 km apart, ranging from 221 to 1,361 m elevation. Using ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, California, USA), we identified all the headwaters of smaller basins that were accessible by rural roads or hiking trails within the Villarrica watershed. We randomly selected 13 of these 19 basins and placed the first site within all basins near the headwater (within 1 km of the tree line). We systematically established the remaining sampling units at every 1.5 km within drainages descending from the headwaters (Ibarra et al. 2014a). We defined the spatial scale of sites according to a 500-m detection radius, capturing the total area within which the detected owl may have occurred, based on the distance over which

we could have detected an owl using callbroadcast surveys (Ibarra et al. 2014a). We conducted owl call-broadcast surveys along rural roads and trails. Playbacks of calls of both species were played two times, in a different random sequence from the center of the site (Ibarra et al. 2014a). Each site was visited repeatedly from October to February for two breeding seasons (2011–2012 and 2012–2013), for a total of 1,145 surveys. In 2011–2012, we conducted 5.85 (range = 3-6) surveys per site. In 2012-2013, we conducted 5.83 (range = 3-6) surveys per site. Temporal, abiotic, and biotic factors that might affect calling rates were collected for each survey, and their influence on owl detectability are detailed in (Ibarra et al. 2014a).

To test the spatial correlation between owls and target biodiversity, we compared probability of occurrence of owl species with three measures of avian biodiversity (1) taxonomic diversity, (2) endemism, and (3) functional diversity. We chose birds because they are often used in biodiversity monitoring and are known to be affected, either taxonomically or functionally, by habitat degradation in temperate forests and elsewhere (Díaz et al. 2005, Flynn et al. 2009). To survey diurnal birds (target biodiversity), each of the 101 sites was surveyed once, from November to January, over the two seasons; 81 (80.2%) sites were surveyed in 2011-2012 and 20 (19.8%) were surveyed in 2012-2013. Based on species accumulation curves, five point-transect surveys per site are considered sufficient to provide a complete characterization of bird species assemblages in temperate forests (Jiménez 2000, Díaz et al. 2005). Therefore, we established five multispecies point-transect surveys systematically separated by 125 m from adjacent point-transects within each site, for a total of 505 point-transect surveys of 50 m radius. We recorded all species heard or seen for a period of 6 min per pointtransect survey. The distances to all birds detected were recorded and grouped into two distance intervals (0-25 and 26-50 m) for analysis. Surveys were conducted from dawn to 10:30. For each point-transect survey, we recorded date, time, temperature (°C), and wind speed (m/s) using a handheld weather monitor (Kestrel 4 200, Kestrel-meters, Birmingham, Michigan, USA). We assigned habitat type within 50 m of each point-transect to one of the following: old growth, mid-successional or early successional forest, mixed shrubland, exotic forestry plantation, or openfield.

Measures of avian functional diversity: habitat-specialization

We used both discrete and continuous measures of functional diversity (Petchey and Gaston 2006). We followed Díaz et al. (2005) to categorize each species into habitat-use guilds based on its primary use of temperate forest structure for nesting and/or feeding at the stand-level. These guilds were: large-tree users, understory users, vertical-profile generalists, and shrub users. Further, we followed Altamirano (2014) to classify species into cavity-nesting and noncavity-nesting species, as the former guild is known to be sensitive to logging (Drever et al. 2008). For continuous functional traits, we followed Julliard et al. (2006) to quantify the degree of habitat-specialization for a species (SSI) as the coefficient of variation (standard deviation/average) of its estimated densities across the six habitat types described previously.

Vegetation and habitat measures

Stand-level structural attributes in temperate forests of southern Chile have been degraded by large-scale farming and plantation forestry, negatively affecting species with the greatest need for large decaying trees, understory vegetation, and coarse woody debris (Reid et al. 2004, Díaz et al. 2005). We used previous studies conducted in southern temperate forests to choose habitat attributes (hereafter covariates) associated with stand-level complexity that could drive a spatial correlation between owls and avian diversity (Martínez and Jaksic 1996, Reid et al. 2004, Díaz et al. 2005, Ibarra et al. 2012). Around each point count-transect, we established a vegetation plot (22.4 m diameter) with the point count-transect located at the center of the plot (N = 505 plots; Table 1). 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).

