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Article

Biotic interactions in species distribution models enhance model performance and shed light on natural history of rare birds: a case study using the straight-billed reedhaunter *Limnoctites rectirostris*

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Species distribution models (SDMs) have become a workhorse to explain, understand and predict distributions of birds. However, SDMs at broad scales are typically built using climatic variables, while ignoring the effects of biotic interactions. Although its role still remains controversial, the inclusion of biotic interactions into SDMs could confirm and/or provide new ecological insights of poorly-known species. We modeled the distribution of the rare South American straight-billed reedhaunter *Limnoctites rectirostris* (Furnariidae), a specialist of marshy areas linked to the spiny herb eryngo (*Eryngium* spp., Apiaceae), which provides the main food and nest resources. To do this, we first modeled the distribution of three eryngo species considered as the main biotic interactors (*E. eburneum*, *E. horridum* and *E. pandanifolium*) and included them into the straight-billed reedhaunter SDM. Second, we analyzed niche overlap between the straight-billed reedhaunter and eryngos in terms of environmental variables using dynamic range boxes, a novel approach to quantify size of n -dimensional hypervolumes. The inclusion of biotic interactions improved model performance relative to a model with climatic variables only. Climatic suitability of *E. eburneum* and mean temperature of wettest quarter were the most important predictors. By contrast, *E. horridum* and *E. pandanifolium* resulted in poor predictors, suggesting that the straight-billed reedhaunter's relative dependence on each eryngo species is different. The three eryngo environmental spaces largely covered the environmental space of the straight-billed reedhaunter, but the opposite was not true. Our findings suggest that biotic interactions play an important role in explaining and predicting the distribution of a rare bird at macro-scales, and that the assessment of niche overlap between interactors may confirm or improve the autoecological understanding of rare and cryptic birds. We advocate the use of an integrative modeling approach including climate and biotic interactions into SDMs to enhance ecological knowledge on poorly-known bird species.

Keywords: Eryngium, Maxent, niche overlap



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Introduction

One central issue in ecology is to understand the abundance and distribution of organisms (Pickett et al. 1994, Guisan and Zimmerman 2000). Due to the conspicuous nature of birds, ornithologists have assembled a great amount of information relating the abundance and distribution of birds to their environments, and ornithology itself has played a key role in the development of ecological theories (Block and Brennan 1993). In the last two decades, species distribution models (SDMs) have been increasingly used to explain, understand and predict species distributions across space and time (Elith and Leathwick 2009). In this sense, SDMs have addressed a wide array of questions, such as quantifying environmental niches of species and predicting their geographic 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). In this field of ecology, birds have been the focus of many SDM studies because of the high availability of freely accessible avian occurrence data (Engler et al. 2017).

SDMs relate species occurrences with environmental variables to create a map depicting relative habitat suitability (Guisan and Zimmerman 2000). However, as autoecology has been historically biased toward reductionism and determinism, ecologists have overlooked the relevance of biotic interactions on the determination of species distributions (Levins and Lewontin 1980). Indeed, most SDMs typically ignore the effects of biotic interactions (Guisan and Thuiller 2005, Elith and Leathwick 2009), mainly as a result of two factors: 1) poor knowledge on biotic interactions at large spatial scales, and 2) assumptions under the Eltonian noise hypothesis, which states that abiotic factors, such as climatic variables, are the only drivers limiting species distributions at large spatial scales and low resolution, whereas biotic interactions would act at smaller spatial scales and higher resolution (Soberón and Nakamura 2009, Boulangeat et al. 2012). Nevertheless, both theory and facts contest such statement because quantifying the fundamental niche does not explain the entire distribution for every species, and numerous studies have shown that the inclusion of biotic interactions improve predictions of species distributions at broad geographical scales (Araújo and Luoto 2007, Heikkinen et al. 2007, Bateman et al. 2012, Hof et al. 2012, Giannini et al. 2013, Araújo and Rozenfeld 2014, Araújo et al. 2014, Crystal-Ornelas et al. 2017, Atauchi et al. 2018). Besides, endotherm distributions may be less directly linked to bioclimatic variables than ectotherm distributions (Engler et al. 2017). Therefore, a critical assessment about the importance of biotic interactions in SDMs, particularly in endotherms, is still needed.

Furthermore, accounting for biotic interactions represents a major challenge for SDMs and it remains unclear how the effects of biotic interactors should be modeled (Guisan and Thuiller 2005, Elith and Leathwick 2009). Recently,

Anderson (2017) proposed some conceptual guidelines to include biotic interactions in SDMs. In the case of predictors (i.e. biotic interactors) not affected by the focal species (e.g. commensalism, amensalism), the suitability of the focal species could be estimated by SDMs, given that they assume that predictors are density-independent factors not affected by habitat suitability. Following Peterson et al. (2011), variables not dynamically affected by the species are termed non-interactive variables, in contrast to variables that are dynamically modified (interactive variables). Under this scenario, including a biotic non-interactive variable should involve obtaining an SDM of the biotic interactor and including this representation as a predictor along with abiotic factors to fit a model for the focal species (Peterson et al. 2011, Anderson 2017). For mutualisms and antagonisms, in contrast, this assumption may not hold, potentially biasing predictions of SDMs (Anderson 2017).

