

Predictive modeling for allopatric *Strix* (Strigiformes: Strigidae) owls in South America: determinants of their distributions and ecological niche-based processes

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ABSTRACT. *Strix* (Strigidae) is a worldwide genus of 17 owl species typical of forested habitats, including Rusty-barred Owls (*S. hylophila*), Chaco Owls (*S. chacoensis*), and Rufous-legged Owls (*S. rufipes*) in South America. These species are distributed allopatrically, but the ecological traits that determine their distributions remain largely unknown and their phylogenetic relationships are unclear. We used species distribution models (SDMs) to identify variables explaining their distribution patterns and test hypotheses about ecological divergence and conservatism based on niche overlap analysis. For Rusty-barred Owls and Chaco Owls, climatic factors related to temperature played a major role, whereas a rainfall variable was more important for Rufous-legged Owls. When niche overlaps were compared, accounting for regional similarities in the habitat available to each species, an ecological niche divergence process was supported for Chaco Owl-Rusty-barred Owl and Chaco Owl-Rufous-legged Owl, whereas a niche conservatism process was supported for Rusty-barred Owl-Rufous-legged Owl. Different ecological requirements support current species delimitation, but they are in disagreement with the two main hypotheses currently envisaged about their phylogenetic relationships (Chaco Owls as the sister taxa of either Rufous-legged Owls or Rusty-barred Owls) and support a new phylogenetic hypothesis (Rufous-legged Owls as sister taxa of Rusty-barred Owls). Our findings suggest that speciation of Rusty-barred Owls and Rufous-legged Owls was a vicariant event resulting from Atlantic marine transgressions in southern South America in the Miocene, but their niche was conserved because habitat changed little in their respective ranges. In contrast, Chaco Owls diverged ecologically from the other two species as a result of their adaptations to the habitat they currently occupy. Ecological and historical approaches in biogeography can be embedded to explain distribution patterns, and results provided by SDMs can be used to infer historical and ecological processes in an integrative way.

RESUMEN. **Modelos predictivos para lechuzas alopatricas del género *Strix* (Strigiformes: Strigidae) en América del Sur: determinantes de sus distribuciones y procesos basados en el nicho ecológico**

Strix (Strigidae) es un género mundial de 17 especies de lechuzas típicas de hábitats boscosos, incluyendo *S. hylophila*, *S. chacoensis* y *S. rufipes* en América del Sur. Estas especies se distribuyen de forma alopatrica, pero las condiciones ambientales que determinan sus distribuciones permanecen en gran parte desconocidas y sus relaciones filogenéticas no están claras. Utilizamos modelos de distribución de especies (MDEs) para identificar variables que expliquen sus patrones de distribución y poner a prueba hipótesis sobre la divergencia ecológica y el conservatismo basado en análisis de superposición de nichos. Para *S. hylophila* y *S. chacoensis*, los factores climáticos relacionados con la temperatura desempeñaron un papel importante, mientras que una variable relacionada con las precipitaciones fue la más importante para *S. rufipes*. Cuando se compararon los solapamientos de nichos teniendo en cuenta las similitudes regionales en el hábitat disponible para cada especie, se apoyó un proceso de divergencia de nicho ecológico para *S. chacoensis* y *S. rufipes*, mientras que un proceso conservador de nicho fue apoyado *S. chacoensis* and *S. hylophila* y para *S. hylophila* y *S. rufipes*. Los requerimientos ecológicos identificados apoyan la delimitación actual de las especies, pero están en desacuerdo con las dos principales hipótesis actualmente consideradas acerca de sus relaciones filogenéticas (*S. chacoensis* como especie hermana de *S. rufipes* o de *S. hylophila*) y apoyan una nueva hipótesis filogenética de *S. rufipes* como especie hermana de *S. hylophila*. Nuestros resultados sugieren que la especiación de *S. hylophila* y *S. rufipes* fue un evento de vicarianza que resultó de las transgresiones marinas del atlántico en el Sur de Sudamérica durante el Mioceno, pero su nicho se conservó porque el hábitat cambió poco en sus rangos correspondientes. Por el contrario, *S. chacoensis* divergió ecológicamente de las otras dos especies como resultado de sus adaptaciones al hábitat que

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ocupa en la actualidad. Los enfoques ecológicos e históricos en la biogeografía pueden complementarse para explicar los patrones de distribución de los organismos, y los resultados proporcionados por los MDE pueden ser utilizados para inferir procesos históricos y ecológicos de una manera integrada.

Key words: MaxEnt, niche overlap, species distribution models, *Strix chacoensis*, *Strix hylophila*, *Strix rufipes*

The distribution and environmental requirements of a species are central issues in biogeography, ecology, and evolution (Godown and Peterson 2000, Anderson et al. 2002, Wiens and Graham 2005). The development of geographic information systems, availability of species databases, and powerful statistical techniques have facilitated the description of species environmental requirements and the prediction of their spatial patterns (Guisan and Zimmermann 2000, Peterson 2001, Soberón 2007). Species distribution models (SDMs) are an example of empirical models that relate field observations to environmental predictors (Guisan and Zimmermann 2000). The most common applications of SDMs include quantifying environmental niches of species and predicting their spatial distributions, assessing the impact of global environmental change on species distributions, predicting suitable areas for rare or endangered species, and supporting appropriate conservation planning (Guisan and Thuiller 2005).

Strix (Strigidae) is a worldwide genus of 17 owl species that occupy diverse forested habitats (Clements et al. 2015, Enríquez et al. 2015). As with other owls in the Neotropics, this group remains understudied (Bodrati and Trejo 2015, Motta-Junior et al. 2015) due to their nocturnal and elusive habits, cryptic nature, and low densities (Marks et al. 1999, Enríquez 2015). In South America, the genus *Strix* is represented by only three closely related species with disjunct distributions (Marks et al. 1999, Clements et al. 2015, Remsen et al. 2015), including Rusty-barred Owls (*S. hylophila*), Chaco Owls (*S. chacoensis*), and Rufous-legged Owls (*S. rufipes*). The distributions, habitat use, population sizes, breeding biology, and diets of these owls remain poorly understood (Trejo et al. 2006, 2012). In addition, their phylogenetic relationships remain unclear. Most authors consider these three owls to be sister species forming a monophyletic group (Marks et al. 1999, Clements et al. 2015, Enríquez 2015, Remsen et al. 2015), but neither morphological nor molecular phylogenies have solved this

issue (e.g., Sibley and Ahlquist 1990, Marks et al. 1999). In this sense, SDMs could shed light on taxonomic affinities based on niche-based processes (i.e., niche divergence or conservatism) (Sites and Marshall 2003, Wiens and Graham 2005, Rissler and Apodaca 2007). Their apparently close phylogenetic relationship suggests that these species would share similar niches, representing a convenient study system to test the hypothesis of ecological conservatism (Peterson et al. 1999, Wiens and Graham 2005, Anderson and Raza 2010). Our objectives, therefore, were to (1) predict the distributions of Rusty-barred, Chaco, and Rufous-legged owls using SDMs, (2) identify environmental variables that explain their current distributions, and (3) compare their niche overlaps under the null hypothesis of niche conservatism to add ecological attributes to their species delimitation and the ongoing discussion of the evolutionary affinities of these species.

METHODS

Study species. Rusty-barred Owls are endemic to the Southern Atlantic forest, present mainly in southern Brazil, but also in southeastern Paraguay and northeastern Argentina (Marks et al. 1999, Bodrati and Trejo 2015, Motta-Junior et al. 2015). They are found in montane and tropical lowland evergreen forests with dense understory as well as in temperate forests (Marks et al. 1999). The global conservation status of Rusty-barred Owls is near threatened, with a moderately rapid and on-going decline suspected due to habitat loss (BirdLife International 2015).