As forest raptors commonly require different habitat patches for breeding and foraging, for owl analyses we added spatial covariates that were correlated with raptor occurrence in other studies (Finn et al. 2002, Henneman and Andersen 2009). We used corrected Landsat (2012-2013) scenes and quantified landscape metrics within two circular areas (180 ha and 1,206 ha) around each site using Fragstat 4.1 (McGarigal et al. 2002). These areas corresponded to the minimum (1.8 km²) and maximum (12.8 km²) home ranges reported for S. rufipes (Martínez 2005). No information exists on home range sizes for G. nana; therefore, we used the same areas considered appropriate for S. rufipes for evaluating habitat associations for G. nana, which allowed us to compare results between the two species. Landscape covariates included: forest extent, shrubland extent, core habitat, forest patch shape index, and relative habitat diversity (Ibarra et al. 2014*b*).

Modeling owl occurrence and bird density

The assumption of perfect detectability can result in misleading inferences about surrogacy relationships as the probability of detecting both top predators and target biodiversity depends on many factors, including wind speed, temperature, and date and time of survey (Ibarra et al. 2014*a*, Martin et al. 2015). Therefore, we used models that adjust for detectability of both surrogate candidates and target biodiversity measures, providing the basis for stronger inferences by removing the need to rely on assumptions of perfect detectability.

Presence/absence data for owls were analyzed using a multi-season occupancy framework (MacKenzie et al. 2003), and bird counts using distance sampling in a multinomial-Poisson mixture model framework (MPMM; Royle et al. 2004). We used the program R-Unmarked (Fiske and Chandler 2011), which uses maximum-likelihood methods to estimate probabilities of occurrence (ψ) and detection (p) for owls, and density (D) and detection (p) for other bird species.

To model ψ and *D*, we first assessed collinearity for reducing the number of covariates (Table 1). We did not use collinear (r > 0.7) covariates in the same model, retaining for analysis only those considered to be most biologically meaningful for most of our study species (Reid et al. 2004, Díaz et al. 2005, Ibarra et al. 2014*b*). In total, four stand-level covariates (SD of tree DBH, canopy cover, volume of coarse woody debris, and bamboo density) were used in the modeling of

Table 1. Stand-level covariates used to examine how the occurrence of owls and the density of all other birds responded to the same set of habitat structural components in Andean temperate forests (details in Ibarra et al. 2014*b*).

| Stand-level covariate | Description |
|--|--|
| Tree density (trees/ha) Standard deviation of tree diameter at breast height (DBH, cm)† Canopy cover (%)† Volume (m ³) of coarse woody debris volume (VCWD)† Banboo understory density (NC)† | density of all trees with DBH > 12.5 cm SD of tree DBH measures the variability in tree size and was considered indicative of stand-level forest complexity proportion of sky covered by canopy estimated from the center of the plot calculated based on the length and diameter of each piece with diameter > 7.5 cm crossing a transect of 22.4 m length density up to 3 m high, expressed as the number of contacts (NC), guantified at |
| Elevation (m a.s.l) | five points of a transect of 22.4 m length meters above sea level measured at the center of the plot |

† Covariates retained for tests of habitat associations after reducing collinearity.

 ψ and *D*. For owls, we included four covariates at the 180 ha landscape-level (forest extent, shrubland extent, forest-patch shape index, and relative habitat diversity) and one at the 1,206 ha landscape-level after reducing collinearity (forest-patch shape index; see Ibarra et al. 2014*b* for details).

For owls, all ψ models contained the topranked sources of variation in p previously identified for both species using the same dataset (Ibarra et al. 2014a). Details of the approach for modeling occurrence (ψ) for both owl species are provided in Ibarra et al. (2014b) and briefly described here. To obtain the best ψ model, we used a stepwise covariate selection procedure linked to R-Unmarked to create a candidate set of models based on model weights (w_i) and the precision of the estimated coefficients, using an information-theoretic approach (Akaike's information criterion [AIC]; Burnham and Anderson 2002). Models within 2 AIC units of the top model were considered as the competitive set of best-supported models (Burnham and Anderson 2002). We analyzed residuals to test for spatial autocorrelation using the Moran's index (Moran 1950). We followed Moore and Swihart (2005) to calculate an autocovariate (Aut) term for G. nana, as only this owl showed spatially correlated residuals. The inclusion of an Aut term resulted in six additional models for G. nana. In total, we evaluated 16 ψ models for *S. rufipes* and 26 models for G. nana (Ibarra et al. 2014b).