Beyond discussions about the inclusion and modeling of biotic interactions in SDMs, most authors agree that ecological knowledge on the species involved represents a key issue in SDMs (Bateman et al. 2012, Giannini et al. 2013, Anderson 2017). Nevertheless, this requires more knowledge of species biology, which is still unavailable for many species. This is especially true for many rare and cryptic birds, for which basic ecological aspects such as distribution, diet and breeding biology remains poorly known (Groombridge and Jenkins 2002). Rather than being a drawback, though, this may represent an opportunity for SDMs to shed light on ecological knowledge on rare and cryptic birds. Indeed, SDMs have shown high performance for identifying important environmental variables explaining the distributions of birds with these characteristics (Gibson et al. 2007, Tinoco et al. 2009, Marini et al. 2010, Botero-Delgado et al. 2012, Wu et al. 2012, Girini et al. 2017). In this context, and given that birds are one of the most well-known taxonomic groups, avian SDMs provide a suitable model into which include biotic interactions (Engler et al. 2017).

The importance of including biotic interactions in SDMs to enhance ecological knowledge on birds has a relatively short history (Heikkinen et al. 2007), considering that monitoring of rare and endangered species has become a priority for conservation agencies. Here, we used a rare South American ovenbird, the straight-billed reedhaunter *Limnortyx rectirostris* (Gould, 1839), to evaluate model performance when including the distribution of three plant species (*Eryngium* sp., Apiaceae) providing the main food and nest resources. We also aimed to identify important climatic variables explaining straight-billed reedhaunter distribution, as well as the most important biotic interactors. To this end, we first modeled SDMs of biotic interactors and then fitted models for the straight-billed reedhaunter with only climatic variables and with climatic and biotic interaction variables. Complementarily, we estimated niche overlap between the straight-billed reedhaunter and eryngos in terms of environmental variables, to analyze the relative dependence between interacting species.



Q1

Q2



Material and methods

Study species

The straight-billed reedhaunter is a rare member of the ovenbird (Furnariidae) family, specialist of marshy areas in southeastern Brazil (eastern Rio Grande do Sul state), southern and eastern Uruguay, and northeastern Argentina (Zimmer et al. 2003). It is a small species (mean body mass = 19.2 g), with a long, straight, slender bill, and a shorter, graduated tail with pointed rectrices (Gerzenstein and Achával 1967, Olson et al. 2005) (Fig. 1). The global conservation status is near threatened, with a moderately small and fragmented population which may be declining due to habitat loss (BirdLife International 2017). Its ecology remains largely unknown, yet all studies agree that it is closely linked to the spiny herb eryngo, *Eryngium* spp. (Apiaceae), which provides arthropods as food resources (Zorrilla de San Martín 1963, López-Lanús et al. 1999) and nest sites (Daguerre 1933, Pereyra 1938, Ricci and Ricci 1984, Babarskas and Fraga 1998, Gonçalves et al. 2017). In particular, it has been mentioned that the straight-billed reedhaunter interacts with three eryngo species: *E. pandanifolium*, *E. horridum* and *E. eburneum* (Olson et al. 2005). The ranges of these species are southern Brazil to northeastern Argentina, with the last two extending to Paraguay (Cabrera 1965). This suggests that the straight-billed reedhaunter's ability to spread to areas where Eryngo species are present is limited by other factors such as habitat quality, climate change, and/or biotic interactions—a hypothesis not previously tested.

Distribution modeling

The fact that eryngo distributions would not be affected by straight-billed reedhaunter distribution (i.e. they represent non-interactive variables) justifies their inclusion into SDMs (Peterson et al. 2011, Anderson 2017). Therefore, we first modeled SDMs of *E. pandanifolium* (n = 107), *E. horridum* (n = 69) and *E. eburneum* (n = 57) using occurrence data sourced from Global Biodiversity Information Facility (2007), and used them as inputs into the straight-billed



Figure 1. Straight-billed reedhaunter *Limnoctites rectirostris*. Ceibas, Argentina. Photo credit: Jorge La Grotteria.