Chaco Owls are endemic to the Chaco region dry woodlands in southern Bolivia, western Paraguay, and north-central Argentina, including the Pantanal of Paraguay and Mato Grosso and the xeric scrublands from the Argentinean Monte desert (Marks et al. 1999, Bodrati and Trejo 2015, Méndez 2015). They are relatively common in both pristine forests and disturbed habitats of the Chaco region (Bodrati and Trejo 2015), and are considered a more generalist species than

either Rusty-barred or Rufous-legged owls (Trejo and Bó 2015). According to Birdlife International (2015), their global conservation status is one of least concern and the population is thought to be stable. Nevertheless, accelerated deforestation and forest fragmentation resulting from agriculture expansion in the Chaco region represent a regional conservation concern (Gasparri and Grau 2009, Bodrati and Trejo 2015, Méndez 2015).

Rufous-legged Owls are endemic to sclerophyllous forests of central Chile and southern temperate forests in Chilean and Argentinean Patagonia (Marks et al. 1999, Trejo et al. 2006). They are found in rainforest, mesophytic forest, parkland, openings in forests, and the forest/steppe ecotone, but prefer old-growth forests with high canopy cover and dense understory (Marks et al. 1999, Trejo et al. 2006, Figueroa et al. 2015, Girini et al. 2016). Their global conservation status is least concern, but the population is thought to be declining due to habitat loss (Birdlife International 2015).

Occurrence data. To fit SDMs, we obtained georeferenced occurrence points from field observations (for Rufous-legged and Chaco owls), museum specimens, literature records, and three online databases, including the Global Biodiversity Information Facility (2007), Administración de Parques Nacionales – Sistema de Información de Biodiversidad (www.sib.gov.ar) (2011), and eBird (2015). Data were checked in the DIVA-GIS software (Hijmans et al. 2002) for bias and errors using known species distribution maps (Marks et al. 1999, BirdLife International and NatureServe 2015). To reduce geographic bias due to different sampling effort, we randomly selected a subsample of records regularly distributed in geographical space (Fourcade et al. 2014). Given that the three species are endemic to phytogeographical regions, we restricted distributions to mask layers (i.e., raster images used to train a model using only a subset of the region) on the basis of the regionalization proposed by Morrone (2014, 2015). Using the shapefile provided by Löwenberg-Neto (2014), we used a mask layer including the Cerrado, Araucaria Forest, and Atlantic and Parana Forest provinces for Rusty-barred Owls, a mask layer including the Chacoan, Pampean, and Monte

provinces for Chaco Owls, and a mask layer of the Patagonian region for Rufous-legged Owls.

Environmental variables. We obtained 19 bioclimatic variables from WorldClim (version 1.4) derived from monthly temperature and rainfall data obtained from global land area interpolation of climate point data (1950–2000; Hijmans et al. 2005). To reduce collinearity among variables, we selected a subset of less correlated variables (Pearson's correlations < 0.8). For each species, correlation matrices between variables were computed based on 10,000 points randomly drawn from each mask. We used two criteria to decide which layers of correlated pairs to retain, i.e., keeping layers with biological interpretation and a similar set of layers for the three species. Bioclimatic variables selected were isothermality (BIO 3), temperature annual range (BIO 7), mean temperature of warmest quarter (BIO 10), mean temperature of coldest quarter (BIO 11), precipitation seasonality (BIO 15), precipitation of warmest quarter (BIO 18), and precipitation of coldest quarter (BIO 19). For Rusty-barred Owls, mean temperature and precipitation of coldest quarter were excluded from the model due to high correlations with the five remaining bioclimatic variables. In addition, we used a global land-cover layer from Global Land Cover-SHARE (Latham et al. 2014) because vegetation is often a strong predictor of owl distributions (Marks et al. 1999). All layers used had a spatial resolution of 2.5 arc-min.

Species distribution models. SDMs were fitted using the MaxEnt version 3.3 (Phillips et al. 2006). MaxEnt is a general-purpose algorithm that generates predictions from an incomplete set of information. This approach assumes that the incomplete empirical probability distribution (based on the species occurrences) can be approximated by a probability distribution of maximum entropy subject to certain environmental constraints, and that this distribution approximates the potential geographic distribution of a species (Phillips et al. 2006). For each species, occurrence data were divided into training data (75% of occurrence points) and test data (25% of occurrence points). We assessed model performance with the Receiver Operating Characteristics Curve (ROC) calculating the area under the curve (AUC) (Phillips

et al. 2006). The AUC is a measure of the area under the ROC ranging from 0.5 (random accuracy) to a maximum value of 1.0 (perfect discrimination; Phillips et al. 2006). We considered models with an $AUC > 0.75$ as potentially useful, acceptable, and with sufficient discriminatory capacity (Elith 2000, Pearce and Ferrier 2000). In addition, we interpreted models as excellent if $AUC > 0.90$ and good if $0.90 > AUC > 0.80$ (Swets 1988). Given that the AUC has several recognized drawbacks that prevent its use as a measure of model performance (Lobo et al. 2008, Peterson et al. 2008), we report not only AUC, but also sensitivity (percentage of true positives) and specificity sensitivity (percentage of true negatives) values (Lobo et al. 2008). Because the default settings in Maxent have been shown to be inferior to tuned settings in simulations, we identified best models in terms of the test AUC. For each species, we fitted multiple models by progressively increasing the regularization parameter β from 1 to 15 by intervals of 1, and from 15 to 40 by intervals of 5 (Cao et al. 2013). For each model, we computed the AUC-value and those models with highest AUC were selected. Regularization parameters selected for modelling were 1 (Rusty-barred Owls), 4 (Chaco Owls), and 2 (Rufous-legged Owls) (See Supplemental Appendix S1).

Relative importance of individual predictors was assessed using jackknife tests that identify the environmental variable with the highest gain (i.e., improvement in penalized average log-likelihood compared to a null model) in the model performance when used in isolation (Elith et al. 2011). For all models, we used the MaxEnt default settings for regularization and selection of feature classes (functions of environmental variables) with 10 replicates generated by cross-validation. Feature classes include linear, quadratic, product, threshold, and hinge features, depending on the number of occurrence points (Phillips et al. 2006). Final models were based on the mean of the 10 replicated models.

We present the species predicted distributions after transforming continuous into binary (presence/absence) predictions according to two different thresholds, the minimum training presence (proportion of test localities with suitability values lower than that associated with the lowest training locality) and the

10 percentile presence (proportion of test localities with suitability values lower than that excluding the 10% of training localities with the lowest predicted suitability) logistic thresholds (Peterson et al. 2011), both of which provide minimum requirements for the species (Liu et al. 2005). In addition, we assessed whether models predicted positive occurrences significantly better than random using threshold-dependent binomial tests (Peterson et al. 2011). To show realized distributions, we reduced the extent of the potential distributions of each species to their intersections with the maps of biogeographic provinces where the species have been recorded (Soberón and Peterson 2005). Finally, we overlapped realized species distributions with species distribution maps (Bird-Life and NatureServe 2015) to allow visual comparison.