For all other birds (data collected by pointtransect surveys), we first used AIC to identify whether the half-normal or the hazard rate was the most suitable distance function for each species (Royle et al. 2004). The half-normal function always received stronger support and thus it was used in all further analyses. To estimate detectability (p), we used four covariates potentially associated with p (covariates affect the scale parameter of the detection function): date (number of days since start of surveys in October), time of survey (minutes since 5:00), wind speed (m/s), and temperature (°C). For each species, we used the stepwise covariate selection procedure described above (without parameterizing density, D) and then ranked each model by AIC to select top-ranked models for further modeling for density (D). To obtain the best models for *D* (covariates affect the Poisson mean), we followed the approach described for owls. We evaluated a range from 16 to 20 D models for each bird species. We averaged models with $\Delta AIC \leq 4$ in the final confidence set for owls and each other bird (Burnham and Anderson 2002). Averaged models were used to predict owl ψ for each site and *D* of all birds for each point-transect survey. Values of D for the five point-transect surveys conducted per site were averaged to obtain one density value per site for each species.

Testing owl surrogacy reliability

We used generalized linear models (GLMs) to relate the averaged ψ of habitat-specialist and generalist owls to avian diversity measures across sites. We also tested second order polynomial models as the association between surrogates and target biodiversity may follow curvilinear relationships (Lindenmayer et al. 2014*a*). We first explored bird richness as a response variable, without accounting for detectability, to examine whether the most commonly reported correlation between top predators and taxonomic diversity (Sergio et al. 2006, Jenkins et al. 2012, Burgas et al. 2014) was also observed in our system. We then related owl occurrence (ψ) to (1) *D* of endemic species, (2) *D* of avian habitat-use guilds, (3) *D* of cavity-nesting species, and (4) community specialization index (CSI) across sites, where CSI for a site *k* was

$$\mathrm{CSI}_k = \frac{\Sigma_1^N(\mathrm{SSI}_i \times D_i)}{\Sigma_1^N(D_i)}$$

with *N* as the total number of bird species in the analysis, SSI as the species specialization index for species *i*, and *D* as the estimated density of species *i* (Devictor et al. 2008). To assess the strength of evidence for each tested model, we calculated the value of AIC for small sample sizes (AIC_c) and model weight (w_i). The latter was used to compare pairs of models by calculating evidence ratios (Burnham and Anderson 2002). All bird data were $\log_{10} (x + 1)$ transformed before statistical analyses to improve normality and variance homogeneity. Species with too few observations to use multinomial-Poisson mixture models were excluded from the analysis.

Results

We recorded 292 detections of *S. rufipes* and 334 detections of *G. nana* over two years. Probabilities of occurrence (ψ ; mean \pm standard error) across sites ranged from 0.05 \pm 0.04 to 1.00 \pm 0.00 for *S. rufipes* and from 0.67 \pm 0.18 to 0.98 \pm 0.04 for *G. nana* (Ibarra et al. 2014*b*).

The density (*D*) of 21 species was estimated using a multinomial-Poisson mixture model (Table 2). Nine (42.9%) species inhabit areas restricted to the southern portion of South America and eight (38.1%) were endemic to South American temperate forests. Seven (33.3%) species were large-tree users, six (28.6%) vertical profile generalists, four (19%) understory users, and four (19%) shrub users. Eleven species (52.38%) were cavity-nesters.

Spatial relationships:

owls and target biodiversity

All biodiversity measures had stronger associations with the specialist owl *S. rufipes* than with the generalist owl *G. nana*. Models using modelaveraged occurrence (ψ) of *S. rufipes* as an independent variable for species richness, density (D) of endemic species, and measures of functional diversity had stronger support from the data than those using ψ of *G. nana*, according to AIC_c values and model weights (w_i ; Table 3, Fig. 2). For overall species richness, the evidence ratio for the linear model S. rufipes relative to a nonlinear model was 2.93, indicating these two models had similar support, such that model fit did not improve with the addition of a second degree quadratic function of S. rufipes occurrence (ψ ; Table 3). Similarly, for the density (*D*) of shrub users we found that the evidence ratio for the nonlinear model S. $rufipes + S. rufipes^2$ relative to a linear model was 1.95, indicating these two models had similar support. The relationship between D of shrub users and occurrence of S. rufipes was negative. There was strong evidence of nonlinearity (second degree quadratic function) for the correlation between occurrence (ψ) of *S. rufipes* and the *D* of (1) endemic species, (2) cavity-nesting species, (3) large-tree users, (4) understory users, and (5) the community specialization index (Table 3). For all these response variables, we found peak values when ψ of *S*. rufipes approximated 1 (Fig. 2). For easier interpretation, we calculated the estimated values of target avian biodiversity that spatially cooccurred with predicted low (0-0.33), moderate (0.34-0.66), and high (0.67-1) occurrence (ψ) of *S*. rufipes in Andean forests based on model averaged predictions (Table 4).