reedhaunter SDM. Straight-billed reedhaunter occurrence data (n = 166) were obtained from literature records (Gould and Darwin 1841, Sanborn 1929, Daguerre 1933, Pereyra 1938, Esteban 1949, Escalante 1956, Zorrilla de San Martín 1963, Gerzenstein and Achával 1967, Canevari et al. 1991, Krapovickas et al. 1992, Chébez 1994, Ricci and Ricci 1994, Babarskas and Fraga 1998, López-Lanús et al. 1999, Sagrera 1999, Accordi and Barcellos 2006, Accordi and Hartz 2006, Pacheco and Olmos 2006, Aldabe et al. 2008, Brummelhaus et al. 2012, Gonçalves et al. 2017), Global Biodiversity Information Facility (2007) and eBird (2016) (Fig. 2). The same procedure was applied to each of the four potential distribution models. Data were checked in the DIVA-GIS software (Hijmans et al. 2005) for errors (erroneous locations), and no data filtering was needed at this step. 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). As a result, 91, 50, 62, and 94 occurrences were used for model fitting of straight-billed reedhaunter, *E. eburneum*, *E. horridum* and *E. pandanifolium*, respectively. For details on the number of records, occurrence resolution, and years of coverage about species occurrences, see Supplementary material Appendix 1 Table A1. We obtained 19 bioclimatic variables from WorldClim ver. 1.4 derived from monthly temperature and rainfall data obtained from global land area interpolation of climate point data (1970–2000 period) (Hijmans et al. 2005). The choice of the accessible area in SDMs is a crucial step in model calibration, and should represent an area that has been available to a species over relevant time periods (Barve et al. 2011). We therefore restricted distributions to the following phytogeographical regions on the basis of the regionalization proposed by Morrone (2014) and the shapefile provided by Löwenberg-Neto (2014): Pampean, Atlantic, Parana Forest and *Araucaria* Forest provinces for straight-billed reedhaunter, and Cerrado, Chacoan, Pampean, Atlantic, Parana Forest and *Araucaria* Forest provinces for *Eryngium* spp. (Fig. 2). To reduce collinearity among variables, a correlation matrix was computed based on 1000 points drawn randomly from each accessible area, and a subset of less correlated variables was selected (Pearson's correlations < |0.8|; Girini et al. 2017). Nine climatic (annual mean temperature range, mean diurnal range, maximum temperature of warmest month, temperature annual range, mean temperature of wettest quarter, annual precipitation, precipitation of driest month, precipitation of wettest quarter and precipitation of warmest quarter) and ten climatic variables (annual mean temperature range, mean diurnal range, isothermality, maximum temperature of warmest month, temperature annual range, mean temperature of wettest quarter, mean temperature of driest quarter, mean temperature of warmest quarter, annual precipitation and precipitation of wettest month) were selected for eryngos and straight-billed reedhaunter distributions, respectively. All layers used had a spatial resolution of 2.5 arc-min. It should be noted that occurrence data ranged between 46 (*E. eburneum*) and 200 (straight-billed reedhaunter) yr, but the WorldClim data only covered 30 yr (1970–2000).



Q3



Q4



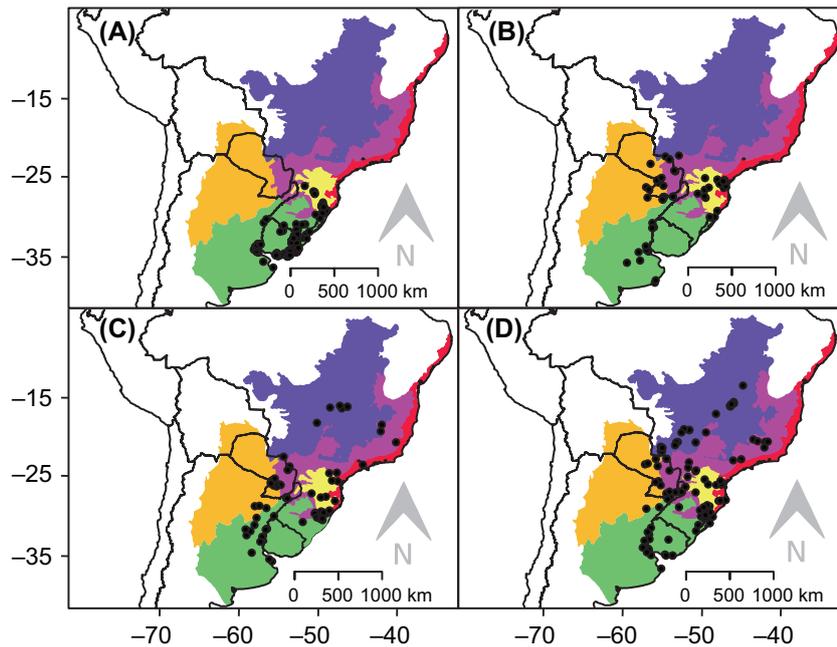


Figure 2. Current distributions of straight-billed reedhaunter (A), *Eryngium eburneum* (B), *E. horridum* (C) and *E. pandanifolium* (D). Points show the total number of occurrences recorded and colored areas show phylogeographical regions (following Morrone 2014) used as accessible areas. Green: Pampean province, orange: Chacoan province, yellow: *Araucaria* Forest province, violet: Parana Forest province, red: Atlantic province, blue: Cerrado province.

In the case of *Eryngo* species, pre-1970 occurrences represented a small number of records (two for *E. horridum* and *E. pandanifolium*, and four for *E. eburneum*), suggesting little impact on the SDMs. In the case of the straight-billed reedhaunter, in contrast, 18 pre-1970 occurrences were recorded. To avoid potential biases due to the presence of historical records (Labay et al. 2011, Faurby and Araújo 2018), the 18 records were confirmed to fall within its known distribution (Zimmer et al. 2013) or have contemporary records in the same locality (most of them).

SDMs were fitted using Maxent ver. 3.3.3k, which uses presence-only data to predict a potential species distribution (Phillips et al. 2006). For a detailed description on how the maximum entropy principle applies to SDMs, see Elith et al. (2011) and Merow et al. (2013). For each species, occurrence data were split into training data (75% of occurrence points) and test data (25% of occurrence points; Phillips et al. 2006). Because the default settings in Maxent have been shown to be inferior to tuned settings in simulations (Warren and Seifert 2011, Radosavljevic and Anderson 2014), we first selected regularization parameters β for optimal model calibration by computing Akaike's information criterion corrected for small sample sizes (AICc) to compare SDMs, which represents a trade-off between goodness-of-fit and model complexity (Warren and Seifert 2011). For each species, we fitted multiple models by progressively increasing the β -value from 1 to 15 by intervals of 1, and from 15 to 40 by intervals of 5 (Warren and Seifert 2011, Cao et al. 2013). For each model, we computed AICc values, and those models with lowest AICc were selected ($\beta_{E. eburneum} = 5$,

