

Predicting potential distributions of two rare allopatric sister species, the globally threatened *Doliornis* cotingas in the Andes

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ABSTRACT. Conservation of rare, elusive species is difficult because of limited knowledge of their biology and distribution. The two species of *Doliornis* cotingas are known from 7 (Chestnut-bellied Cotinga, *D. remseni*) and 13 (Bay-vented Cotinga, *Doliornis sclateri*) locations, respectively. Their limited ranges in combination with habitat loss make them vulnerable to extinction. We modeled the potential distribution of these two rare, allopatric sister species separated by an orographic barrier using species distribution modeling with an ensemble forecast approach using eight modeling techniques. Predicted distributions (with conservative thresholds of probability of presence, i.e., lowest presence thresholds) for these sister species showed virtually no overlap, although their respective niches were statistically not dissimilar. Hence, the existence of the recently discovered Chestnut-bellied Cotinga could not have been predicted from the range of its sister species, unless using very crude distribution models (with extensive extrapolation). New areas of likely occurrences were identified for both species, and the genus, and will be useful for directing future field searches. The estimates of potentially suitable range for both species still qualify both species as “vulnerable to extinction.” Our study illustrates how opportunistic records collected by field ornithologists can be objectively transformed, with the help of existing software, into information potentially useful in the conservation of rare species.

RESUMEN. Predicción de las distribuciones potenciales de dos especies hermanas alopatricas, los globalmente amenazados cotingas *Doliornis* en los Andes

Conservación de especies escasas es difícil por falta de documentación de su biología y su distribución. Las dos especies de cotingas *Doliornis* son conocidas de solo 7 (Cotinga de Remsen, *D. remseni*) y 13 (Cotinga de Sclater, *D. sclateri*) registros localizados precisamente. Su pequeña área de distribución y desaparición de su hábitat hace que son vulnerables a la extinción. Modelamos la distribución potencial de esas dos especies hermanas alopatricas, separadas por una barrera orográfica, utilizando ocho técnicas de modelo de distribución con un método de pronóstico de ensamble. Las distribuciones predichas (con niveles umbrales de probabilidad de presencia conservativos, el nivel umbral mínimo de presencia) para cada especie hermana eran casi completamente distintas. Así, el rango de distribución de la especie descubierta recientemente, *D. remseni*, no hubiera podido ser predicho con los registros de su especie hermana, *D. sclateri*, aunque hayamos utilizado modelos muy básicos (con extensiva sobre-predicción). Nuevas áreas de alta probabilidad de ocurrencia fueron identificadas para cada especie, y el género, y podrán servir para orientar futuros inventarios de campo. Las estimaciones de los rangos potencialmente favorables para cada especie siguen calificándolas como ‘vulnerables a la extinción’. Este estudio ilustra como registros masivamente colectados de manera oportunista por ornitólogos de campo pueden ser transformados objetivamente, con programas existentes, en conocimientos útiles para la investigación y la conservación de especies escasas.

Key words: allopatric sister taxa, alloprediction, BIOMOD, distribution range, species distribution modeling, tropical montane forest

Field ornithologists are the very first providers of distributional data for rare or elusive species. Following the discovery of new sites of occurrence, revisions of species distribution ranges are regularly published. Often, only a descriptive or mapping interpretation of these records is

provided. Conclusions are highly sensitive to reporting biases, such as stochastic nondetection or inaccessibility of potentially suitable areas (a common problem in the tropics). One method for making a parsimonious use of these scattered, anecdotal data is to identify probabilistic species distributions with models. These models combine occurrence data with environmental data to statistically identify areas resembling the

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locations where the species is known to occur (Araújo and New 2007, Pearson et al. 2007, Thuiller et al. 2009). Such niche modeling is becoming an important tool in conservation and biogeography, providing spatially explicit, predicted distribution ranges that are robust to the usual lack of previous ecological and distributional knowledge of poorly known taxa (Guisan et al. 2006). This feature is particularly useful for species known from a limited number of locations, including poorly detectable, inconspicuous or low-density species, species in remote, poorly investigated habitats, or recently discovered species (Raxworthy et al. 2003, Engler et al. 2004, Franklin et al. 2009, Marini et al., 2010). These models are increasingly used by field ornithologists to exploit bird distributional data (e.g., Rojas-Soto et al. 2008, Henry and Aznar 2009).

From a conservation perspective, niche modeling provides a methodological framework for identifying spatially optimal conservation strategies, such as designing networks of priority areas (Marini et al. 2009a) or targeting conservation efforts for threatened species (Peterson and Robins 2003, Thorn et al. 2009, Marini et al. 2009b) and regional diversity hotspots (Myers et al. 2000, García 2005). From a biogeographical perspective, one achievement of niche modeling is the ability to predict the distribution of unknown, still to be discovered, species from modeled distributions of closely related known species in cases of niche conservatism in evolutionary time (Raxworthy et al. 2003) or niche similarity between phylogenetically closely related species (Warren et al. 2008). Theory supports this assumption of niche conservatism, or similarity between closely related species, predicting low niche differentiation between vicariant species over evolutionary time scales (Ricklefs and Latham 1992). Further empirical work documented the conservative nature of ecological niche evolution by successfully extrapolating distributions of closely related species using data from the other species (Peterson et al. 1999), and phylogenetic information has been combined with species distribution modeling to explore speciation mechanisms (Graham et al. 2004). Indeed, in practice, for closely related allopatric species pairs, niche conservatism can be deduced from areas of overprediction (i.e., areas where presence is predicted outside of the actual range) in one-species

models that actually fit the known description range of the other species (Peterson et al. 1999, Raxworthy et al. 2003, Pearson et al. 2007).