Ecological mechanisms:

habitat correlates for owls and target biodiversity

Details on results for habitat relationships for both owl species are provided in Ibarra et al. (2014b) and briefly described here. Strix rufipes responded more strongly to stand-level whereas G. nana to landscape-level covariates. Model selection results indicated that occurrence (ψ) for S. rufipes responded positively to both the variability (SD) in the DBH distribution of trees (logit-scale estimates: intercept [SE] = -3.29[0.93], beta coefficient = 2.59 [1.12]) and bamboo understory density (beta coefficient = 0.98 [0.49]; Ibarra et al. 2014b). Landscape-level habitat data did not improve our ability to predict S. rufipes occurrence in Andean temperate forests as the estimated beta coefficients were imprecise (i.e., 95% CI overlapped zero). For G. nana, the spatial Table 2. Avian species with their geographical and ecological attributes, and stand-level covariates associated with the density (D) of bird species in Andean temperate forests, according to model selection statistics based on Akaike's information criterion (AIC).

| | | | | | Forest stand-structural components | | | |
|---|-----------------------------|-----------------------|----------------------------|------|---|---------------------|--------------------------------------|----------------------------|
| Name | Geographic distribution† | Habitat-use guild‡ | Cavity-nesting species§ | SSI | Volume of coarse woody debris (m ³) | Canopy cover (%) | Bamboo understory density (NC) | SD of DBH of trees (cm) |
| Chilean pigeon | SSA | VPG | Ν | 0.12 | | | | |
| Austral parakeet (Enicognathus ferrugineus) | E | LTU | Y | 2.68 | | | | +0.07 [0.03] |
| Green-backed firecrown(Sephanoides | SSA | VPG | Ν | 0.23 | -0.21 [0.11] | -0.12 [0.03] | | |
| Striped woodpecker(Veniliornis | SSA | LTU | Y | 1.21 | | -0.64 [0.15] | | +0.07 [0.02] |
| Chilean flicker (<i>Colaptes</i> | SSA | LTU | Y | 0.37 | | -0.21 [0.08] | | |
| Magellanic woodpecker (<i>Campephilus</i> magellanicus) | E | LTU | Y | 1.96 | | -1.51 [0.35] | | +0.19 [0.09] |
| Thorn-tailed rayadito | Е | LTU | Y | 0.41 | | -0.23 [0.02] | | |
| Des Murs's wire-tail (Sylviorthorhynchus desmursii) | E | UU | Ν | 0.72 | +0.63 [0.31] | | | +0.04 [0.01] |
| White-throated treerunner (<i>Pygarrhichas</i> alboqularic) | Е | LTU | Y | 0.38 | | -0.22 [0.04] | | |
| Black-throated huet-huet | Е | UU | Y | 0.96 | | -0.44 [0.06] | + 0.13 [0.04] | + 0.04 [0.01] |
| (Pteroptocnos tarnii) Chucao tapaculo (Scelorchilus rubecola) | Е | UU | Y | 0.78 | | -0.44 [0.04] | + 0.05 [0.01] | +0.02 [0.01] |
| Magellanic tapaculo (Scytalopus | SSA | UU | Y | 0.57 | | -0.25 [0.05] | | +0.03 [0.01] |
| White-crested elaenia (Elaenia albicens) | SA | VPG | Ν | 0.16 | -0.25 [0.07] | -0.06 [0.01] | | |
| Tufted tit-tyrant (Anairetes parulus) | SA | SU | Ν | 0.32 | | $+0.11 \ [0.04]$ | | |
| Fire-eyed diucon (<i>Xolmis</i> pyrope) | SSA | SU | Ν | 0.11 | | | | |
| Chilean swallow (Tachycineta meyeni) | SA | LTU | Y | 0.23 | | -0.07 [0.03] | | +0.02 [0.01] |
| Southern house wren (Troglodytes aedon) | PA | SU | Y | 0.24 | | +0.12 [0.03] | | |
| Austral thrush (<i>Turdus</i> falcklandii) | SSA | VPG | Ν | 0.03 | | | | |
| Patagonian sierra-finch (<i>Phrugilus natagonicus</i>) | Е | VPG | Ν | 0.60 | | -0.34 [0.05] | | |
| Austral black bird | SSA | VPG | Ν | 0.25 | | +0.09 [0.04] | | +0.02 [0.01] |
| Black-chinned siskin (Sporagra barbata) | SSA | SU | Ν | 0.09 | | | +0.06 [0.03] | |

Notes: Parameter estimates [SE] for covariates present in the top model set with Δ AIC values < 2 and with estimates of their 95% confidence intervals that do not overlap 0 are shown. The + and - indicate the direction of the relation. SSI is species specialization index, and DBH is diameter at breast height.