Comparisons of niche overlap. We compared niches of the three species of owls in both geographic G-space (i.e., representation of the fundamental niche in space) and ecological E-space (i.e., fundamental niche comprising all environmental traits) (Rödder and Engler 2011). To compare niche overlap in G-space, we computed Schoener (1968) D index between SDMs using ENMtools version 1.3 (Warren et al. 2010). This measure ranges from 0 (no overlap) to 1 (total overlap). We first performed the “identity test” in ENMtools to assess whether distribution models were statistically different between two species. This test compares the observed niche overlap value to a null distribution of 100 expected overlap values generated by pooling occurrence data for both species and creating two new randomized samples of the same size as the original samples. Observed niche overlap values are then compared to the null distribution of expected niche overlap values. We also performed a “background test” to test whether niche differences were due to differences in habitat availability. In contrast with the “identity test”, this compares the observed niche overlap value to a null distribution of 100 overlap values created by comparing a SDM of one species (species A) to a SDM generated from random points within the geographic range of the other species (species B). We repeated this procedure in the opposite direction because it is directional in comparisons. The geographic range

of each species corresponded to the mask layers used in SDM fitting (see above). If the null hypothesis is rejected, then observed niche overlap can be explained by habitat selection and/or suitability, thus supporting niche divergence (Warren et al. 2008). If the null hypothesis is accepted, then niche overlap can be explained by regional differences in the habitat available to each species, and thus niche conservatism is supported (Warren et al. 2008).

To compare niche overlap in E-space, we used the approach proposed by Rödder and Engler (2011). We first computed a Principal Component Analysis (PCA) on the pooled species occurrences using the 19 bioclimatic variables, and then performed a Linear Discriminant Analysis (LDA) on PCs with eigenvalues ≥ 1 (five PCs were retained). These PCs account for environmental variation in species occurrences, therefore representing E-space. In LDA, species were defined a priori as groups with equal prior probabilities and compared through PCs. Data were divided into training data (70% of occurrence points) and test data (30% of occurrence points). Total overlap in E-space was derived by summing all falsely classified values and dividing them by the total of all values resulting in a metric ranged between 0 (no overlap) to 1 (total overlap). This procedure was repeated 1000 times to account for possible variations caused by data splits. All graphs, bias correction, and niche overlap in E-space were performed in R version 3.2.1 (R Development Core Team 2015) using the packages *ggplot2* (Wickham 2009), *dismo* (Hijmans et al. 2015), and *MASS* (Venables and Ripley 2002).

RESULTS

Rusty-barred Owls. We recorded 153 occurrence points for Rusty-barred Owls, and 110 points were used as a result of bias correction (Fig. 1). Average AUC was 0.952 ± 0.015 , indicating excellent predictive power and discriminatory capacity of the model. Isothermality and mean temperature of the warmest quarter were the most important single predictors. In contrast, land cover was a poor isolated predictor (Fig. 2A). Isothermality values between 50% and 60%, and mean temperatures between 12°C and 21°C in the warmest quarter had higher climatic suitability (Fig. 3A, B). Compared to the known species

distribution, the realized distribution was slightly different, extending northwest into the Parana Forest, and not stretching to the Pampean and Chacoan provinces in the south and the west respectively (Fig. 4). The minimum training presence threshold was 0.036 (average sensitivity = 95.2%, average specificity = 76.7%, threshold dependent test P -value < 0.0001) and the 10 percentile training presence threshold was 0.173 (average sensitivity = 82.7%, average specificity = 89.2%, threshold dependent test P -value < 0.0001).

Chaco Owls. We recorded 136 occurrence points for Chaco Owls, and 105 points were used as a result of bias correction (Fig. 1). Average AUC was 0.870 ± 0.038 , indicating good predictive power and discriminatory capacity of the model. Mean temperatures of both the warmest and the coldest quarter were the most important single predictors (Fig. 2B). In contrast, land cover was a poor isolated predictor. Areas with mean temperatures between 29 and 33°C in the warmest quarter and between 17 and 22°C in the coldest quarter had higher climatic suitability (Fig. 3C, D). Compared to its known distribution, the realized distribution was slightly larger, covering areas of Monte and Pampean provinces to the southwest and southeast respectively (Fig. 4). The minimum training presence threshold was 0.041 (average sensitivity = 98.0%, average specificity = 35.6%, threshold dependent test P -value = 0.001) and the 10 percentile training presence threshold was 0.272 (average sensitivity = 84.5%, average specificity = 73.6%, threshold dependent test P -value = 0.037).

Rufous-legged Owls. We recorded 345 occurrence points for Rufous-legged Owls, and 201 points were used as a result of bias correction (Fig. 1). Average AUC was 0.889 ± 0.023 , indicating good predictive power and discriminatory capacity of the model. Precipitation during the coldest quarter was the most important predictor, whereas land cover was a poor isolated predictor (Fig. 2C). Rufous-legged Owls were strongly associated with areas with precipitation of the coldest quarter between 400 and 1500 mm (Fig. 3E). Compared to the known distribution, the realized distribution was similar, but extended to the north in Chile and did not cover near zones of Monte scrublands in northwestern Argentinean Patagonia or Patagonian steppes