Our objective was to improve our knowledge of two rare sister, tropical humid montane forest bird species, Bay-vented Cotingas (*Doliornis sclateri*) and Chestnut-bellied Cotingas (*D. remseni*), by analyzing previously reported (Appendix 1) and new (Henry 2008) occurrence data. These species are restricted to humid montane forests at elevations ranging from 2740—to 3800 m in the central and northern Andes (Ridgely and Tudor 1994, Ridgely and Greenfield 2001, BirdLife International 2010). Bay-vented Cotingas were discovered in 1871 at Maraynioc, Peru (Taczanowski 1874; see Appendix 1) and subsequently reported at 13 other locations, all on the east slope of the eastern Peruvian Andes (Appendix 1). Chestnut-bellied Cotingas were first observed in the field in 1989 and described as recently as 1994 (Robbins et al. 1994), and are known from only 10 locations on the eastern slope of the Andes in Ecuador and from the central Andes of Colombia (Appendix 1). These two species are separated by an orographic barrier, that is, an area of low elevation (2000–3000 m) and arid habitats delimiting the northern and central Andes called the North Peru Low (NPL). The NPL is regarded as a major biogeographic barrier, and a transitional area for many sister-species pairs of the high-elevation montane forest (Cracraft 1985, Stotz et al. 1996; but see Parker et al. 1985, García-Moreno and Fjeldså 1999). We first modeled the distribution range of the two sister species, then tested for evolutionary niche similarity (Warren et al. 2008) between the two species on both sides of the biogeographic barrier. We also tested the hypothesis that the existence and distribution of the most recently discovered species (Chestnut-bellied Cotinga; first described by Robbins et al. 1994) could have been predicted with location data from its sister species described 120 yr earlier (Bay-vented Cotinga). We further used all 20 reported locations for both species to model the potential distribution of the genus *Doliornis*. If a more robust prediction of the overall lineage's potential distribution could be achieved (Graham et al. 2004), it may be possible to identify areas where one of the two species, or a still unknown congeneric species, may remain to be discovered. Identifying such gaps

should ensure that most of the remnant patches of humid montane forest that potentially still host a *Doliornis* cotinga can be identified and considered in conservation planning. Our study illustrates how species distribution modeling could be used for assessing the distribution and conservation status of rare species known only from scattered, opportunistic records collected by field ornithologists (Bourg et al. 2005, Peterson and Papes 2007, Rojas-Soto et al. 2008, Marini et al., 2010).

METHODS

Study species and occurrence localities.

Both *Doliornis* species are rare to locally uncommon, with population sizes in the range of 2500–9999 individuals (BirdLife International 2010). They are confined to dense thickets in the páramo-cloud forest ecotone at elevations of 2875–3650 m for Chestnut-bellied Cotingas (Appendix 1; *contra* Ridgely and Greenfield 2001) and 2740–3800 m for Bay-vented Cotingas. The low number of known localities for *Doliornis* cotingas is likely due to their low density and their inconspicuous, low-volume calls, lethargic perching behavior, and remote habitats. The biology of both *Doliornis* species is poorly known (Henry 2008, BirdLife International 2010).

Data for presence records (Appendix 1) were extracted from original publications, complemented with direct contact with observers and collection curators, to assess the precision of the published coordinates. For niche modeling to be as robust as possible when the number of occurrence records is very low, geographical coordinates of sites need to be precise and species identification verified. Three Chestnut-bellied Cotinga records were therefore discarded: locations 3 and 9 (Appendix 1) because of imprecise locations, and location 4 because of lack of appropriate habitat in the area and a posteriori identification (J.F. Freile in Henry 2008). Two Bay-vented Cotinga records were obtained in the same pixel of the study area (locations 2 and 3; Appendix 1) so were not replicated in the data we used for modeling. We thus used 13 locations for Bay-vented Cotingas and seven for Chestnut-bellied Cotingas.

Environmental variables. To model the potential distribution of the two species, we considered a geographic area defined by country

borders, including Peru, Ecuador, Colombia, and Venezuela. Within this area, we obtained data concerning 11 environmental variables obtained at a resolution of 2.5 s (i.e., about a 4.5 km × 4.5 km pixel). We restricted the study area to pixels with an average altitude over 2000 m to consider only the altitudinal range where both species may occur. We extracted three topographical variables from the Hydro-1K dataset of the USGS (<http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html>), namely slope, aspect, and the compound topographic index. The slope describes the maximum change in elevation between each cell and its eight neighbors. The slope is expressed in integer degrees between 0 and 90. The aspect describes the direction of maximum rate of change in the elevations between each cell and its eight neighbors and gives the slope direction, measured in positive integer degrees from 0 to 360 (clockwise from north). The compound topographic index, commonly referred to as the wetness index, is a function of the upstream contributing area and the slope of the landscape. We further used eight climatic variables from the BioClim database (<http://cres.anu.edu.au/outputs/anuclim/doc/bioclim.html>) that are integrative annual or seasonal climatic variables: annual mean temperature (BIO1), temperature seasonality (BIO4), maximum temperature of the warmest month (BIO5), minimum temperature of the coldest month (BIO6), annual precipitation (BIO12), precipitation seasonality (BIO15), and amount of precipitation during the wettest (BIO13) and driest (BIO14) months. We did not consider vegetation layers in the modeling runs because of a large temporal mismatch between the bird occurrence data (mostly collected in the 1970s, but one in the 19th century) and available vegetation layers (like the Leaf Area Index or the NDVI, for the 2000s; see Myneni et al. 2002, Parra et al. 2004). Massive deforestation occurred between these two periods (Stotz et al. 1996, Renjifo et al. 2002, BirdLife International 2010). As a result, this temporal mismatch could lead to, at best, a weak and, at worst, a false modeled effect of vegetation on bird occurrence. We wanted, first, to objectively identify the potential distribution areas with relatively stationary ecoclimatic variables and, second, to include a posteriori the relationship to current, suitable habitat availability (cf.

section “Extents of occurrence and vegetation coverage”), hence identifying areas where the species may have disappeared due to habitat loss.

