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# Effects of climate change on species distribution, community structure, and conservation of birds in protected areas in Colombia

Jorge Velásquez-Tibatá · Paul Salaman · Catherine H. Graham

**Abstract** Climate change is expected to cause shifts in species distributions worldwide, threatening their viability due to range reductions and altering their representation in protected areas. Biodiversity hotspots might be particularly vulnerable to climate change because they hold large numbers of species with small ranges which could contract even further as species track their optimal habitat. In this study, we assessed the extent to which climate change could cause distribution shifts in threatened and range-restricted birds in Colombia, a megadiverse region that includes the Tropical Andes and Tumbes-Choco-Magdalena hotspots. To evaluate how climate change might influence species in this region, we developed species distribution models using MAXENT. Species are projected to lose on average between 33 and 43 % of their total range under future climate, and up to 18 species may lose their climatically suitable range completely. Species whose suitable climate is projected to disappear occur in mountainous regions, particularly isolated ranges such as the Sierra Nevada de Santa Marta. Depending on the representation target considered, between 46 and 96 % of the species evaluated may be adequately represented in protected areas. In the future, the fraction of species potentially adequately represented is projected to decline to 30–95 %. Additional protected areas may help to retain representativeness of protected areas, but monitoring of species projected to have the largest potential declines in range size will be necessary to assess the need of implementing active management strategies to counteract the effects of climate change.

**Keywords** Conservation · Species distribution modeling · Tropical Andes hotspot · Tumbes-Choco-Magdalena hotspot

## Introduction

Climate change is expected to cause shifts in the geographic distribution of species worldwide as species track their optimal habitat which will likely shift as a result of rearrangement of climate zones (Peterson et al. 2002; Thomas et al. 2004; Loarie et al. 2008). In the tropics, species may be pushed to higher elevations, effectively shrinking their distributions as the climate warms (Peh 2007; Seimon et al. 2007; Chen et al. 2009, 2011). Such shifts in species distributions might threaten their persistence through range reduction or fragmentation which can cause decreases in population size (Gaston 1994). Reductions in range size are particularly harmful for endemic species, which already have small ranges (Manne and Pimm 2001). Moreover, new regions that species move into may not be protected and could provide less suitable habitats than those in their current distribution (Araújo et al. 2004, 2011; Thuiller et al. 2006). Therefore, regions with large concentrations of species with small ranges and high levels of habitat transformation, such as biodiversity hotspots, may be particularly vulnerable to climate change (Raxworthy et al. 2008). Here, we explore the potential

J. Velásquez-Tibatá (✉) · C. H. Graham
Department of Ecology and Evolution, Stony Brook University,
Stony Brook, NY 11794-5245, USA
e-mail: jivelasquezt@gmail.com

P. Salaman
World Land Trust-US, 2806 P Street, NW, Washington,
DC 20007, USA

conservation consequences of climate change on threatened and range-restricted birds across two biodiversity hotspots in Colombia.

Located in the northwest of South America, Colombia has one of the most unique and diverse biotas on Earth and has been highlighted in all global conservation assessments (Myers et al. 2000; Olson and Dinerstein 1998). The Tropical Andes and Tumbes-Choco-Magdalena hotspots contain most of this diversity. Under conservative assumptions, Malcolm et al. (2006) projected that at least 2.7 % of the species that occur in the Tropical Andes may become extinct as a result of doubling of $CO_2$ atmospheric concentrations, although this figure could be as high as 47 %. Considering that only 25 % of the original vegetation in this region remains and that 15 % of the total area is protected (Brooks et al. 2009), the actual proportion of species that may become extinct might be even greater due to ongoing habitat loss in the region. Therefore, climate change presents a clear threat to biodiversity in this South American hotspot. However, in contrast to well-studied temperate regions, only a few studies have quantified the potential extent of range shifts for species in South America (e.g., Anciães and Peterson 2006; Graham et al. 2011; Forero-Medina et al. 2011) and none have evaluated how these shifts might impact community composition or the effectiveness of current reserve systems (Hoffmann et al. 2011). Successful mitigation of the impact of climate change on biodiversity in hotspots will depend on our ability to anticipate species responses to climate change. To do this, we must address two important questions: (i) what species and regions will be more at risk due to climate change? (ii) How well will species be represented in protected areas (PAs) under future climate conditions?