$\beta_{E. horridum} = 9$, $\beta_{E. pandanifolium} = 7$). Two models for the straight-billed reedhaunter were fitted: one model with climatic variables only (climate-only model) and another model with climatic variables and *eryngo* potential distributions (climate+biotic interactions model). Final models were based on the mean of 10 replicated models generated by cross-validation. Since several drawbacks of the AUC prevent its use as a measure of model performance (Lobo et al. 2008), models were calibrated on the training data and evaluated on the test data following two steps: we first tested whether model predictions were better than random expectations using the area under the partial receiver operating characteristics curve (pROC), which prioritizes omission error over commission error in estimating model robustness (Peterson et al. 2008). To do this, we used an acceptable omission error rate of 10% and 1000 bootstrap replicates on 50% of the test data to assess whether pROC values were significantly above 1.0 (α set at 0.05; Peterson et al. 2008). We then considered best models as those passing this filter and with smallest AICc in a range such that $\Delta AICc < 2$. Relative importance of individual predictors was assessed using jackknife tests, which compare the change in gain (a measure of model fit) of a model with a variable in isolation against a model without this variable but including the remaining ones (Phillips et al. 2006, Elith et al. 2011). The variable that causes the largest drop in training gain after being removed is considered the most important variable (Phillips et al. 2006). We also report percent contribution and permutation importance of each predictor to model performance (Phillips et al. 2006). Because the Eltonian noise hypothesis states that abiotic

factors are the only drivers limiting species distributions at large spatial scales (Soberón and Nakamura 2009), we accepted the hypothesis when all eryngo distributions were irrelevant to predict straight-billed reedhaunter distribution, and rejected it when at least one of eryngo distribution was important. A total of 130 models were run (four species, 20 regularization parameters, and 10 replicates for the best models).

Except for the SDMs, analyses and graphs were performed in R 3.3.1 (R Core Team) using the packages *dismo* (Hijmans et al. 2016), *maps* (Brownrigg 2016), *ENMeval* (Muscarella et al. 2014), *ENMGadgets* (Barve and Barve 2013) and *ggplot2* (Wickham 2009).

Niche overlap analysis

Under the supposed asymmetric nature of the relationship between the straight-billed reedhaunter and eryngos (i.e. the straight-billed reedhaunter would strongly depend on eryngos, but not the opposite), we would not only expect a low niche overlap between these species, but also that the straight-billed reedhaunter would largely be embedded within the n -dimensional hypervolumes of the eryngo species, termed asymmetric niche overlap (Kuppler et al. 2017). To test this hypothesis, we computed asymmetric niche overlap using dynamic range boxes, a novel robust nonparametric approach to quantify size of n -dimensional hypervolumes (Junker et al. 2016). Under an SDM framework, each environmental variable (climate and species interactions) represents one dimension of the hypervolume. Classical range boxes envelope all observed data per environmental variable delimited by the minimum and maximum value (Hutchinson 1957). However, this approach is highly sensitive to outliers and does not account for the distribution of the data (Junker et al. 2016). Dynamic range boxes overcome these problems by using quantiles in their computations, and thus both being little affected by outliers and considering the distribution of the data. The essence of the method is as follows: consider a dataset of n dimensions (i.e. environmental variables). For each dimension, the minimum and maximum (quantile 0–100%) are computed and then standardized to the range 0–1. The resulting intervals are defined as range boxes (Junker et al. 2016). As an example, imagine two environmental variables and a box around the data encompassing the quantile range 0–100% for each variable. Notice that for this quantile range, this represents a classical range box. The novelty of dynamic range boxes is that the procedure described is repeated for different quantiles containing a decreasing number of occurrences (e.g. 12.5–87.5%, 25.0–75.0%, 37.5–62.5%) until reaching a degenerated interval only containing the medians (Junker et al. 2016; see also Fig. 2 in Blonder 2017). A range box of a given dimension (i.e. side length of the box) is a measure of niche breadth, whereas the product of range boxes for the n dimensions reflects the hypervolume of the environmental space. Given that there is one range box per quantile per dimension, the resulting values are averaged across all the quantile

ranges. The overlap $port(A, B)$ is the portion of the volume of species B $vol(B)$ covered by the volume of species A $vol(A)$ (Junker et al. 2016). This is quantified as the mean volume of the intersection of $vol(A)$ and $vol(B)$ relative to $vol(A)$, and it is therefore asymmetric relative to $port(B, A)$. For instance, the portion of $vol(E. eburneum)$ covered by $vol(\text{straight-billed reedhaunter})$, i.e. $port(E. eburneum, \text{straight-billed reedhaunter})$, will be different to the portion of $vol(\text{straight-billed reedhaunter})$ covered by $vol(E. eburneum)$, i.e. $port(\text{straight-billed reedhaunter}, E. eburneum)$. For a full description of the method see Junker et al. (2016), and for an application see Kuppler et al. (2017). Asymmetric niche overlaps were computed with the package *dynRB* (Junker et al. 2016) using the 19 bioclimatic variables on occurrence data and default settings (number of range boxes = 201). Correlations between dimensions were reduced using a principal component analysis (Cruz-Cárdenas et al. 2014) and original dimensions were replaced with the first two principal components (explained variance >70%); otherwise, these may overestimate niche sizes and thus overlaps (Junker et al. 2016).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.XXXXXX>> (Palacio and Girini 2018).