Species distribution modeling. We used eight different niche-based modeling techniques with the BIOMOD computational framework (detailed by Thuiller et al. 2009): (1) generalized linear model (GLM), a regression method with polynomial terms for which a stepwise procedure is used to select the most significant variables, (2) generalized additive model (GAM), another regression method with four degrees of freedom and a stepwise procedure to select the most parsimonious model, (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance, (4) artificial neural networks (ANN), a machine-learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results, (5) mixture discriminant analysis (MDA), a classification method based on mixture models, (6) multivariate adaptive regression splines (MARS), a regression method, (7) generalized boosting model (GBM), a machine-learning method that combines a boosting algorithm and a regression tree algorithm to construct an “ensemble” of trees, and (8) Random Forest (RF), a machine-learning method that is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all trees in the forest. All models require information about presence and absence to be able to determine suitable conditions for a given species, so a set of 10,000 pseudo-absences was selected at random from the overall area to calibrate the models. The models compute a probability distribution based on environmental variables spread over the entire study area and assign a probability of suitability to each cell in the study area.

Presence threshold and Jackknife testing. To validate and interpret models, distinguishing suitable from unsuitable areas is necessary and is achieved by setting a decision threshold above which the model output is interpreted as predicting presence (Pearson et al. 2004). Different approaches have been employed for setting thresholds (Liu et al. 2005), and they must be chosen carefully

because receiver operating characteristic (ROC) tests can be weak at discerning models able to predict species’ distributions in broad, unsampled areas from those that cannot (Peterson et al. 2007), and are difficult to implement when presence data are scarce. The threshold we used was the lowest predicted value associated with any one of the observed presence records, called the “lowest presence threshold” (LPT). This approach can be interpreted ecologically as identifying pixels predicted to be at least as suitable as those where a species has been recorded as present; it is thus conservative, identifying the minimum predicted area possible while maintaining zero omission error in the data set of known occurrences (Pearson et al. 2007). Such a threshold may be too conservative for species known from very few locations, that is, where available records may not represent the whole range of ecoclimatic conditions where the species might occur. In that case, the variability of the output among the different modeling techniques can be used to further assess the robustness of the predictions of species presence.

Because of the importance of model assessment and small numbers of locations for both species, the predictive performances of our models were tested with a jackknife (or “leave-one-out”) procedure (Pearson et al. 2007). Each observed location was removed from the data once, and a model was built using the remaining $n - 1$ localities. Predictive performance was then assessed based on the ability of each model to predict the single location excluded from the data set. We tested the statistical predictive performance of a model with the program of Pearson et al. (2007). For each modeling technique and each species, this program returns a P value that is the probability of predicting randomly the known locations, according to the total area predicted as suitable by the model using a given threshold and the success in predicting the single excluded location. This procedure was conducted for all eight modeling techniques for each data set (Bay-vented Cotinga, Chestnut-bellied Cotinga, and *Doliornis* sp.) using the LPT as threshold.

Ensemble forecast and contribution of variables. Ensemble forecast techniques attempt to account for variability among species distribution models to determine the central tendency (Araújo and New 2007). For each

taxon, the consensus distribution was obtained by selecting the outputs of those modeling techniques validated by the jackknife tests (leave-one-out procedure), that is, those modeling techniques with P -values < 0.05 . We then produced maps reporting the unweighted average suitability of the selected models (Marmion et al. 2009). Contributions of the variables to the models were obtained with the BIOMOD computer platform. Independently, we characterized the contributions of the variables to the definition of the bioclimatic niche of each species and the genus by running a principal component analysis (PCA) and plotting coordinates of the 20 independent *Doliornis* locations along the first and second principal components.

Interpredictivity and genus distribution model. To assess ecological similarity between the two sister species, we used one of the statistical tests of niche conservatism described by Warren et al. (2008). We tested the equivalency of the niches of the two species by looking at the similarity between the modeled niches. We calculated two similarity indices, D and I (ranging from 0 when there is no overlap to 1 when niche models are identical), that allow the plausibility of niche equivalency between the two species (i.e., no statistical difference between alternative niche models) to be assessed. To know if these similarity measures were different from what could be obtained randomly, we created 100 null distributions, as proposed by Warren et al. (2008), by considering 100 randomly partitions of the 20 locations in groups of 13 and seven locations for which the same similarity indices were estimated. We then compared the D and I values obtained for the species-specific data and the distributions of those obtained for the 100 null distributions.

Finally, we used a data set containing all 20 locations from both species to model the potential distribution of the genus *Doliornis* as a whole, potentially helping to identify new areas of occurrence for both species or undescribed related taxa. This model was evaluated using the same leave-one-out procedure, and we produced the same ensemble forecast maps.

Extents of occurrence and vegetation coverage. The extent of occurrence is defined as the area within the shortest continuous imaginary boundary that can be drawn to encompass all known, inferred, or projected sites of present occurrence of a species, excluding

cases of vagrancy (IUCN 2001). We estimated the potential extent of occurrence using the ensemble forecast predictions for each species in the study area. We summed the suitability values of all pixels where a given species was predicted as present by models retained in the ensemble forecast prediction, considering only suitability values above the LPT. By multiplying these sums by the pixel area (ca. $4.6 \text{ km} \times 4.6 \text{ km}$, or 21.16 km^2 , in the latitudinal range 10°N to 10°S), we obtained an estimate of the potential extent of occurrence of each species in km^2 . These estimates were compared to previous estimates of extent of occurrence (BirdLife International 2010).

To account for actual habitat suitability, we used land-cover data from the vegetation map for South America published by Eva et al. (2002). This cover is a layer of 73 vegetation types at a $1 \text{ km} \times 1 \text{ km}$ scale. In a conservative approach, we retained as suitable all vegetation types that could include some of the habitat of *Doliornis* cotingas at the pixel level, including mosaic agriculture/degraded forests, closed shrublands, closed and open montane grasslands, and all montane forests ($> 1000 \text{ m}$, the only available elevation threshold) except closed and open deciduous forests. Several of these habitats are not suitable for *Doliornis* cotingas, but, given the square kilometer scale used, their habitat (páramo-cloud forest ecotone) might occur within squares dominated by these vegetation types. To obtain estimates of potential distribution sizes corrected for habitat suitability, we first redefined pixel size of the distribution output with a bilinear interpolation to fit that of the vegetation map (so a $1 \text{ km} \times 1 \text{ km}$ scale). We then recalculated the estimate of extent of occurrence for each species for pixels that (1) had a suitable habitat (from the vegetation map), and (2) were considered suitable for a species given the threshold (LPT).