† Geographic distribution abbreviations are E, endemic; SSA, southern South America; SA, wide spread South America; and PA, Pan America (Vuilleumier 1985).

‡ Habitat-use guild abbreviations are SU, shrub user; VPG, vertical profile generalist; LTU, large tree user; and UU, understory user (Díaz et al. 2005).

§ Cavity-nesting species abbreviations are Y, yes; N, no. Y considered species relying on tree cavities for more than 10% of their nests (Altamirano 2014).

| Model specification | K† | AIC _c | ΔAIC_c ‡ | w _i § | $-2 \times LL\P$ | ER# |
|--|----|------------------|------------------|------------------|------------------|----------|
| Species richness | | | | | | |
| Strix rufipes | 3 | -50.10 | 0.00 | 0.75 | -56.35 | 2.93 |
| Strix rufipes + Strix rufipes ² | 4 | -47.95 | 2.15 | 0.25 | -56.36 | |
| Glaucidium nana | 3 | -11.49 | 38.61 | 0.00 | -17.74 | |
| Glaucidium nana + Glaucidium nana ² | 4 | -9.32 | 40.77 | 0.00 | -17.74 | |
| NULL | 2 | 7.91 | 58.01 | 0.00 | 3.79 | |
| Density of endemic species | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -7.15 | 0.00 | 1.00 | -15.57 | 518.14 |
| Strix rufipes | 3 | 5.35 | 12.50 | 0.00 | -0.90 | |
| Glaucidium nana | 3 | 55.55 | 62.70 | 0.00 | 49.31 | |
| Glaucidium nana + Glaucidium nana ² | 4 | 57.20 | 64.35 | 0.00 | 48.78 | |
| NULL | 2 | 126.92 | 134.07 | 0.00 | 122.80 | |
| Density of cavity-nesting species | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -104.24 | 0.00 | 1.00 | -112.66 | 3610.36 |
| Strix rufipes | 3 | -87.86 | 16.38 | 0.00 | -94.11 | |
| Glaucidium nana | 3 | -40.82 | 63.43 | 0.00 | -47.06 | |
| Glaucidium nana + Glaucidium nana ² | 4 | -38.71 | 65.54 | 0.00 | -47.12 | |
| NULL | 2 | 31.23 | 135.47 | 0.00 | 27.10 | |
| Density of large-tree users | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -110.07 | 0.00 | 0.99 | -118.48 | 95.99 |
| Strix rufipes | 3 | -100.94 | 9.13 | 0.01 | -107.18 | |
| Glaucidium nana | 3 | -50.10 | 59.96 | 0.00 | -56.35 | |
| Glaucidium nana + Glaucidium nana ² | 4 | -48.57 | 61.49 | 0.00 | -56.99 | |
| NULL | 2 | 20.66 | 130.73 | 0.00 | 16.54 | |
| Density of understory users | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -20.65 | 0.00 | 1.00 | -29.06 | 1618.26 |
| Strix rufipes | 3 | -5.87 | 14.78 | 0.00 | -12.12 | |
| Glaucidium nana | 3 | 46.72 | 67.37 | 0.00 | 40.48 | |
| Glaucidium nana + Glaucidium nana ² | 4 | 48.51 | 69.15 | 0.00 | 40.09 | |
| NULL | 2 | 118.57 | 139.21 | 0.00 | 114.44 | |
| Density of vertical profile generalists | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -263.98 | 0.00 | 0.94 | -272.40 | 14.47 |
| Strix rufipes | 3 | -258.64 | 5.34 | 0.06 | -264.89 | |
| Glaucidium nana | 3 | -230.58 | 33.40 | 0.00 | -236.83 | |
| Glaucidium nana + Glaucidium nana ² | 4 | -228.58 | 35.40 | 0.00 | -237.00 | |
| NULL | 2 | -196.34 | 67.64 | 0.00 | -200.46 | |
| Density of shrub users | | | | | | |
| Strix rufipes + Strix rufipes ² | 4 | -337.99 | 0.00 | 0.66 | -346.41 | 1.95 |
| Strix rufipes | 3 | -336.66 | 1.33 | 0.34 | -342.91 | |
| Glaucidium nana + $Glaucidium$ nana ² | 4 | -312.78 | 25.21 | 0.00 | -321.20 | |
| Glaucidium nana | 3 | -300.79 | 37.21 | 0.00 | -307.03 | |
| NULL | 2 | -284.82 | 53.17 | 0.00 | -288.94 | |
| Community specialization index (CSI) | | | | | | |
| Strix rufives + Strix rufives ² | 4 | -263.76 | 0 | 1.00 | -272.18 | 82941.05 |
| Strix rufives | 3 | -241.11 | 22.65 | 0.00 | -247.36 | |
| Glaucidium nana | 3 | -211.39 | 52.37 | 0.00 | -217.64 | |
| Glaucidium nana + $Glaucidium$ nana ² | 4 | -209.71 | 54.05 | 0.00 | -218.12 | |
| NULL | 2 | -141.79 | 121.97 | 0.00 | -145.92 | |
| | - | | | | | |