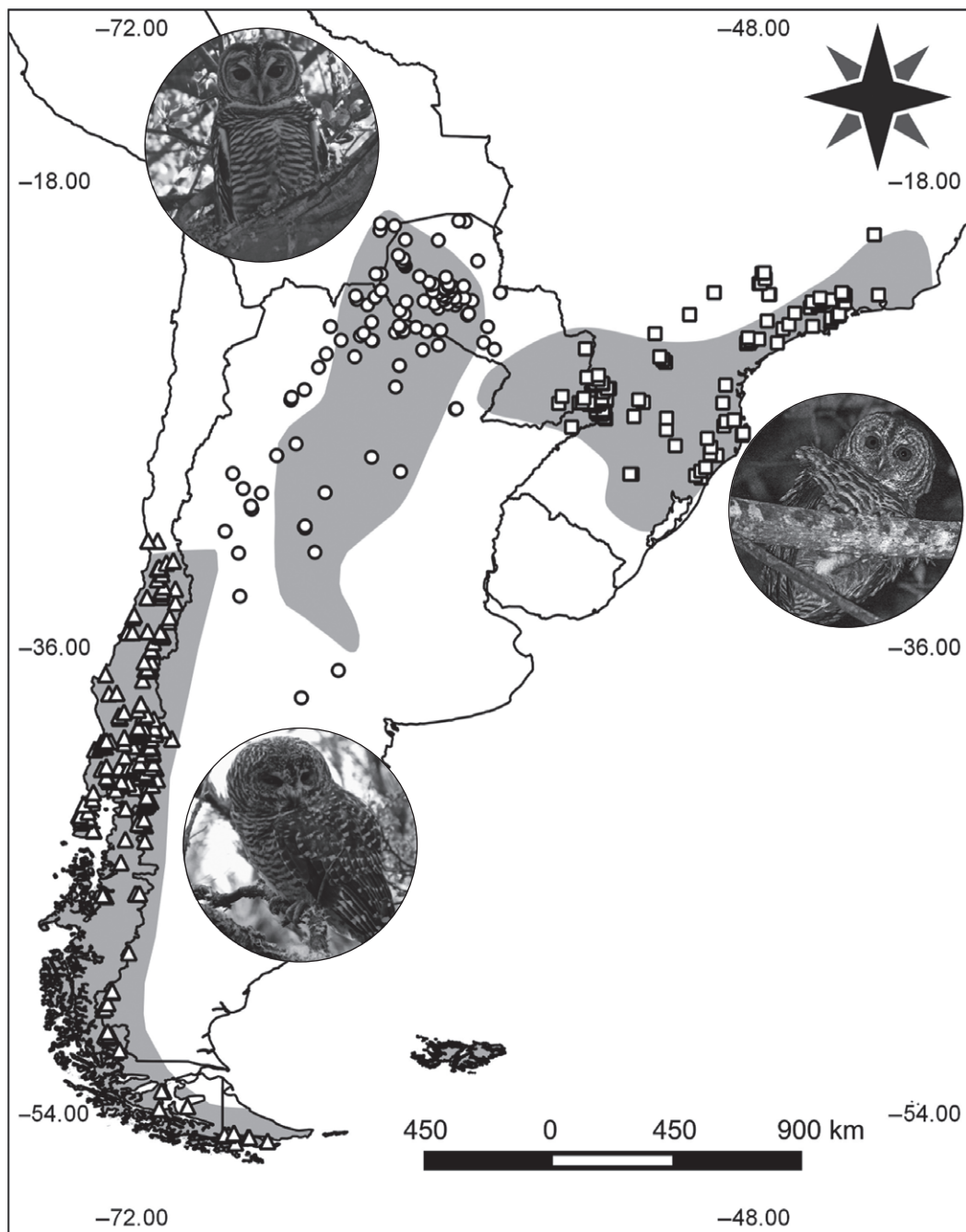


Fig. 1. Current distribution of the genus *Strix* in South America, showing records for Rusty-barred Owls (*S. hylophila*; squares), Chaco Owls (*S. chacoensis*; circles), and Rufous-legged Owls (*S. rufipes*; triangles) on species distribution maps (dark gray) from Birdlife International and NatureServe (2015). Photo credits: R. M. Jensen (Rusty-barred Owl), G. N. Montellano (Chaco Owl), and D. Barroso (Rufous-legged Owl).

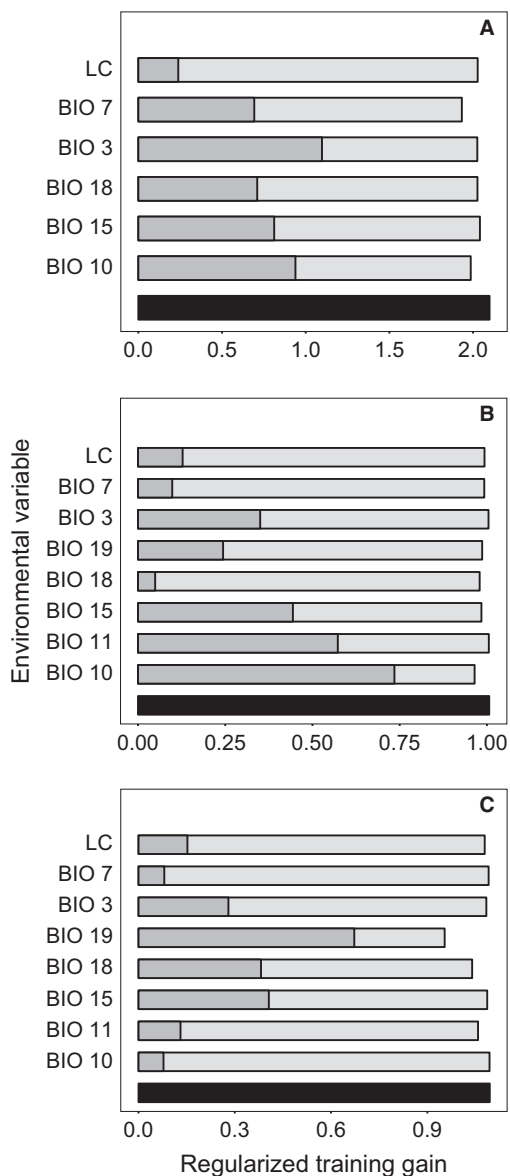


Fig. 2. Jackknife tests of environmental variable importance in SDM relative to all environmental variables (black bars) for each predictor variable alone (dark gray bars), and the drop in training gain when the variable is removed from the full model (light gray bars) for (A) Rusty-barred Owls (*Strix hylophila*), (B) Chaco Owls (*S. chacoensis*), and (C) Rufous-legged Owls (*S. rufipes*). LC: land cover; BIO 3: isothermality; BIO 7: temperature annual range; BIO 10: mean temperature of warmest quarter; BIO 11: mean temperature of coldest quarter; BIO 15: precipitation seasonality; BIO 18: precipitation of warmest quarter; BIO 19: precipitation of coldest quarter.

in southwestern Argentina (Fig. 4). The minimum training presence threshold was 0.059 (average sensitivity = 98.9%, average specificity = 57.9%, threshold dependent test P -value < 0.0001) and the 10 percentile training presence threshold was 0.351 (average sensitivity = 83.6%, average specificity = 78.8%, threshold dependent test P -value < 0.0001).

Niche overlap. Niche overlap in G-space was very low, as expected given their allopatric distributions. Highest overlap was detected between Rusty-barred Owls and Rufous-legged Owls, but the three species differed significantly in their niche overlaps (Table 1). In the background test, the null hypothesis was not rejected for Rusty-barred Owls-Rufous-legged Owls (Table 1), meaning that niche differences between their SDMs may be explained by variability in the available habitat, and thus support the niche conservatism hypothesis. In contrast, Rusty-barred Owls-Chaco Owls and Chaco Owls-Rufous-legged Owls differed significantly from the null model, supporting the niche divergence hypothesis (Table 1).

Similar to niche overlap in G-space, niche overlap in E-space was very low. The first five axes explained 95.25% of variation in bioclimatic variables. PCA-LDA resulted in a niche overlap value of 0.019 ± 0.013 for Chaco Owls-Rusty-barred Owls, 0.010 ± 0.008 for Chaco Owls-Rufous-legged Owls, and 0.00 ± 0.00 for Rusty-barred Owls-Rufous-legged Owls. Although very low niche overlap values, they suggest that Chaco Owls and Rusty-barred Owls are the most similar species in E-space.

DISCUSSION

Predicted distributions of South American *Strix*. The potential distributions of the three South American species of *Strix* owls predicted by our SDMs were comparable to the known distributions. Observing the 10 percentile training presence, this is especially true for Rufous-legged Owls and Rusty-barred Owls, whereas the predicted distribution of Chaco Owls extended outside the known range in southeastern Bolivia, southeastern Paraguay, and northwestern Argentina. The minimum training presence gave similar qualitative results, but, for Chaco Owls, included the southern portion of