RESULTS

Jackknife model testing. The jackknife tests of the ability of the different models to predict excluded localities were implemented with prediction thresholds set at the LPT. The results of the tests are presented in Table 1, with the success rate and associated P -values for each modeling technique per species and for the genus. To produce the ensemble forecast

Table 1. Jackknife tests of the ability of the different models to predict excluded localities, and performed to validate or not the modeling techniques for each data set. Models in bold are those used in the ensemble forecasts. See the “Methods” section for descriptions of the different models.

Group		GLM	GAM	CTA	ANN	MDA	MARS	GBM	RF
<i>D. sclateri</i>	Success rate	0.85	0.77	0.69	0.77	1	0.85	0.62	0
	<i>P</i> value	<0.001	<0.001	<0.001	<0.001	0.46	<0.001	<0.001	1
<i>D. remseni</i>	Success rate	0.71	1	0.86	0.14	0.71	0.43	0.14	0
	<i>P</i> value	0.006	1	<0.001	0.42	1	0.88	1	1
<i>Doliornis</i> sp.	Success rate	0.84	0.84	0.95	0.79	0.95	0.89	0.47	0
	<i>P</i> value	<0.001	<0.001	<0.001	<0.001	0.48	<0.001	<0.001	1

predictions, we first retained the modeling techniques with significant *P*-values ($P < 0.05$), then restrained the subset to the four models with the best success rates: GLM, GAM, ANN and MARS for Bay-vented Cotingas, GLM and CTA for Chestnut-bellied Cotingas, and GLM, GAM, CTA and MARS for *Doliornis* sp.

Predicted distribution ranges. For both species, variables that contributed most to the models were maximum temperature of the

hottest month (BIO5) and minimum temperature of the coldest month (BIO6). For Bay-vented Cotingas, precipitation seasonality (BIO15) contributed to the same extent. The graphic output of the PCA conducted on the values of the 11 environmental variables for the 20 locations (7 for Chestnut-bellied Cotinga—DR, and 13 for Bay-vented Cotinga—DS) is provided in Figure 1, and reveals that locations of the two species already segregate along the first

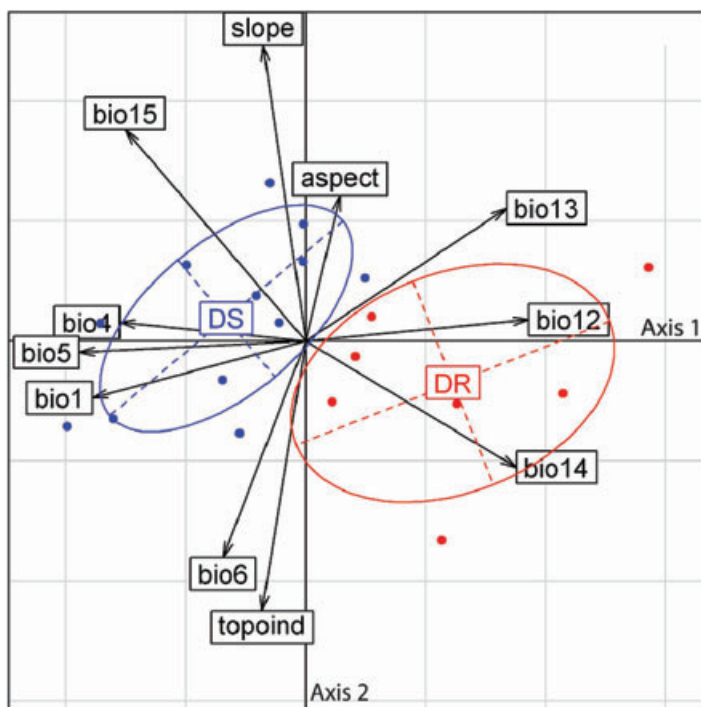


Fig. 1. Graphic output of a principal component analysis (the two axes are the first two principal components) based on 11 environmental variables (see Methods for details) for the 20 locations where *D. remseni* and *D. sclateri* have been observed (7 for *D. remseni*—DR, in red; 13 for *D. sclateri*—DS, in blue). Ellipses of 95% confidence interval are shown for each species.