Results

Models for each eryngo species showed high partial ROC values, indicating good model performance (pROC = 1.401–1.698, all $p < 0.001$). Precipitation of the driest month was the most important single predictor when used in isolation for *E. eburneum*, showing a positive relationship with climatic suitability (Fig. 3). However, the gain with and without this variable is unchanged and at its largest, which makes it uninterpretable. This entails a very high correlation with straight-billed reedhaunter suitability. Mean diurnal range, annual mean temperature and annual precipitation were the most important variables for *E. horridum*, showing negative (temperature predictors) and positive (annual precipitation) relationships with climatic suitability (Fig. 3). For *E. pandanifolium*, precipitation variables (annual precipitation and precipitation of the wettest quarter) were the most important predictors, showing positive and negative relationships, respectively, with climatic suitability (Fig. 3). Percent contribution and permutation importance showed similar results (Supplementary material Appendix 1 Table A2).

For the straight-billed reedhaunter, the climate-only model and the climate + biotic interactions model had pROC values averaging 1.737 ± 0.066 ($p < 0.001$) and 1.675 ± 0.043 ($p < 0.001$), respectively, indicating good model performance. Model evaluation revealed that including biotic interactions improved model fit. In particular, the inclusion of the three eryngo species into the model decreased AICc from 2036.8, for the climate-only model, to 1971.4, for the