Different approaches have been used to assess the impact of climate change on species diversity and community composition (Guisan and Zimmermann 2000). Species distribution models (SDMs), which are based on the statistical relationship between records of current distribution and their associated climate, can be used to project species potential distributions under new environmental conditions based on the assumption that species responses to particular environmental variables remain unchanged, or in other words, that the niche is conserved. Criticism has been raised that these models may be overly simplistic because they generally ignore inter-specific interactions (Araújo and Luoto 2007; Davis et al. 1998; Pearson and Dawson 2003); may not capture the correct species-environment relationships, because they are correlative and not mechanistic (Kearney and Porter 2009); and do not consider long-term population viability (Keith et al. 2008). Nonetheless, they are able to project with reasonable accuracy whether species ranges will increase or decrease under changing climate (Green et al. 2008; Araújo et al. 2005) and have the

advantage that they require relatively little information and thus can be applied to large numbers of species. As such, they provide valuable insight into how climate change will affect diversity patterns, particularly in data poor but highly diverse regions.

A number of bioinformatics initiatives have made high-quality data for almost all birds of Colombia easily accessible. We used data from these initiatives to estimate the response of threatened and range-restricted bird species of Colombia to impending climate change using SDMs. Specifically, we modeled the consequences of climate change on species range size and structure, species richness and composition, and species representation in PAs. Our goal was to determine which species and regions are likely to be most affected by climate change, and to use this first assessment to provide insights useful in guiding species conservation efforts and research in this diverse country.

## Methods

### Study species

We assessed distribution changes in all continental, non-aquatic, globally threatened, and near-threatened bird species (146 spp.), following BirdLife International (2008), and range-restricted species (173 spp.; range <50,000 km$^2$) following Stattersfield et al. (1998) that occur in the western half of Colombia (Fig. 1). Species occurring in either of these two listing schemes were considered in our analyses. Threatened species are those that meet the International Union for the Conservation of Nature (IUCN) criteria (IUCN 2001) for the categories "Critically Endangered" (CR), "Endangered" (EN), and "Vulnerable" (VU). We also included "Near-Threatened" (NT) species because they are likely to qualify for a threatened category in the near future. The species considered in this study have on average 62 % of their distribution range in the country. The core of the distribution for 34 % of these species lies in neighboring countries, mainly Ecuador (13 %), Venezuela (9 %), and Peru (6 %). We decided to include those species in our analysis because they are considered in national conservation action plans (e.g., Renjifo et al. 2002).

We compiled point locality data for these species throughout their entire distribution in Latin America from ornithological databases (Project Biomap, Fundación ProAves, DATAves, eBird, and xeno-canto), literature, and unpublished records (see "Acknowledgments"). Project BioMap database contains 230,000 records of Colombian bird specimens from 87 collections worldwide. All specimens in the database were hand-examined by museum curators or by taxonomic experts who visited the museums. Fundación ProAves, DATAves, eBird, and xeno-canto