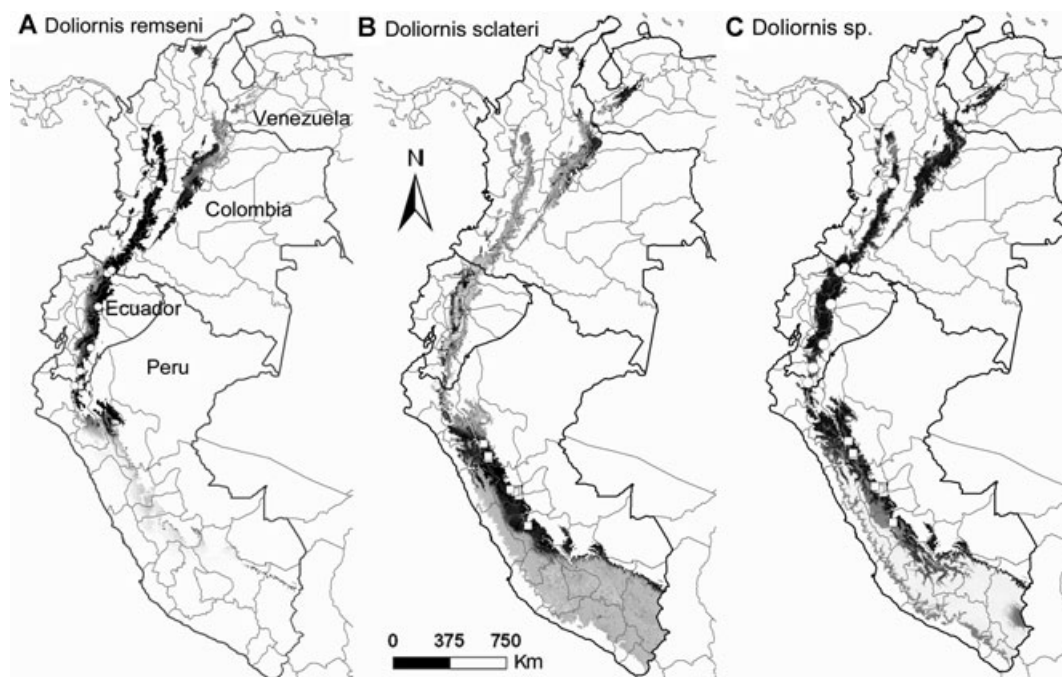


Fig. 2. Predicted distribution ranges of (A) Chestnut-bellied Cotingas (*Doliornis remseni*), (B) Bay-vented Cotingas (*Doliornis sclateri*), and (C) the genus *Doliornis* sp. (combining the data from the two species) in the Andes as the average suitability across models contributing to the ensemble forecast predictions and for those areas where the suitability values overpass the mean lowest presence threshold (LPT). The color gradient (light, medium, and dark) represents the increasing average niche suitability (ranging from 0 to 1). Also depicted are record locations used in modeling (dots and squares) and country and province borders.

axis (51.5% of explained variance) characterized by a positive association with precipitation (BIO12-13-14) and a negative association with temperature (BIO1-4-5). Chestnut-bellied Cotingas is positively associated with this axis, whereas Bay-vented Cotingas loads negatively. The distribution maps obtained by the ensemble forecast predictions are presented in Figure 2A (Chestnut-bellied Cotinga) and Figure 2B (Bay-vented Cotinga). The ensemble forecast predictions were also obtained for the complete set of all *Doliornis* locations ($N = 20$) to model the potential distribution range of the genus (Fig. 2C).

Niche similarity between sister species.

The PCA already revealed that locations of both species largely diverged for at least four bioclimatic variables. With the conservative LPT threshold, species-specific models could not predict any occurrence of the other species. When considering the ensemble forecast model calibrated with the data for Chestnut-bellied

Cotingas, the average suitability of Chestnut-bellied Cotinga locations was 0.806, whereas the average suitability of the 13 Bay-vented Cotinga locations was 0.102. Similarly, when considering the ensemble forecast model calibrated with the data for Bay-vented Cotingas, the average suitability of Bay-vented Cotinga locations was 0.873 and the average suitability of the seven Chestnut-bellied Cotinga locations was 0.051. Finally, the two indices of niche similarity had low values ($D = 0.241$ and $I = 0.526$), smaller than any of the values obtained for the 100 null distributions. Hence, the niches of the two species can be considered dissimilar.

Estimated extents of occurrence. Estimated extents of occurrence—the sum of suitability values for pixels with values above the LPT as predicted by the ensemble forecast—were 22 498 km² for Bay-vented Cotingas and 62 616 km² for Chestnut-bellied Cotingas. After accounting for habitat suitability within these probabilistic ranges (i.e., discarding pixels with

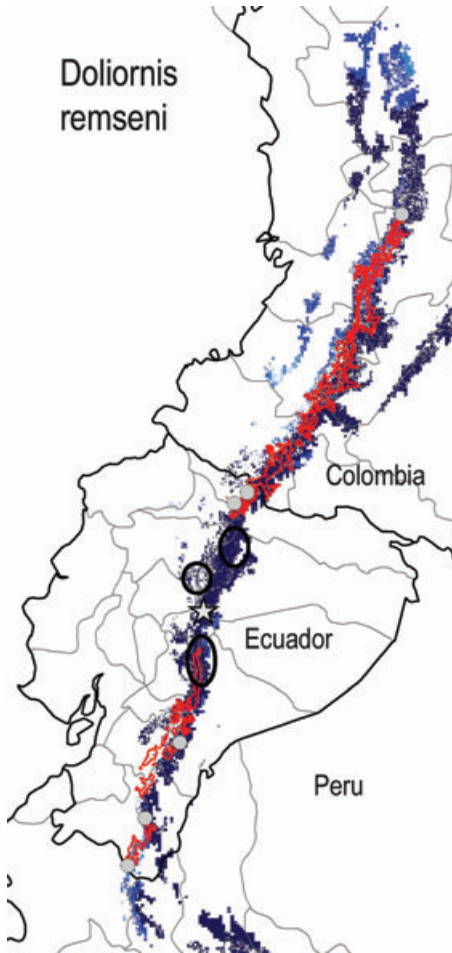


Fig. 3. Predicted distribution of *D. remseni* restricted to suitable vegetation cover, overlaid on the BirdLife International (2010) range map (in red). The blue color gradient (light, medium, and dark) indicates the increasing average niche suitability (ranging from 0 to 1) within the ensemble forecast predictions. Also shown are country (black) and province (gray) borders, and species records, including those used in modeling (gray dots), imprecise locations (black ovals), and a doubtful record (black circle, in Henry 2008). The gray star outside the BirdLife International's range is a new location (Henry 2008).

predicted presence, but unsuitable habitat and further restricting the range to the north or south of the NPL according to the species), predicted extents of occurrence were down to 37 672 km² for Chestnut-bellied Cotingas (Fig. 3) and 14 790 km² for Bay-vented Cotingas (Fig. 4).