Q8

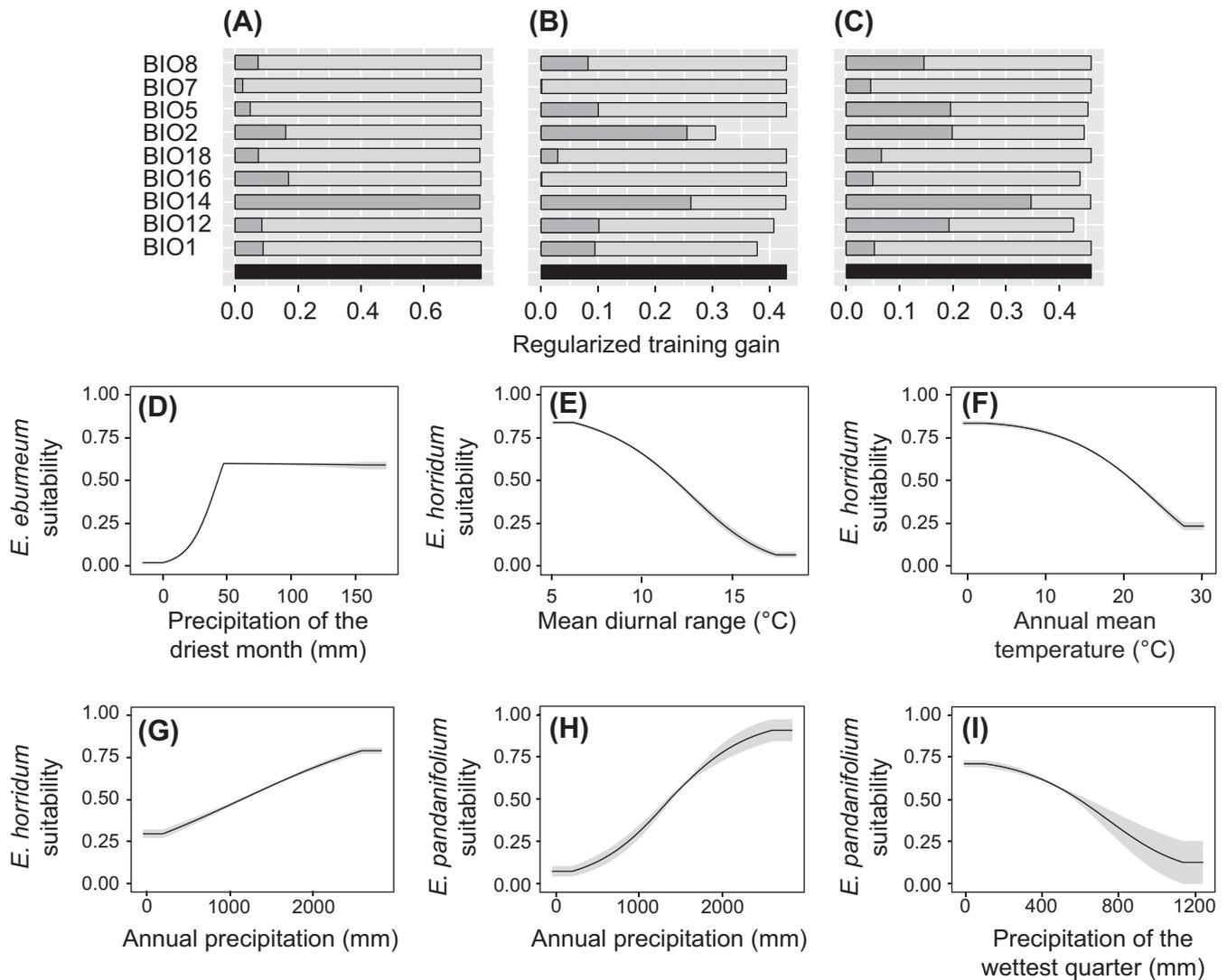


Figure 3. Important predictors for eryngo SDMs. Jackknife tests of environmental variable importance in SDMs relative to all environmental variables (black bars) for each predictor variable alone (dark gray bars), and the drop in training gain when the variable is removed from the full model (light gray bars) for (A) *Eryngium eburneum*, (B) *E. horridum* and (C) *E. pandanifolium*. Response-curves of the most important predictors for (D) *Eryngium eburneum*, (E-F) *E. horridum* and (G) *E. pandanifolium*. Black lines depict curves of each variable used in isolation to fit the model. BIO1: annual mean temperature, BIO2: mean diurnal range (mean of monthly (maximum temperature – minimum temperature)), BIO5: maximum temperature of warmest month, BIO7: temperature annual range, BIO8: mean temperature of wettest quarter, BIO12: annual precipitation, BIO14: precipitation of driest month, BIO16: precipitation of wettest quarter, BIO18: precipitation of warmest quarter. Gray bands depict one standard deviation.

climate + biotic interactions model (Table 1). Climatic suitability of *E. eburneum* and mean temperature of the wettest quarter were the most important predictors (Fig. 4). Straight-billed reedhaunter suitability showed positive relationships with the three interactor species, as expected, and a negative relationship with mean temperature of the wettest quarter (Fig. 4). Nevertheless, only *E. eburneum* was an important predictor, whereas *E. horridum* and *E. pandanifolium* resulted in poor predictors. Areas with mean temperatures between 9.42 and 16.32 °C in the wettest quarter, high climatic suitability of *E. eburneum* (0.54–0.59) had higher straight-billed reedhaunter suitability (Fig. 4). Both model predictions

matched well the known distribution of the straight-billed reedhaunter, yet the climate + biotic interactions model predicted highly suitable areas at the southeastern limit of Brazil

Table 1. Model comparison between straight-billed reedhaunter SDMs with climatic variables only and with climatic variables plus biotic interactions (*E. eburneum*, *E. horridum* and *E. pandanifolium* suitabilities). β indicates the optimal regularization parameter used by Maxent to fit models (see Methods).

Model	β	AICc	Δ AICc
Climate-only	4	2036.8	65.40
Climate + biotic interactions	8	1971.4	0.00

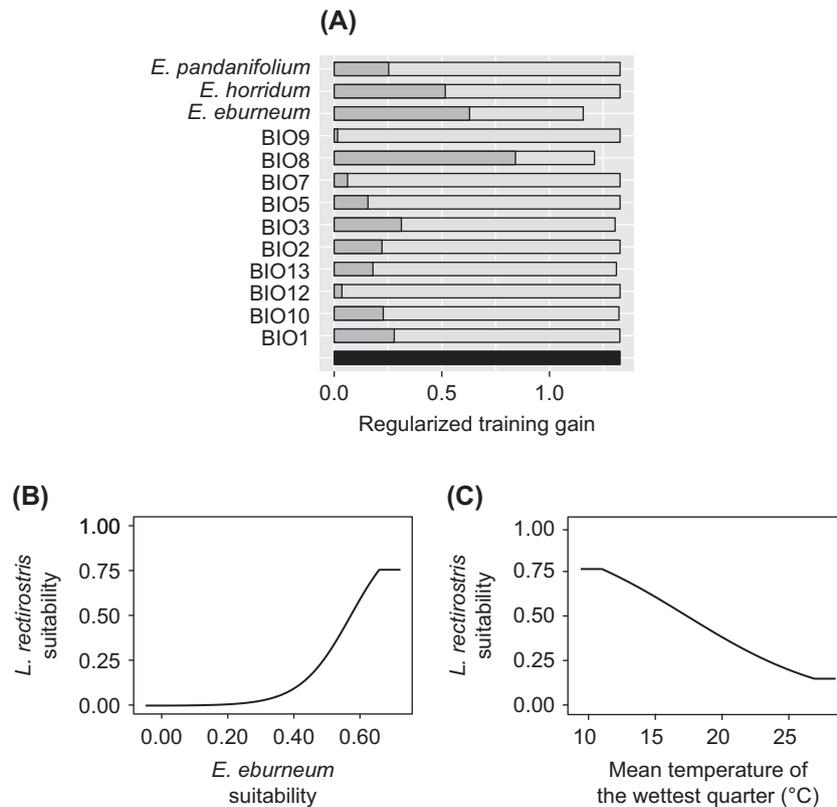


Figure 4. Important predictors for straight-billed reedhaunter SDM with climate + biotic interactions data. Jackknife tests of environmental variable importance in SDMs relative to all environmental variables (black bars) for each predictor variable alone (dark gray bars), and the drop in training gain when the variable is removed from the full model (light gray bars) is shown in (A) and response-curves of the most important predictors are shown in (B-C). BIO1: annual mean temperature, BIO2: mean diurnal range (mean of monthly (maximum temperature – minimum temperature)), BIO3: isothermality $100 \times (\text{BIO2}/\text{BIO7})$, BIO5: maximum temperature of warmest month, BIO7: temperature annual range, BIO8: mean temperature of wettest quarter, BIO9: mean temperature of driest quarter, BIO10: mean temperature of warmest quarter, BIO12: annual precipitation, BIO13: precipitation of wettest month. Gray bands depict one standard deviation.

(on the Atlantic shore and at the boundary between Brazil, Argentina and Uruguay), as well as at northwestern Uruguay, not predicted by the climate-only model (Fig. 5). Jackknife tests, percent contribution and permutation importance of the climate-only model showed identical qualitative results relative to the climate + interactions model (Supplementary material Appendix 1 Fig. A1, Table A3).