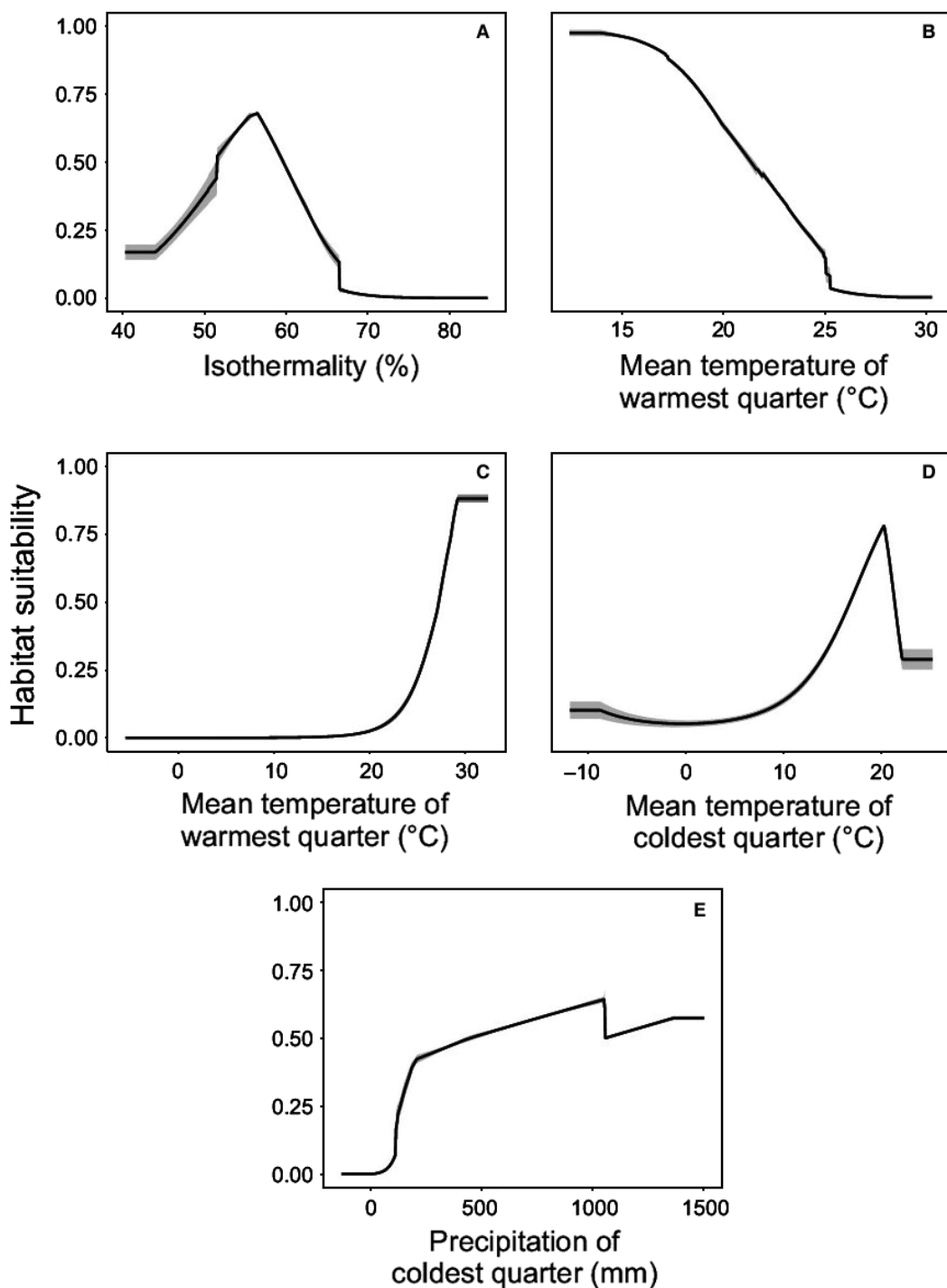


Fig. 3. Response-curves of the most important environmental variables for the Rusty-barred Owl (*Strix hylophila*; A–B), Chaco Owl (*S. chacoensis*; C–D), and Rufous-legged Owl (*S. rufipes*; E) SDMs. Black lines depict curves of each variable used in isolation to fit the model, and gray bands represent one standard deviation.

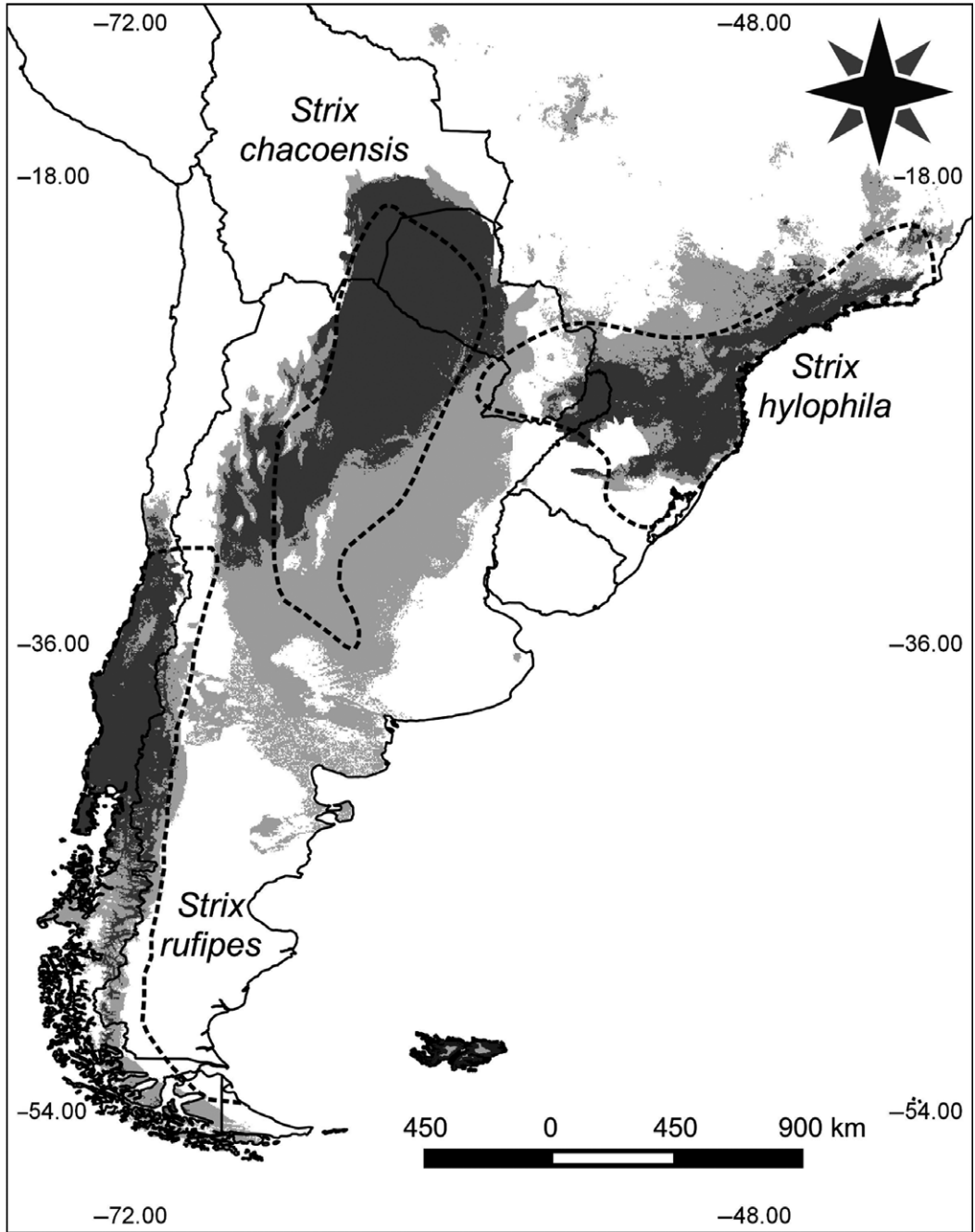


Fig. 4. Realized geographic distributions of *Strix* owls. Species distribution maps (dotted black lines) from BirdLife International and NatureServe (2015) are shown on values above the minimum training presence logistic threshold (light gray), and 10 percentile training presence logistic threshold (dark gray).

Monte province, the central portion of the Chacoan province, and central and northeastern Argentina.

Of the three species, the distribution of Chaco Owls is the least known, with few records from the center and southern

Table 1. Niche overlap analysis in G-space between *Strix* species.