Fig. 1 Study area and main geographic regions
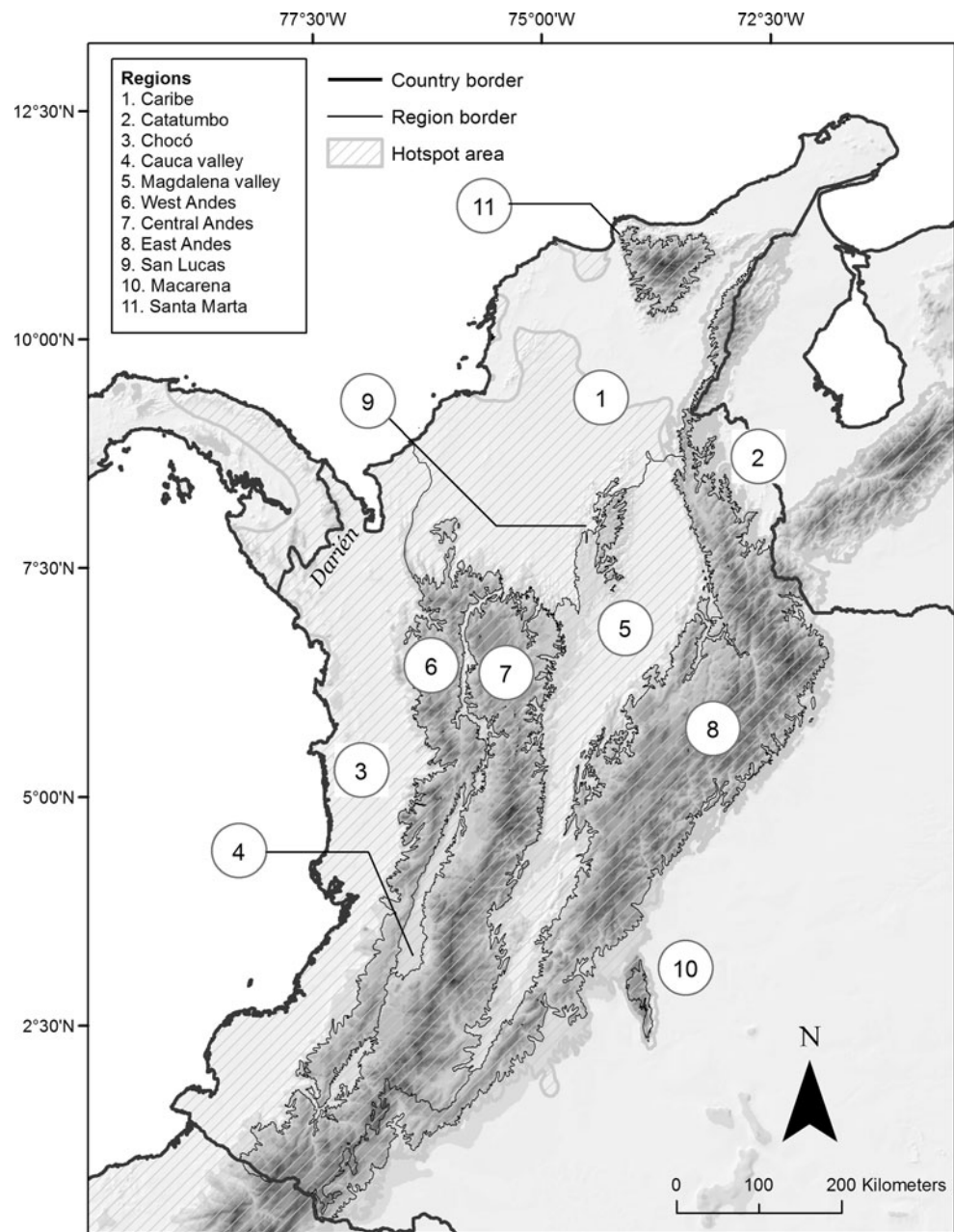


contain records of bird observations, sound recordings, and captures by field ornithologists and birdwatchers. Records were georeferenced using ornithological gazetteers (Paynter 1982, 1997; Paynter and Traylor 1977), topographic maps, and the GEONet Names Server (http://earth-info.nga.mil/gns/html/). Records for each species were mapped and examined by JV to identify potential georeferencing errors. We eliminated records that represented considerable range extensions or were >500 m outside a species' known altitudinal range as reported by Stotz et al. (1996). Additional data cleaning was done by setting up a webpage where ornithologists provided feedback about the accuracy of locality points for each species. After data cleaning, we had

4,542 unique records for 219 out of all 233 threatened, near-threatened, and range-restricted birds occurring in Colombia, with 1–86 records per species (median = 15 records). We excluded species with <5 points from further analyses; therefore, we ran distribution models for 199 species.

Study area

This study focused on the western region of Colombia, defined here as the area west of the 500-m contour line on the east slope of the East Andes (492,203 km$^2$; Fig. 1) and encompasses the Colombian part of the Tropical Andes and Tumbes-Choco-Magdalena hotspots. For analyses

including dispersal scenarios, we divided our study region into 11 main regions, delimited by major environmental or geographic breaks: the Andes mountains (West, Central, and East cordilleras), the inter-Andean valleys (Cauca and Magdalena), Caribe, Catatumbo, Chocó, San Lucas, Serranía de Macarena, and Sierra Nevada de Santa Marta. To summarize our community analyses, we further subdivided the Andes cordilleras and Sierra Nevada de Santa Marta in middle elevations (1,000–3,000 m) and highlands (>3,000 m) and East and West Slopes for the middle elevations of the Andes, resulting in a total of 18 subregions.