When comparing asymmetric niche overlap between species, the three eryngo environmental spaces largely covered the environmental space of the straight-billed reedhaunter whereas the opposite was not true, supported also by relatively large *port*(eryngo species, straight-billed reedhaunter) values (0.53–0.69) and low *port*(straight-billed reedhaunter, eryngo species) values (0.26–0.62) (Fig. 6).

Discussion

Our results suggest that biotic interactions play an important role in predicting the distribution of a rare bird at a geographical scale. These agree with previous findings, which

have shown that biotic interactions significantly improved predictions of SDMs of a wide array of taxa, including ectotherms (birds: Araújo and Luoto 2007, Heikinnen et al. 2007, Crystal-Ornelas et al. 2017, Atauchi et al. 2018; mammals: Bateman et al. 2012, Hof et al. 2012; reptiles: Delean et al. 2013; amphibians: Cunningham et al. 2008; insects: Giannini et al. 2013; plants: Boulangeat et al. 2012). This would be particularly true for specialist species depending on a small number of resources (Bateman et al. 2012, Giannini et al. 2013), although their assessment in SDMs of generalist species remains unexplored (but see Araújo et al. 2014).

Despite the controversial role of biotic interactions in SDMs, our results do not support the Eltonian noise hypothesis. As Soberón and Nakamura (2009) have pointed out, the Eltonian noise hypothesis is falsified when local interactions have an impact on distributions at geographic extents. In our case, one interactor species (*E. eburneum*) emerged as the most important predictor for the straight-billed reedhaunter distribution. Thus, it is likely that the interaction with eryngo species had an important effect on the distribution

Q6



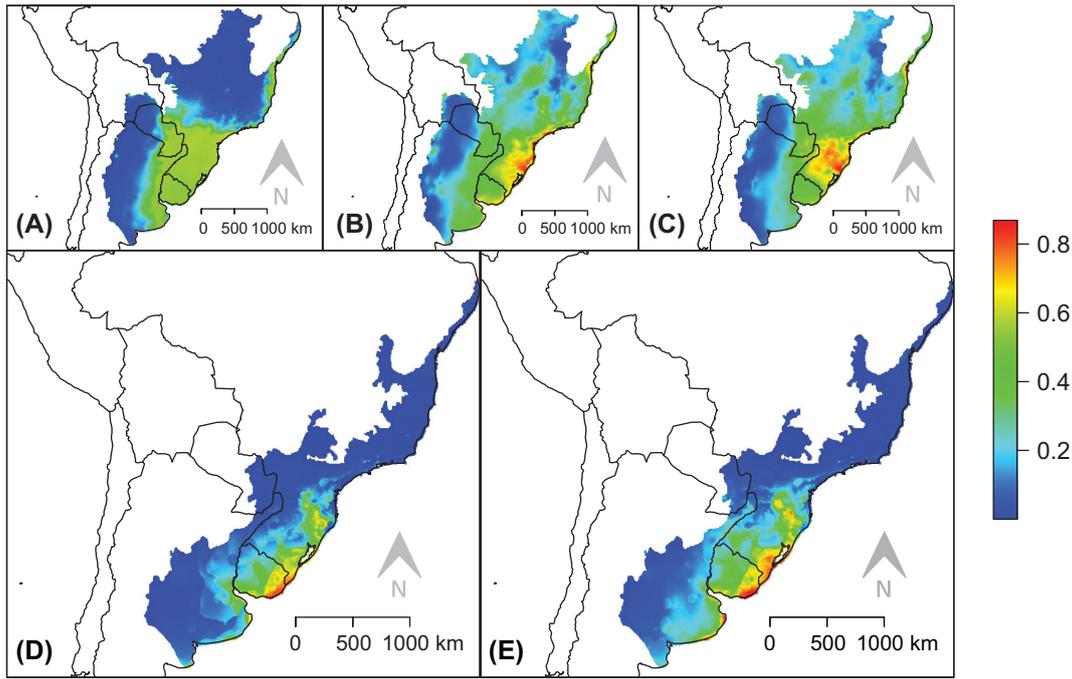


Figure 5. Potential distributions of (A) *Eryngium eburneum*, (B) *E. horridum*, (C) *E. pandanifolium*, (D) straight-billed reedhaunter with climate-only data, and (E) straight-billed reedhaunter with climate + biotic interactions data.

of the straight-billed reedhaunter, a specialist of marshy areas dominated by eryngo herbs which provide food and nest sites (Zimmer et al. 2003).

It should be noted that the approach adopted here, as well as the examples cited before, included habitat suitabilities or the presence-absence of interactors as proxies of biotic interactions. Biotic interactions are complex and dynamic to be accurately represented by a static model (Peterson et al. 2011,

Boulangeat et al. 2012, Anderson 2017). Therefore, a plausible explanation for the lesser importance of other biotic predictors (*E. horridum*, *E. pandanifolium*) relative to climatic predictors is the less accurate representation of biotic interactions through SDMs than climatic variables. In a recent and similar study, Atauchi et al. (2018) also found that biotic interactions (five plant SDMs used as inputs) improved the potential distribution of an endemic bird, the Peruvian Plantcutter (*Phytotoma raimondii*, Cotingidae), rejecting the Eltonian noise hypothesis. Although both studies support the relevance of biotic interactions in SDMs, the Eltonian noise hypothesis remains open to debate, highlighting the need to further both theoretical justification and empirical evidence.