Table 3. Ranking of models relating measures of avian diversity and owl probabilities of occurrence (ψ) in Andean temperate forests.

† Number of parameters estimated.

 $\ddagger \Delta AIC_c$ is the difference in AIC_c values between each model and the lowest AIC_c model.

§ AIC_c model weight. ¶ $-2 \times log-likelihood.$

Evidence ratio among two best models.

auto-covariate (Aut) term (beta coefficient [SE] = 1.84 [1.04]) controlled for intra-landscape data dependence as it improved the AIC weight of best models (0.09 and 0.07 units higher than models without the Aut term). The best models for *G. nana* indicated that ψ responded positively to both forest shape index at 1206 ha (intercept

[SE] = -1.09 [2.22], beta coefficient = 0.72 [1.61]) and forest cover extent at 180 ha (beta coefficient = 0.16 [1.43]) and negatively to shrubland cover at 180 ha (intercept [SE] = -0.02 [1.47], beta coefficient = -0.57 [2.67]). However, none of beta coefficients for any covariates were informative for G. nana ψ , as they all overlapped zero (see



Fig. 2. Relationship between probabilities of occurrence (ψ) of habitat-specialist owls *Strix rufipes* and (1) species richness/site, (2) density (individuals/ha × site), and (3) community specialization index/site in Andean temperate forests.

Ibarra et al. 2014*b* for details).

Model selection results for all other birds indicated that canopy cover, followed by the variability (SD) in the DBH of trees were the most frequent covariates associated with density of birds, with 12 species responding negatively and three positively to canopy cover. Nine species responded positively to SD in DBH of trees, three species responded positively to bamboo density, and two species responded negatively and one responded positively to volume of coarse woody debris (Table 2).

Discussion

Evidence for a reliable surrogacy relationship

We found that owls were reliable predictors of local avian endemism, species richness, and functional biodiversity in South American temperate forests, consistent with the hypothesis that avian top predators act as biodiversity surrogates at the forest stand-level (Sergio et al. 2006, Burgas

| Т | able 4. Estimated mean [SE] for (1) species richness/site, (2) density (individuals/ha \times site) of different diversity |
|---|--|
| | measures, and (3) community specialization index/site, associated with low (0-0.33), moderate (0.34-0.66), |
| | and high (0.67–1) probabilities of occurrence (ψ) for <i>Strix rufipes</i> in Andean temperate forests, based on model- |
| | averaged predictions. |

| | | | Community | | | | | |
|----------------------|---------------------|----------------|-----------------|---------------------|---------------------|------------------------------|----------------|-------------------------|
| Predicted ψ | Species richness | Endemics | Cavity nesters | Large-tree users | Understory users | Vertical profile generalists | Shrub users | specialization index |
| Low (0–0.33) | 4.77 [1.16] | 3.04 [0.81] | 10.30 | 6.48 [0.91] | 1.95 [0.53] | 15.93 [1.24] | 7.46 [0.45] | 0.38 |
| Moderate (0.34-0.66) | 5.49 | 4.08 | 11.89 | 7.64 | 2.66 | 17.00 | 7.01 | 0.44 |
| High (0.67–1) | 7.12 [1.57] | 8.06 [3.29] | 17.46 [4.27] | 10.96 [2.41] | 5.42 [2.23] | 19.66 [2.18] | 6.15 [0.57] | 0.67 [0.19] |

et al. 2014). However, our empirical assessment stresses that the degree of habitat-specialization of top predators will likely affect their reliability as biodiversity surrogates.