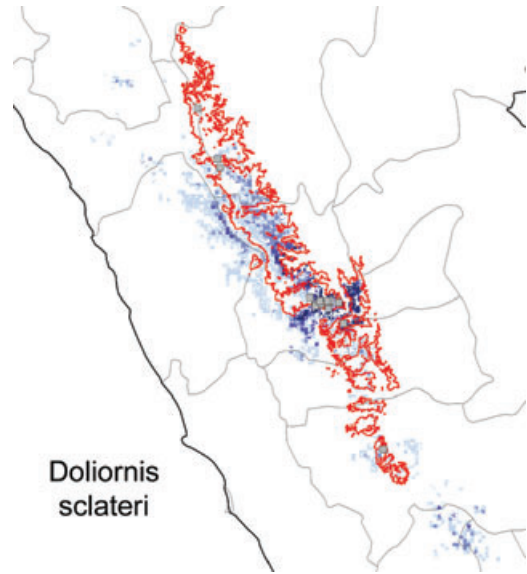


Fig. 4. Predicted distribution of *D. sclateri* restricted to suitable vegetation cover, overlaid on the Nature-Serve (Young et al. 2009) range map (in red). The blue color gradient (light, medium, and dark) indicates the increasing average niche suitability (ranging from 0 to 1) within the ensemble forecast predictions. Also shown are country (black) and province (gray) borders, and species records used in modeling (gray squares).

DISCUSSION

Modeling performance and predicted distributions. When trying to predict the distribution ranges of rare species, having a small number of occurrence locations available for modeling is a problem. However, for the rare cotingas in our study, the predicted distributions were statistically powerful, that is, they predicted distributions better than expected even with few locations. This could be due to the highly specific habitat used by *Doliornis* cotingas, that is, mainly treeline of Andean humid montane forest (Henry 2008). This habitat is confined to a very narrow ecoclimatic zone, making delimitation with climatic variables easy and robust (Parra et al. 2004). Robustness of models is illustrated when projecting known localities that were excluded from the analysis onto the predicted distribution range of Chestnut-bellied Cotingas. This species was known to occur at two additional locations (3 and 9 in Appendix 1),

but precise locations for these records were lacking. Approximate locations (Fig. 3), owing to location names, indeed point to large areas of continuous suitable areas (over 0.80 probability of suitability for the species in darker blue). The record from location 4 (see Appendix 1) was considered doubtful because of a lack of appropriate habitat in surrounding areas (J.F. Freile in Henry 2008). This is supported by the intermediate (0.5) probability of bioclimatic suitability in this area, mostly below the LPT (Fig. 2A), and the actual lack of suitable habitat (Fig. 3). For Bay-vented Cotingas, we compared our model output with those of the NatureServe project (Young et al. 2009; Fig. 4). Again, the core areas of the distribution range of Bay-vented Cotingas are congruent among both distribution-modeling projects. The comparison also reveals major western overpredictions by our model, even with the LPT. Note that thresholds for the NatureServe project were defined a posteriori, according to expert judgment. Reviewers were asked to choose the predicted distribution maps that looked the most reasonable. Thus, by construction, overpredictions are strongly minimized in such predicted distribution ranges compared to our models' output.

Based on the current state of knowledge of *Doliornis* distributions (Ridgely and Tudor 1994, Ridgely and Greenfield 2001, Henry 2008), these species avoid the western slopes of the Andes (except at locations 2 and 5; see Appendix 1). However, our models predict their occurrence further west than actually known (e.g., western Colombia, west side of the central inter-Andean valley in Ecuador, and west of the Río Marañón valley in Peru). Several factors suggest that these western extrapolations are unwarranted (unless future inventories provide supportive evidence for them). First, according to field visits by J. Fjeldså (pers. comm.), climatic conditions seem inappropriate for *Doliornis* cotingas in these western areas. At similar elevation, the habitat is much drier on the western slope than the eastern slope. In addition, no *Doliornis* was recorded in these western areas despite several intensive investigations (e.g., Imbabura, Pichincha, and Azuay provinces in Ecuador; Krabbe et al. 1998, Ridgely and Greenfield 2001; several departments in Peru, J. Fjeldså, pers. comm.). Also, if we consider the occurrence of vegetation types (compare Figs. 2A—and B

and 3–4), the western part of the predicted range turns out to be largely unsuitable for *Doliornis*. And, finally, for Chestnut-bellied Cotingas, the western part of the predicted distribution appears highly fragmented, with few continuous areas of high occurrence probability. This is particularly evident when comparing fragmentation of the eastern versus western parts of the range. This suggests that the western overprediction areas are unlikely to host *Doliornis* populations. Even though these areas may have hosted suitable humid montane forest in the past, humans may have largely modified these habitats, rendering them unsuitable for *Doliornis* (Stotz et al. 1996, Renjifo et al. 2002, BirdLife International 2010). Actually, the western overprediction areas fit well with zones of dense, traditional, rural human populations (cf. Fig. 7b in Fjeldså et al. 1999).

Environmental niches of allopatric sister species. We found a common ecological influence of environmental components when defining the ecological niches of the two sister species, corresponding to the hottest and the coldest temperatures of the year. Overall, observed locations of one species could not be predicted by the niche model developed for the sister species. Hence, the existence of the recently described Chestnut-bellied Cotinga (Robbins et al. 1994) could not have been predicted by extrapolation from a species distribution model calibrated with occurrence data for its previously described sister species, the Bay-vented Cotinga. This is also supported by the nonequivalence of the niches of the two species.

Peterson et al. (1999) showed conservatism in ecological niches evolution for 37 pairs of sister bird, mammal, and butterfly species isolated on either side of a lowland barrier in southern Mexico. In contrast, niche divergence was revealed in some sympatric sister species (Sattler et al. 2007). Indeed, conservatism or divergence of ecological niches depends on the speciation mechanisms involved. Strict vicariant speciation depends simply on geographic isolation, and niche conservatism is expected (e.g., Peterson et al. 1999). Other scenarios, such as the peripheral isolates model of speciation and many models of sympatric speciation (Futuyma 1997), invoke invasion of novel ecological situations as part of the speciation process. In the case of *Doliornis*, sister taxa are found in similar habitats (east slope, humid montane forest) on

both sides of a low-elevation orographic barrier, the NPL, proposed as a major biogeographic barrier for high-elevation montane forest species (Cracraft 1985, Parker et al. 1985, García-Moreno and Fjeldså 1999). Their phenotypes are similar, with limited differentiation (Robbins et al. 1994). Along with simple vicariant isolation and low phenotypic differentiation, niche conservatism was expected. Molecular data suggest that the *Doliornis* clade (Ohlson et al. 2007) dates back to the mid-Miocene (García-Moreno and Fjeldså 1999), and vicariance of the *Doliornis* species would date from the mid-Pleistocene (García-Moreno and Fjeldså 1999). Thus, vicariance would be just posterior to the late Miocene uplift of the northern Andes and to the formation of the NPL (García-Moreno and Fjeldså 1999). To resolve the incongruence between vicariance and observed niche divergence, we hypothesize that niches differentiated after the isolation event, while species adapted to north–south variations in bioclimatic conditions of their habitat, the páramo-cloud forest ecotone. To test the generality of niche conservatism/divergence in the Andes, similar patterns of ecological divergence could be tested among other sister allopatric taxa occurring north and south of the NPL, for example, with the 21 species pairs identified by Parker et al. (1985) and García-Moreno and Fjeldså (1999).