Furthermore, the inclusion of biotic interactions into SDMs has confirmed previous knowledge on the natural history of a rare bird. Sparse data on the ecology of the straight-billed reedhaunter have shown that this species strongly depends on *E. eburneum*, *E. horridum* and *E. pandanifolium* to feed and nest (Zimmer et al. 2003, Olson et al. 2005), but its relative dependence on each plant was completely unknown. In particular, our SDM showed that one eryngo species was a more important predictor than the others, as it may be observed in the field (M. Gavensky pers. obs.). Specifically, *E. eburneum* was the main biotic interactor explaining straight-billed reedhaunter distribution, whereas *E. horridum* and *E. pandanifolium* had little predictive power. This suggests that the straight-billed reedhaunter would depend more on *E. eburneum* than on *E. horridum* and *E. pandanifolium*, at least at a geographical scale. It is worth mentioning that *E. eburneum* distribution may represent a confounding factor with the precipitation of the driest quarter, evidenced by its

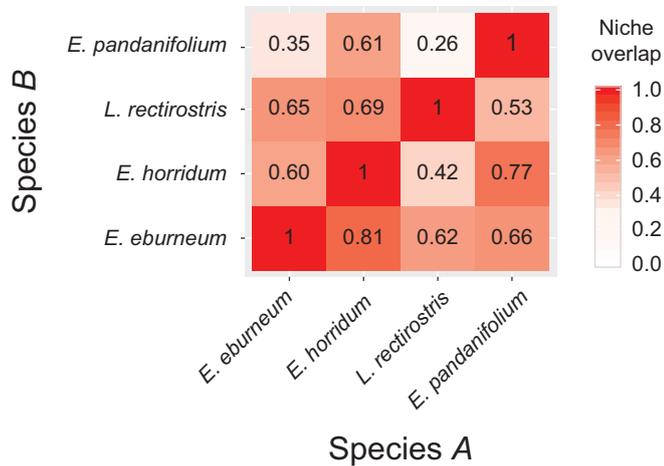


Figure 6. Heatmap showing the asymmetric niche overlap $port(A, B)$ of n-dimensional hypervolumes defined by the first two principal components on the 19 bioclimatic variables (scale bar). $port(A, B)$ sensu Junker et al. (2016) is defined as the portion of the niche volume of species B covered by the niche volume of species A (see Methods).

high correlation ($r=0.87$, $n=1000$). Moreover, precipitation is expected to be an important factor explaining its distribution, as areas inhabited by this species periodically flood (López-Lanús et al. 1999). Therefore, it is likely that both factors contribute to explain the distribution of the straight-billed reedhaunter, mediated by both direct (resources provided by *E. eburneum* and periodic floods resulting from precipitations) and indirect effects (the effect of precipitation on the distribution of *E. eburneum*) of these variables. In this case, a biotic factor correlated closely with an abiotic variable, which captured an important part of the biotic signature (Soberón and Nakamura 2009).

Niche overlap analysis supported an asymmetric relationship between the straight-billed reedhaunter and the three eryngo species, i.e. the straight-billed reedhaunter largely depended on eryngo distributions, but not the opposite. This is expected assuming that this interaction represents a commensalism rather than a mutualism (i.e. non-interactive variable), and suggests that other factors limit the expansion to areas where eryngo species are present, including historical and present-day factors. The approach adopted here also underscores another overlooked aspect of the inclusion of biotic interactions into SDMs, namely, the degree of dependence between interactors. In this sense, previous calculation of asymmetric niche overlap between interactors may provide a rapid assessment of potential species to be included as SDM inputs, especially if the number of interactors under scrutiny is large. Intuitively, a positive covariation between the relative importance of biotic interactors into SDMs and the degree of niche overlap is expected, because these both reflect the level of association between interactors. Although we found a high correlation between training gain and niche overlap despite a low sample size ($r=0.86$, $n=3$), studies assessing a greater number of interactors are needed to effectively determine the magnitude of this correlation.

From a philosophical perspective, both reductionism (i.e. the view that few mechanistic laws can explain and predict all the observable phenomena) and determinism (i.e. the view that every observable phenomenon has a single efficient cause) have had a prominent importance in classical philosophy of science, constraining the development of ecological theories (Pickett et al. 1994). Autoecology, for instance, has explained species distributions focusing on physiological responses of organisms to few abiotic factors along environmental gradients. Nevertheless, it has ignored the universal statement of ecology that organisms interact directly and indirectly with each other, being able to occur in sub-optimal conditions (Levins and Lewontin 1980). Overall, our study supports the idea that biotic interactions are relevant for SDMs at macro-scales, thus improving the understanding of species distributions. Although climatic conditions and other abiotic factors may also explain this ecological phenomenon, as the Eltonian noise hypothesis claims, biotic interactions seem to play an important role in modeling the distributions of many organisms, including rare and cryptic birds, such as the straight-billed reedhaunter. We therefore advocate the use of an integrative modeling approach, whenever possible,

including climate and biotic interactions into SDMs to enhance ecological knowledge on poorly-known birds.

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Supplementary material (Appendix JAV-01743 at <www.avianbiology.org/appendix/jav-01743>). Appendix 1.

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