This is the first study on terrestrial vertebrates that has accounted for detectability of both potential surrogates and target biodiversity. Our results indicate that habitat-specialist S. rufipes always had a stronger relationship with target biodiversity than did the habitat-generalist G. nana. The broad range of predicted occurrence probabilities (ψ) across our sites for specialist owls suggests that they may act as reliable surrogates across a wide range of sites in temperate forests: from highly degraded habitat to structurally complex old-growth forests, with low and high values for both owl occurrence (ψ) and avian diversity, respectively. In contrast, the relatively high occurrence for generalist owls across all sites makes them less reliable surrogates. This result for the generalist owl is similar with patterns suggested by Ozaki et al. (2006) for Accipiter gentilis, who found that this raptor was not an efficient biodiversity surrogate because it often used anthropogenically degraded habitat that were poor in taxonomic diversity. The latter study, however, did not account for the detectability of both the surrogate candidate and target biodiversity, and it did not test for other dimensions of target biodiversity such as endemism or functional diversity.

Our findings suggest that the habitat-specialist *S. rufipes* could be used as a surrogate for avian endemism. Biodiversity in South American temperate forests evolved in isolation from other similar forests within the continent since at least the late Tertiary (Vuilleumier 1985). This isolation

explains the particularly high rates of endemism (e.g., 41% for forest bird species; Vuilleumier 1985). Our analysis included a high proportion (38.1%) of endemics, all of which have been reported as habitat-specialists in previous studies (Díaz et al. 2005).

The use of functional diversity rests on the assumption that the density of functional traits will provide insight into ecosystem stability and processes beyond that given by taxonomic diversity (Petchey and Gaston 2006, Devictor et al. 2010). Focusing on a diversity of functional traits rather than on species richness facilitates the synthesis between community ecology and ecosystem ecology (e.g., monitoring from functional traits through niche relationships to communities can generate links to an ecosystem-based view) and allows applied ecologists to make predictive statements of community assembly that may help policy makers make informed conservation decisions (McGill et al. 2006). We chose discrete and continuous habitatspecialization traits for all target avian species, which can inform us about niche relationships and ecosystem stability (Julliard et al. 2006). For example, in a niche context species fall on different places along a specialist-generalist continuum, with specialists being favored under relatively stable conditions and generalists under unstable conditions and degraded habitats (Devictor et al. 2010). We found that measures of avian functional diversity that were associated with habitat-specialization increased nonlinearly and peaked at sites with highest occurrence of habitat-specialist owls. Julliard et al. (2006) also found that specialist species tend to disproportionately aggregate at sites that are expected to be more stable. Our results suggest that such a pattern of specialist aggregation might be driven by high stand structural complexity in temperate forests.

Untangling ecological mechanisms

Understanding the mechanisms underlying surrogacy relationships is a key component for improving the use of the surrogate species in conservation efforts (Lindenmayer and Likens 2011). In Andean temperate forests, relatively low densities of canopy cover, high variability (SD) in tree diameter at breast height (DBH), and relatively high density of bamboo understory may drive a positive correlation between owls and avian taxonomic and functional diversity. When compared to early and mid-successional forests, structurally complex older forests tend to have less dense canopy cover due to a mosaic of canopy gaps produced by tree-falls in midelevations (500-900 m altitude) and naturally open canopies (54-81% canopy cover) and a lack of shade-tolerant trees in high-elevations (>900 m altitude; Veblen et al. 1980, Ibarra et al. 2012). Complex Andean forest-stands are also characterized by their variability (SD) in DBH (i.e., multi-aged forest stands), with relatively high frequency of large old-living and dead trees, combined with dense clumps of bamboo understory in mid-elevations and a homogeneously distributed bamboo in high-elevation stands (Veblen et al. 1980).

Stand structural complexity in Andean temperate forests relates to the habitat requirements of both the surrogate owl and target biodiversity species. For example, nesting S. rufipes occupy cavities available in large trees (mean DBH = 122.8 \pm 36.2 cm) that are >100 years old (Beaudoin and Ojeda 2011). Similarly, species in the large tree-user guild of birds also rely on large trees for both nesting and foraging (Díaz et al. 2005). Cavity-excavating species Colaptes pitius, Campephilus magellanicus, Veniliornis lignarius, and Pygarrhichas albogularis feed disproportionately more on larger and more decayed trees than on healthy trees with smaller diameters (Ojeda et al. 2007, Altamirano 2014). These four excavators produce cavities that are subsequently used by several secondary cavity nesters, including owls, parakeets, swallows, rayaditos, ducks, and small mammals (Altamirano 2014). Therefore, the validated-surrogate *S. rufipes* and cavityexcavator species rely on old-living and dead trees, and the latter group of birds positively influences the richness of other forest vertebrates (Drever et al. 2008).