Distributions and conservation. According to IUCN (2001) Red List criteria, Chestnut-bellied Cotingas is classified as vulnerable because of its small, decreasing population, and restricted, declining extent of occurrence, area of occupancy, and area/extent/quality of habitat (BirdLife International 2010). Bay-vented Cotingas also qualified as vulnerable for the same reasons, but less evidence of critical habitat loss is available for this species (BirdLife International 2010). The potential extent of occurrences that we estimated (about 37 000 km² for Chestnut-bellied Cotingas and 15 000 km² for Bay-vented Cotingas), with the LPT threshold and after accounting for habitat availability, are different from the estimated Extents of Occurrence provided by BirdLife International (2010; 10 900 km² for Chestnut-bellied Cotingas, 13 100 km² for Bay-vented Cotingas). For Chestnut-bellied Cotingas, the new record locations (Henry 2008) explain this difference to some extent. However, our estimate includes

large, northern areas of predicted occurrence (in Colombia) that are supported by only one location and, therefore, may be unwarranted. Hence, the actual extent of occurrence may still be close to the 20 000-km² threshold used when evaluating extinction risk (IUCN 2001). For Bay-vented Cotingas, our estimated value is similar to the formerly available estimate. Thus, our estimates support a Red List status as “vulnerable to extinction” for both species (BirdLife International 2010, IUCN 2010).

Our models suggest a relatively continuous distribution of Chestnut-bellied Cotingas north of the NPL where habitat is suitable. The southern part of the range is highly fragmented. Fit between the predicted distribution range and the range provided by BirdLife experts is relatively good in the highly fragmented, outer parts of the range (cf. northern and southern margins). The major discrepancy is the large, continuous area of high probability of occurrence in central Ecuador. This omission by BirdLife International is due to the lack of precise occurrence data in the intervening area, data first documented after BirdLife International had produced their map (Henry 2008). Our maps of potential distribution will be important for guiding searches for each species in areas where they are currently not known to occur.

Species distribution modeling, using location records and readily available environmental variables, provides objective biogeographic information for poorly known tropical landscapes, and offers an innovative tool for the refinement of species distribution ranges and the search of unknown species (Raxworthy et al. 2003, Engler et al. 2004, Bourg et al. 2005, Guisan et al. 2006, Peterson and Papes 2007). Models calibrated for the two *Doliornis* species, in our study, revealed areas of likely occurrence that remain to be validated in the field. The range of Bay-vented Cotingas may actually extend further to the southeast, reaching the Peruvian Department of Cusco, and to the northwest, with an area of high probability of occurrence in the Department of Cajamarca. Chestnut-bellied Cotingas is likely to be found between the Colombian provinces of Cauca and Huila, as well as in several parts of Ecuador and northernmost Peru. Two areas of overprediction in the northern Andes deserve specific comments. First, a *Doliornis* cotinga is predicted to occur, with an extended area of high probability, in the

eastern Andes of Columbia, south of Bogotá. High Andean bird species are poorly differentiated among the three Colombian Andean Ridges (Cracraft 1985, Ridgely and Tudor 1994) and, if a *Doliornis* sp. was to be found there, we suggest it would be Chestnut-bellied Cotingas and not a new species. Second, the models of Bay-vented Cotingas predict the occurrence of the species in the Andes of Venezuela (La Culata or Nevada Sierras), whereas models of the closest species (Chestnut-bellied Cotinga) do not predict this population. It suggests that, if a *Doliornis* sp. was to be discovered in this area, it may be a third species, with bioclimatic requirements closer to Bay-vented Cotingas than Chestnut-bellied Cotingas.

To conclude, by modeling the ecological niche of two allopatric, rare Andean endemics, we identified the most suitable areas where these species should occur based on climatic and topographic modeling, some of which have been confirmed as occupied by one species. Such species distribution modeling can play a major role in identifying the probable distributions of rare species and helping to focus searches for them and inform conservation planning. Our study illustrates how the observations of field ornithologists can be used objectively, with the help of existing statistical software, to transform anecdotal records into knowledge of the distribution, ecology, and conservation of rare species.

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APPENDIX 1. Locations where Bay-vented Cotingas (*D. sclateri*; DS) and Chestnut-bellied Cotingas (*D. remseni*; DR) have been reported.