Species A	Species B	Identity test			Background test			Interpretation	
		Observed D	Mean expected D	P	Mean expected $D_{A,B}$	P	Mean expected $D_{B,A}$		P
Rusty-barred Owl	Chaco Owl	0.057	0.879	<0.001	0.110	<0.001	0.220	<0.001	Niche divergence
Rusty-barred Owl	Rufous-legged Owl	0.054	0.906	<0.001	0.053	0.29	0.050	0.23	Niche conservatism
Chaco Owl	Rufous-legged Owl	0.025	0.907	<0.001	0.057	<0.001	0.102	<0.001	Niche divergence

Results of identity and background tests using Schoener's D index (D) and P -values (P) are shown. Mean expected D represents the average of 100 expected niche overlap values under a null distribution (see Methods for details). For the background test, the distribution of species B is first considered as background ($D_{A,B}$), and then the test is repeated in the opposite direction ($D_{B,A}$).

extremes of their distribution range. Moreover, and although they are considered endemic to the dry Chaco woodland (Marks et al. 1999, Méndez 2015, Trejo and Bó 2015), the SDM also indicates the presence of suitable areas in the humid Chaco. For Rusty-barred Owls, the SDM predicts suitable areas outside the known range into the Cerrado biogeographic province (central-west region of Brazil). Moreover, their distribution in Paraguay would be restricted to a small region in the southeast. The distribution of Rufous-legged Owls is relatively well-known, but their northern limit still remains unclear and has been reported as 31°55'S (Trejo et al. 2006, Figueroa et al. 2015). In support of this, our model indicated suitable areas for Rufous-legged Owls even further north, up to ~30°S. In addition, in agreement with other authors (Vuilleumier 1985, Girini et al. 2016), there are also some suitable areas in the forest-steppe ecotone and the steppe. Finally, the southern limit of the range of Rufous-legged Owls would be the Falkland Islands (Islas Malvinas) (Johnson and Goodall 1965, Strange 1972), where the minimum training presence of the SDM shows suitable areas for the species.

At the scale of our study, predicted distributions of the three South American *Strix* owls were mainly determined by climatic factors. In particular, temperature variables were more important in explaining the distributions of Rusty-barred Owls and Chaco Owls, whereas precipitation was more important for Rufous-legged Owls. In contrast, land-cover type played a secondary role in their potential distributions. These results seem to contradict the general assumption that the distribution of *Strix* owls depends primarily on the availability of forest habitat (Marks et al. 1999, Trejo et al. 2006). In addition, the results of several studies suggest that features related with forest vegetation structure (e.g., forest age, number of strata, and forest cover) have an important effect on the abundance and distribution of *Strix* owls (e.g., Carroll 2010, Ibarra et al. 2014). Nevertheless, the distribution and abundance of bird species are known to strongly depend on climatic factors (Watkinson et al. 2004), and several investigators have found that climatic variables are important in explaining the distribution of *Strix* owls (e.g., Diniz-Filho et al. 2004,

Carroll 2010, Jepsen et al. 2011, Ackers et al. 2015). In addition, the responses of species and factors influencing distributions of environmental resources operate in a hierarchical way at different spatial scales (Mackey and Lindenmayer 2001). The distribution and availability of the primary environmental resources involve both larger scaled abiotic physical inputs and smaller scaled biotic-driven processes and, at the global- and meso-scales, climatic factors are the major drivers that determine the distribution of animals, including terrestrial vertebrates that inhabit forested habitats (Mackey and Lindenmayer 2001).

***Strix* species delimitation and niche-based processes.** As expected for species with allopatric distributions, the three species of owls in our study differed in ecological space (i.e., fundamental niche comprising all environmental features in multidimensional space) and, as a result, there was low niche overlap. The identity test also indicated that the SDMs were nonequivalent in geographic space (i.e., representation of the fundamental niche available in space), and showed low niche overlap values. In this sense, an inference of nonequivalency of SDMs, especially in allopatric species, may largely be the result of differential availability of habitat (McCormack et al. 2009, Warren et al. 2010). The background test addresses this issue and, when niche overlaps were compared accounting for regional similarities in the habitat available to each species, an ecological niche divergence process was supported for Chaco Owls and Rusty-barred Owls and for Chaco Owls and Rufous-legged Owls, whereas a niche conservatism process was supported for Rusty-barred Owls and Rufous-legged Owls. This suggests that Rusty-barred Owls and Rufous-legged Owls would be the two most closely related species in this group. Formerly, Chaco Owls were treated as a subspecies of Rufous-legged Owls, but they were split into distinct species based on differences in plumage color, morphology, and vocalizations (Straneck and Vidoz 1995). Some investigators have proposed that Chaco Owls are more closely related to Rusty-barred Owls on the basis of similar vocalizations (Straneck and Vidoz 1995, Remsen et al. 2015). Our results support the current species delimitation, but do not support a close relationship between

Chaco Owls and Rufous-legged Owls or between Chaco Owls and Rusty-barred Owls. Instead, our results support a new phylogenetic hypothesis, with Rufous-legged Owls the sister taxon of Rusty-barred Owls.

Beyond the actual phylogenetic affinities between South American *Strix* owls, we hypothesize that events in South America during the Cenozoic could have played a role in the speciation processes of this group. Speciation of South American *Strix* owls seems to have taken place after the late Miocene (9–8 mya; Sibley and Ahlquist 1990, Diniz-Filho and Sant'ana 2000). During the middle to late Miocene (17–11 mya), three successive Atlantic marine transgressions formed the “Paranean Sea” that spread over eastern Argentina, western Uruguay, southern Paraguay, and southeastern Bolivia (Ortiz-Jaureguizar and Cladera 2006). This event separated terrestrial environments currently inhabited by Rusty-barred Owls and Rufous-legged Owls, and flooded the Chaco areas currently inhabited by Chaco Owls (Supplemental Appendix S2). The late Miocene–early Pliocene (11–3 mya) is known as the “Age of Southern Plains” because the area formerly flooded by the “Paranean Sea” became a large area of grassland habitat (Ortiz-Jaureguizar and Cladera 2006). In addition, the uplift of the Andean Cordillera beginning in the middle Miocene (17 mya) had profound effects on climatic conditions in southern South America, forming a major barrier to moisture-laden South Pacific winds (Ortiz-Jaureguizar and Cladera 2006). The “Paranean Sea”, the southern plains, and the uplift of Andean Cordillera have played a role in speciation and diversification of many different taxa (mammals: Ortiz-Jaureguizar and Cladera 2006, reptiles: Morando et al. 2015, arthropods: Donato 2006, Ferretti et al. 2012, plants: Ortiz-Jaureguizar and Cladera 2006, Apodaca et al. 2015), including birds (Tambussi and Degrange 2012).

Assuming that the ancestor of present-day species of *Strix* was widely distributed in southern South America (given the large extent of forest habitat from the Paleocene to early Pliocene; Ortiz-Jaureguizar and Cladera 2006), we propose that the “Paranean Sea” acted as a geographic barrier for Rusty-barred Owls and Rufous-legged Owls, leading to a vicariant event. These species have since

remained isolated from each other due to niche conservatism in climatic tolerances and the dry conditions in the southern plains produced by the uplift of Andean Cordillera, leading to allopatric speciation (Wiens and Graham 2005). In contrast, the different climatic conditions and vegetation in the Chaco province since the middle Miocene (Cabrera 1976, Pennington et al. 2000, Ortiz-Jaureguizar and Cladera 2006) are consistent with a divergence niche process for Chaco Owls. Overall, and although SDMs and comparisons of niche overlaps cannot by itself provide definitive phylogenetic affinities between different taxa (e.g., Rissler and Apodaca 2007), our findings suggest that different niche-based processes have taken place in the evolution of South American *Strix* owls, and that abiotic processes at the global-scale could have played an important role in their speciation.

CONCLUSIONS

Traditionally, two isolated approaches have been used to explain distribution patterns: historical biogeography and ecological biogeography (Crisci et al. 2006). Because both evolution and ecology are basic pillars for explaining and predicting these patterns (Wiens and Graham 2005, Crisci et al. 2006), this dichotomy seems too restricting. Our study provides an example of the integration of historical and ecological approaches in biogeography (e.g., Cao et al. 2013, Fuentes-Hurtado et al. 2016). Results provided by SDMs can be used to infer historical and ecological processes in an integrative way, given that (1) niche conservatism in climatic tolerances plays a role in allopatric speciation and historical biogeography (Wiens and Graham 2005), (2) SDMs represent a useful technique for inferring space-time processes in ecological biogeography (Crisci et al. 2006), and (3) construction and comparison of SDMs can serve to test niche-based processes (Warren et al. 2008). We advocate for an integrative framework on biogeography to investigate both practical as theoretical problems, and that species distribution modeling represents a useful tool to bridge historical and ecological approaches in biogeography.