As detailed by Ibarra et al. (2014b), S. rufipes are more likely to occur in forest stands with a relatively dense bamboo understory (Martínez and Jaksic 1996, Ibarra et al. 2012, 2014b). Native bamboo provides habitat for arboreal and scansorial rodents and marsupials, which constitute the main prey of S. rufipes in temperate forests (Figueroa et al. 2006). Bamboo understory has also been identified as providing critical protective cover and feeding habitat for ground-gleaner birds such as Pteroptochos tarnii and Scelorchilus *rubecula*, and leaf-gleaners *Scytalopus magellanicus* and Sylviorthorhynchus desmursii; all species with poor flying abilities (Reid et al. 2004). In our study, bamboo understory was a good predictor of the density of P. tarnii and S. rubecula. Further, the four understory specialists responded positively to the variability (SD) in DBH. Because P. tarnii, S. rubecula, and S. magellanicus nest in cavities available in trees with DBH ranging from 61.3 to 193.8 cm (Altamirano 2014), our results suggest that understory users, as well as S. rufipes, require stands that combine a relatively dense bamboo understory with large old-living trees and snags (Ibarra et al. 2014b). Thus, the cooccurrence of these species likely results from similar habitat requirements.

Meeting the requirements of habitat-specialists is expected to also provide for the needs of habitat-generalist species, unless the validated surrogate species is so highly specialized it has a very narrow niche (Martin et al. 2015). This may be the case in our study system as the habitatspecialist owl was positively associated with species included in the vertical-profile generalist guild. These species use the entire vertical profile of forests for most of their activities including the canopy, sub-canopy, and understory vegetation (Díaz et al. 2005). Interestingly, we found a negative spatial correlation between forest-specialist owls and species included in the shrub user guild, which comprises species that exploit degraded areas but occasionally use forests; therefore, S. rufipes potentially can be considered as an anti-surrogate (sensu Lindenmayer et al. 2014b) for species using degraded or open stands

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in temperate forests.

Life history and breeding ecology of forest owls have been poorly studied in south-temperate systems (Figueroa et al. 2014). Owl individuals of different ages or different breeding status (e.g., breeding pair in a reproductive site vs. juveniles getting established in new territories) may not have the same surrogacy value. Therefore, we suggest that future studies of surrogacy relationships may consider assessing potential intra-specific differences in surrogacy reliability (Burgas et al. 2014).

Application for conservation

Worldwide, the current loss of ecological specialists is considered one the most important forms of biotic impoverishment (Olden et al. 2004). Our empirical study suggests that the habitat-specialist S. rufipes fulfills the "a priori defined criteria" to be used as a biodiversity surrogate in temperate forests (see Introduction; Caro 2010): (1) Strix rufipes is sensitive to heavy land-use practices that reduce the availability of large old-living and dead trees and that remove or burn the understory vegetation, as are several other avian species inhabiting temperate forests (Díaz et al. 2005, Ibarra et al. 2012); (2) the wide range of predicted occurrence rates for S. rufipes make them reliable surrogates across a range of habitat conditions as they can tolerate some habitat disturbance; (3) conducting repeated nocturnal surveys of owls can readily and costeffectively be done in temperate forests (S. rufipes has relatively high detection probabilities and recommendations to improve survey protocols are available in Ibarra et al. 2014a), and repeated surveys may also be established as a volunteerbased roadside survey program; (4) S. rufipes occurs extensively across South American temperate forests from sea level to near the tree line (0–1500 m of elevation; Ibarra et al. 2014b); these broad latitudinal and elevation ranges are shared by >75% of avian species inhabiting southern temperate forests (Vuilleumier 1985) and, therefore, this surrogacy relationship may hold across the South American temperate forest distribution; and (5) management actions tailored to promote occurrence rates of S. rufipes may be linked to enhanced density of endemic species, specialized communities and, likely, ecosystem stability.

The maintenance of multi-aged stands with a variety of tree sizes (SD of DBH = 19.9 ± 9 cm or mean DBH = 37.6 ± 12.5 cm), including large old-growth trees, with relatively high bamboo understory cover (34.2 \pm 26.6%), will promote high occurrence of S. rufipes (Ibarra et al. 2014b). These habitat attributes will likely benefit other avian habitat-specialists of conservation concern in South American temperate forests (Reid et al. 2004, Díaz et al. 2005). Therefore, our surrogatevalidated study can enable wildlife and forest managers to use S. rufipes to more reliably monitor avian diversity patterns and functions, and to address the challenge of determining the impacts of habitat degradation on biodiversity in temperate forests.

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