Species	No.	Location	Coordinates ^a	Elevation (m asl)	First record, references, and comments ^b
DS	1	Near source of Aynamayo [=Río Vítoc], Marayntoc, Depto. Junín, Peru	c. 11°22'S 75°24'W*	3310 ^{ANSP,AMNH}	9 June 1871, type locality (Taczanowski 1874); April 1921, ANSP, AMNH
DS	2	Pan de Azúcar, c. 5–10 km north-east of Acomayo, Depto. Huánuco, Peru	c. 09°42'S 76°00'W*	—	26 February 1972; FMNH
DS	3	Bosque Cutieragra (or Cutirragra), south of Huaylaspampa, Carpish Mountains, Acomayo region, Depto. Huánuco, Peru	c. 09°42'S 76°02'W*	2740 ^{LSUMZ} , 2775 ^{LSUMZ} , 3050 ^{ANSP}	10 August 1972; FMNH, LSUMZ, ANSP
DS	4	Bosque Shaiga, Depto. Huánuco, Peru	—	—	20 July 1973; LSUMZ
DS	5	Bosque Quiulacocho, near crest of Carpish Mountain, c. 10 km north of Acomayo, Depto. Huánuco, Peru	c. 09°44'S 76°06'W*	3000; 3800	23 June 1974; LSUMZ
DS	6	Bosque Unchog, pass between Churubamba and Hacienda Paty, c. 14 km north-north-west of Acomayo, Depto. Huánuco, Peru	09°43'45"S 76°10'04"W ^{Ahlman} , 09°45'21"S 76°09'51"W ^{Schmitt}	3350 ^{LSUMZ} , 3450 ^{LSUMZ} , 3450 ^{Ahlman} , 3440 ^{Schmitt}	18 July 1975, LSUMZ; R. Ahlman, pers. comm., F. Schmitt, pers. comm., GPS geolocation
DS	7	Mashua, east Tayabamba, on trail from Tayabamba to Ongón, east Depto. La Libertad, Peru	c. 08°12'S 77°14'W*	3350	23 September 1979, LSUMZ
DS	8	Puerta del Monte, c. 30 km north-east of Los Alisos (LSUMZ), Depto. San Martín, Peru	07°32'S 77°29'W ^{LSUMZ}	3250	5 August 1981, LSUMZ, coordinates provided by LSUMZ
DS	9	Laguna Quiulacocho (or Quiulacocho), north-north-west of Acomayo, Carpish Mountains, Depto. Huánuco, Peru	c. 09°42'S 76°07'W*	3600	28 July 1984, LSUMZ
DS	10	Millpo, 2–6 km down of Abra Porta Chuela Pass, east Tambo de Vacas, Pozuzo-Chaglla trail, Depto. Pasco, Peru	09°57'S 75°51'W	3100 ^{Davis} , 3450 ^{LSUMZ}	8 July 1985, LSUMZ; T. Davis (pers. comm.) provided details that allowed precise geolocation with GoogleEarth (<0°01')
DS	11	1 and 2 km northwest of Punta de Saria on Pozuzo-Chaglla trail (LSUMZ); Sariapunta (Stephens and Traylor 1983), Depto. Pasco, Peru	09°43'S 75°54'W*	3100; 3200	4 August 1985, LSUMZ
DS	12	La Montaña, near Buldiboyo, above Yacuabamba, south of Abiseo NP, Carpish Mountains, Depto. La Libertad, Peru	08°06'00"S 77°15'30"W	3300; 3550	10 August 2000, S. Allen, http://maybank.tripod.com/SouthAmerica/Peru/Peru-07-08-2000.htm , GPS geolocation
DS	13	Chuchunpunta, within 10 km of Acomayo, Depto. Huánuco, Peru	c. 09°47'S 76°01'W*	3050	1 August 1973, FMNH

Continued

APPENDIX 1. Continued.

Species	No.	Location	Coordinates ^a	Elevation (m asl)	First record, references, and comments ^b
DS	14	Bosque Unchog, Depto. Huánuco, Peru	09°39'41"S 76°13'42"W	–	29 July 2006, eBird database, <i>field</i> Global Biodiversity Information Facility website
DR	1	Cajamarca, Podocarpus National Park, Loja/Zamora-Chinchipec prov., Ecuador	04°06'S 79°09'W	2875; 3100	7 March 1989, Robbins et al. (1994), Rasmussen et al. (1996), published coordinates
DR	2	Cañon del Quindío Nature Reserve, Quindío dept., west slope of the Central Cordillera, Colombia	04°36'33"N 75°27'09"W	3520; 3620	31 August 1989; Renjifo (1994); Renjifo et al. (2002)
DR	3	Cayambe-Coca Ecological Reserve, Ecuador	c. 00°17'S 78°12'W –0°14'N	–	1990, no detail on original record; Freile and Santander (2005), coordinate precision: 0°07'
DR	4	Entrance of Cotopaxi National Park, Cotopaxi prov., Ecuador	77°58'W** c. 00°39'S 78°31'W**	c. 3400–3600	July 1991, M. Honick and J. C. Matheus, http://www.birdlifeforums.org/ , coordinate precision: 0°03'
DR	5	3 km south-east of Impueran, west slope of Cerro Mongus, south-east of Carchi prov., Ecuador	00°27'N 77°52'W	3550; 3575; 3650	March 1992; Robbins et al. (1994), published coordinates
DR	6	Cajamarca, east slope of Cordillera Las Lagunillas, south of Zamora-Chinchipec prov., Ecuador	04°47'S 79°24'W	3350	28 October 1992; Robbins et al. (1994), published coordinates
DR	7	Guandera Biological Reserve, Carchi prov., Ecuador	c. 00°36'N 77°42'W	c. 3600–3700	1997; Cresswell et al. (1999), coordinates in Freile and Santander (2005), precision: 0°01'
DR	8	Below the pass of Gualacoe-Limón (Macas) road, within 1–2 km of the pass, eastern slope, Morona-Santiago prov., Ecuador	c. 03°00'S 78°39'W**	c. 3500	2 January 1999, G. H. Rosenberg (pers. comm.), http://vireo.acnatsci.org/ , coordinates identified with a map (precision: 0°02')
DR	9	Sangay National Park, Ecuador	c. 01°30'S 78°20'W –02°30'S 78°50'W**	–	2002, no detail on original record; Freile and Santander (2005), coordinate precision: 0°30'
DR	10	Yanacocha Lake, east slope, Llanganates National Park, Napo prov., Ecuador	01°05'55"S 78°18'27"W	3390	23 February 2006, Henry (2008), GPS geolocation

^aThe number of decimals of the coordinates indicates their precision. * and ** indicate geographical coordinates extracted from Stephens and Traylor (1983; coordinate precision not specified) or deduced from locality names (see comments for details about coordinate precision), respectively.

^bCollections hosting specimens are the Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH) in New York, and Field Museum of Natural History (FMNH) in Chicago. Website resources were accessed on 28 June 2010. – indicates missing data.