Overall, our results indicate that Rusty-barred Owls, Chaco Owls, and Rufous-legged

Owls have different ecological requirements, and that historical events together with ecological constraints have played a role in their speciation. Although SDMs and spatially explicit analyses of environmental data are valuable tools that allow tests of the role of ecology in niche-based speciation processes (Wiens and Graham 2005, Beukema et al. 2010, McCormack et al. 2009, Blair et al. 2013), they cannot provide definitive conclusions regarding phylogenetic affinities (e.g., Rissler and Apodaca 2007). In this sense, further research based on molecular data will be needed to definitively reveal the evolutionary history and phylogenetic relationships of these endemic owls of South America.

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LITERATURE CITED

- ACKERS, S. H., R. J. DAVIS, K. A. OLSEN, AND K. M. DUGGER. 2015. The evolution of mapping habitat for Northern Spotted Owls (*Strix occidentalis caurina*): a comparison of photo-interpreted, Landsat-based, and lidar-based habitat maps. *Remote Sensing of Environment* 156: 361–373.
- ADMINISTRACIÓN DE PARQUES NACIONALES [online]. 2011. Sistema de Información de Biodiversidad. Proyecto de Conservación de la Biodiversidad - Donación GEF-BIRF-TF 028372- AR. <<http://www.sib.gov.ar>> (Accessed 21 August 2015).
- ANDERSON, R. P., M. GOMEZ-LAVERD, AND A. T. PETERSON. 2002. Geographical distributions of spiny pocket mice in South America: insights

- from predictive models. *Global Ecology and Biogeography* 11: 131–141.
- , AND A. RAZA. 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. *Journal of Biogeography* 37: 1378–1393.
- APODACA, M. J., J. V. CRISCI, AND L. KATINAS. 2015. Andean origin and diversification of the genus *Perezia*, an ancient lineage of Asteraceae. *Smithsonian Contributions to Botany* 102: 1–28.
- BEUKEMA, W., P. DEPOUS, D. DONAIRE, D. ESCORIZA, S. BOGERTS, A. G. TOXOPEUS, C. A. J. DEBIE, J. ROCA, AND S. CARRANZAS. 2010. Biogeography and contemporary climatic differentiation among Moroccan *Salamandra algira*. *Biological Journal of the Linnean Society* 101: 626–641.
- BIRDLIFE INTERNATIONAL [online]. 2015. IUCN Red List for birds. <<http://www.birdlife.org>> (Accessed 17 November 2015).
- BIRDLIFE INTERNATIONAL AND NATURESERVE. 2015. Bird species distribution maps of the world. BirdLife International, Cambridge, UK and NatureServe, Arlington, VA, USA.
- BLAIR, M. E., E. J. STERLING, M. DUSCH, C. J. RAXWORTHY, AND R. G. PEARSON. 2013. Ecological divergence and speciation between lemur (*Eulemur*) sister species in Madagascar. *Journal of Evolutionary Biology* 26: 1790–1801.
- BODRATI, A., AND A. TREJO. 2015. Búhos de Paraguay. In: *Los búhos Neotropicales: diversidad y conservación* (P. L. Enríquez, ed.), pp. 563–572. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- CABRERA, A. L. 1976. Regiones fitogeográficas argentinas. Acme, Buenos Aires, Argentina.
- CAO, Y., R. E. DEWALT, J. L. ROBINSON, T. TWEDDALE, L. HINZ, AND M. PESSIMO. 2013. Using Maxent to model the historic distributions of stonefly species in Illinois streams: the effects of regularization and threshold selections. *Ecological Modelling* 259: 30–39.
- CARROLL, C. 2010. Role of climatic niche models in focal-species-based conservation planning: assessing potential effects of climate change on Northern Spotted Owl in the Pacific Northwest, USA. *Biological Conservation* 143: 1432–1437.
- CLEMENTS, J. F., T. S. SCHULLENBERG, M. J. ILIFF, D. ROBERSON, T. A. FREDERICKS, B. L. SULLIVAN, AND C. L. WOOD [online]. 2015. The eBird/Clements checklist of birds of the world: v2015. <<http://www.birds.cornell.edu/clementschecklist/download/>> (Accessed 16 November 2015).
- CRISCI, J. V., O. E. SALA, L. KATINAS, AND P. POSADAS. 2006. Bridging historical and ecological approaches in biogeography. *Australian Systematic Botany* 19: 1–10.
- DINIZ-FILHO, J. A. F., T. F. RANGEL, AND B. A. HAWKINS. 2004. A test of multiple hypotheses for the species richness gradient of South American owls. *Oecologia* 140: 633–638.
- , AND C. E. R. SANT'ANA. 2000. Phylogenetic correlograms and the evolution of body size in South American owls (Strigiformes). *Genetic and Molecular Biology* 23: 285–292.
- DONATO, M. 2006. Historical biogeography of the family Tristiridae (Orthoptera: Acridomorpha) applying dispersal–vicariance analysis. *Journal of Arid Environments* 66: 421–434.
- EBIRDBASIC DATASET. 2015. Version: EBD_relMay-2015. Cornell Lab of Ornithology, Ithaca, NY.
- ELITH, J. 2000. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. In: *Quantitative methods in conservation biology* (S. Ferson and M. A. Burgman, eds.), pp. 39–58. Springer, New York, NY.
- , S. J. PHILLIPS, T. HASTIE, M. DUDÍK, Y. E. CHEE, AND C. J. YATES. 2011. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43–57.
- ENRÍQUEZ, P. L. 2015. Los búhos Neotropicales: diversidad y conservación. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- , K. EISERMANN, J. C. MOTTA-JUNIOR, AND H. MIKKOLA. 2015. Una revisión de la taxonomía y sistemática de los búhos Neotropicales. In: *Los búhos Neotropicales: diversidad y conservación* (P. L. Enríquez, ed.), pp. 29–38. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- FERRETTI, N., A. GONZÁLEZ, AND F. PÉREZ-MILES. 2012. Historical biogeography of the genus *Cyriocosmus* (Araneae: Theraphosidae) in the Neotropics according to an event-based method and spatial analysis of vicariance. *Zoological Studies* 51: 526–535.
- FIGUEROA, R. A., S. ALVARADO, E. CORALES, D. GONZALEZ-ACUÑA, R. SCHLATTER, AND D. R. MARTÍNEZ. 2015. Los búhos de Chile. In: *Los búhos Neotropicales: diversidad y conservación* (P. L. Enríquez, ed.), pp. 173–272. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- FOURCADE, Y., J. O. ENGLER, D. RÖDDER, AND J. SECONDI. 2014. Mapping species distributions with MAXENT using a geographically biased sample of presence data: a performance assessment of methods for correcting sampling bias. *PLoS ONE* 9: e97122.
- FUENTES-HURTADO, M., A. R. HOF, AND R. JANSSON. 2016. Paleodistribution modeling suggests glacial refugia in Scandinavia and out-of-Tibet range expansion of the Arctic fox. *Ecology and Evolution* 6: 170–180.
- GASPARRI, N. I., AND H. R. GRAU. 2009. Deforestation and fragmentation of Chaco dry forest in NW Argentina (1972–2007). *Forest Ecology and Management* 258: 913–921.
- GBIF – GLOBAL BIODIVERSITY INFORMATION FACILITY [online]. 2007. Free and open access to biodiversity data <<http://www.gbif.org/>> (Accessed 24 August 2015).
- GIRINI, J. M., A. TREJO, AND D. MONTALTI. 2016. Nuevos registros de Lechuzas Batarez Austral *Strix rufipes* en ambientes no-boscosos del norte de la Patagonia andina. *Cotinga* 38: 55–57.

- GODOWN, M. E., AND A. T. PETERSON. 2000. Preliminary distributional analysis of US endangered bird species. *Biodiversity and Conservation* 9: 1313–1322.
- GUISAN, A., AND W. THUILLER. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8: 993–1009.
- , AND N. E. ZIMMERMANN. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.
- HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- , L. GUARINO, AND E. ROJAS. 2002. DIVA-GIS. A geographic information system for the analysis of biodiversity data. Manual-International Potato Center, Lima, Perú.
- , S. PHILLIPS, J. LEATHWICK, AND J. ELITH [online]. 2015. Species distribution modeling. R package version 1.0-12. <<http://CRAN.R-project.org/package=dismo>> (Accessed 4 August 2015).
- IBARRA, J. T., K. MARTIN, M. C. DREVER, AND G. VERGARA. 2014. Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: a multi-scale approach. *Forest Ecology and Management* 331: 281–291.
- JEPSEN, E. P., J. KEANE, AND H. B. ERNEST. 2011. Winter distribution and conservation status of the Sierra Nevada Great Gray Owl. *Journal of Wildlife Management* 75: 1678–1687.
- JOHNSON, A. W., AND J. D. GOODALL. 1965. The birds of Chile and adjacent regions. Buenos Aires University, Buenos Aires, Argentina.
- LATHAM, J., R. CUMANI, I. ROSATI, AND M. BLOISE. 2014. FAO global land cover (GLC-SHARE) Beta-release 1.0 Database, Division LaW.
- LIU, C., P. M. BERRY, T. P. DAWSON, AND R. G. PEARSON. 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385–393.
- LOBO, J. M., A. JIMÉNEZ-VALVERDE, AND R. REAL. 2008. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography* 17: 145–151.
- LÖWENBERG-NETO, P. 2014. Neotropical region: a shapefile of Morrone's (2014) biogeographical regionalisation. *Zootaxa* 3802: 300.
- MACKEY, B. G., AND D. B. LINDENMAYER. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. *Journal of Biogeography* 28: 1147–1166.
- MARKS, J. S., R. J. CANNINGS, AND H. MIKKOLA. 1999. Family Strigidae (Typical Owls). In: *Handbook of the birds of the world* (J. del Hoyo, A. Elliott, and J. Sargatal, eds.), pp. 76–242. Vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona, Spain.
- MCCORMACK, J. E., A. J. ZELLMER, AND L. L. KNOWLES. 2009. Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation? Insights from tests with niche models. *Evolution* 65: 184–202.
- MÉNDEZ, D. R. 2015. Búhos de Bolivia. In: *Los búhos Neotropicales: diversidad y conservación* (P. L. Enríquez, ed.), pp. 93–110. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- MORANDO, M., M. OLAVE, L. J. AVILA, E. BAKER, AND J. W. SITES, JR. 2015. Molecular phylogeny of the lizard clade Leiosaurae endemic to southern South America. *Herpetologica* 71: 322–331.
- MORRONE, J. J. 2014. Biogeographical regionalization of the Neotropical region. *Zootaxa* 3782: 1–110.
- . 2015. Biogeographical regionalization of the Andean region. *Zootaxa* 3936: 207–236.
- MOTTA-JUNIOR, J. C., A. C. ROCHA BRAGA, AND M. A. MONTEIRO GRANZINOLLI. 2015. Owls of Brazil. In: *Los búhos Neotropicales: diversidad y conservación* (P. L. Enríquez, ed.), pp. 115–169. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- ORTIZ-JAUREGUIZAR, E., AND G. A. CLADERA. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66: 498–532.
- PEARCE, J., AND S. FERRIER. 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling* 128: 127–147.
- PENNINGTON, R. T., D. E. PRADO, AND C. A. PENDRY. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27: 261–273.
- PETERSON, A. T. 2001. Predicting species geographic distributions based on ecological niche modeling. *Condor* 103: 599–605.
- , M. PAPEŞ, AND J. SOBERÓN. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213: 63–72.
- , J. SOBERÓN, R. G. PEARSON, R. P. ANDERSON, E. MARTÍNEZ-MEYER, M. NAKAMURA, AND M. B. ARAÚJO. 2011. Ecological niches and geographic distributions. Princeton University Press, Princeton, NJ.
- , J. SOBERÓN, AND V. SÁNCHEZ CORDERO. 1999. Conservatism of ecological niches in evolutionary time. *Science* 285: 1265–1267.
- PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231–259.
- R DEVELOPMENT CORE TEAM [online]. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- REMSEN, J. V., JR., J. I. ARETA, C. D. CADENA, A. JARAMILLO, M. NORES, J. F. PACHECO, J. PÉREZ-EMÁN, M. B. ROBBINS, F. G. STILES, D. F. STOTZ, AND K. J. ZIMMER [online]. 2015. A classification of the bird species of South America. American Ornithologists' Union. <<http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>> (Accessed 15 November 2015).
- RISSLER, L. J., AND J. J. APODACA. 2007. Adding more ecology into species delimitation: ecological niche

- models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). *Systematic Biology* 56: 924–942.
- RÖDDER, D., AND J. O. ENGLER. 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography* 20: 915–927.
- SCHOENER, T. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704–726.
- SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven, CT.
- SITES J. W., JR., AND J. C. MARSHALL. 2003. Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution* 18: 462–470.
- SOBERÓN, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10: 1115–1123.
- , AND A. T. PETERSON. 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Information* 2: 1–10.
- STRANECK, R. J., AND F. VIDOZ. 1995. Sobre el estado taxonómico de *Strix rufipes* (King) y de *Strix chacoensis* (Cherrie and Reichenberger) (Ave: Strigidae). *Nótulas Faunísticas* 74: 1–5.
- STRANGE, I. 1972. Wildlife in the Falklands. *Oryx* 11: 241–257.
- SWETS, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.
- TAMBUSSI, C. P., AND F. DEGRANGE. 2012. South American and Antarctic continental Cenozoic birds: paleobiogeographic affinities and disparities. Springer, New York, NY.
- TREJO, A., AND M. S. BÓ. 2015. Los Búhos de Argentina. In: Los búhos Neotropicales: diversidad y conservación (P. L. Enríquez, ed.), pp. 43–58. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.
- , ———, AND L. BIONDI. 2012. Búhos de Argentina: estado de conservación y prioridades de investigación. *Ornitología Neotropical* 23: 225–232.
- , R. A. FIGUEROA, AND O. S. ALVARADO. 2006. Forest-specialist raptors of the temperate forests of southern South America: a review. *Revista Brasileira de Ornitologia* 14: 317–330.
- VENABLES, W. N., AND B. D. RIPLEY. 2002. Modern applied statistics with S. Springer, New York, NY.
- VUILLEUMIER, F. 1985. Forest birds of Patagonia: ecological geography, speciation, endemism and faunal history. *Ornithological Monographs* 36: 255–304.
- WARREN, D., R. GLOR, AND M. TURELLI. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* 62: 2868–2883.
- , ———, AND ———. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.
- WATKINSON, A., A. J. GILL, AND M. HULME. 2004. Flying in the face of climate change: a review of climate change, past, present and future. *Ibis* 146: 4–10.
- WICKHAM, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, NY.
- WIENS, J. J., AND C. H. GRAHAM. 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution and Systematics* 36: 519–539.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Model selection of species distribution models.

Appendix S2. Potential distributions of *Strix* owls in South America and “Paranean Sea”.