### Environmental data

We used 15 of the 19 bioclimatic variables from the WorldClim database (www.worldclim.org) that represent biologically meaningful measures for characterizing species distributions as follows: annual mean temperature, mean diurnal temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, mean temperature of the wettest quarter (i.e., wettest consecutive 3-month period), mean temperature of the driest quarter, mean temperature of the warmest quarter, mean temperature of the coldest quarter, annual precipitation, precipitation of the wettest month, precipitation of the driest month, precipitation of the wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter, and precipitation of the coldest quarter (Hijmans et al. 2005). These data are available at a resolution of 1-km$^2$ worldwide, and for Colombia, they have been interpolated from weather station data averaged mostly over a 30-year period (1960–1990; Hijmans et al. 2005). We excluded 4 bioclimatic variables present in the database that measured climatic variability because the behavior of any dispersion variable must be understood in the context of the mean (or any other location measurement) of the data. Since we did not consider interactions between variables in our modeling (i.e., product features), we could not model the interaction between location (e.g., mean annual temperature) and dispersion variables (e.g., standard deviation of temperature), and thus, including dispersion variables on their own could have induced spurious results when projecting to future climates with different average values. Furthermore, aspects of climate variability were already captured by other variables in the database. Given that the number of variables used for distribution models is optimized within MAXENT (see range prediction below) to avoid overfitting (Elith et al. 2011), we opted to let MAXENT chose the most statistically informative variables from the set of 15 variables. In MAXENT, if variables are close to a uniform distribution, they are not weighted heavily in the model or are not used at all. As a result, most models used only a subset (4–5) of the variables.

For future climates, we used downscaled predictions available in the WorldClim database from three general circulation model (GCM) outputs for the 2040–2069 period (referred to as 2050 thereafter) used in IPCC's Third Assessment Report (TAR; Houghton et al. 2001): the Hadley Center Coupled Model 3 (HadCM3), the Commonwealth Scientific and Industrial Research Organisation model Mk2 (CSIRO-Mk2), and the Canadian Centre for Climate Modelling and Analysis model CGCM2 (CCCma-CGCM2). In the absence of objective criteria to select GCM outputs (Loiselle et al. 2010), we used all of the aforementioned models because they have been widely used to model future species distributions (e.g., Iverson et al. 2008; Loarie et al. 2008; Thuiller et al. 2006), thus allowing us to compare across studies. For each GCM, we considered the A2 and B2 emission scenarios. The A2 emission scenario predicts a fourfold increase in $CO_2$ levels with respect to their 1990 levels by the year 2100, while the B2 emission scenario assumes a doubling in $CO_2$ emission by the year 2100 (Nakicenovic and Swart 2000). Finally, changes in the correlation structure within environmental variables may present a challenge for prediction in future times when such correlation structure changes (i.e., environmental variables become decoupled; Elith et al. 2010). We tested whether there were differences in the correlation structure between present and future bioclimatic datasets using a test of homogeneity among correlation coefficients (Sokal and Rohlf 1995), and found no significant differences at $\alpha = 0.05$.

Downscaled future climate layers (at a 1-km$^2$ resolution) used in IPCC's Fourth Assessment Report (AR4; Solomon et al. 2007) became available after the completion of our analyses (http://www.ccafs-climate.org/). However, we chose to present our analyses using the TAR GCMs because downscaled climate predictions for emission scenario B2 were not yet available and exploratory comparisons between TAR and AR4 bioclimatic layers for the aforementioned GCMs in our study region were, although significantly different, also highly and positively correlated (Appendix 2).

Vegetation cover for Colombia was obtained from the Global 2000 landcover dataset for South America (GLC 2000; Eva et al. 2002). This dataset contains a landcover classification based on satellite imagery from the SPOT and other sensors at a resolution of 1-km$^2$ for the year 2000.

### Distribution modeling

We used MAXENT version 3.2.1, a software based on the maximum entropy method, to predict changes in species

distributions as a result of climate change (Phillips et al. 2006). MAXENT estimates the conditional density of the covariates (or functions of covariates) at the presence sites which maximizes entropy (i.e., is closest to uniform), under the constraint that the mean of each covariate should match the empirical average generated from covariates associated with species occurrence data (Phillips and Dudik 2008). We used the relationship developed in MAXENT between current climate and species localities to predict where species would occur under current and future climate conditions. For all species, we ran the models using the default regularization values which have been tuned to perform well across a variety of organisms and regions (Phillips and Dudik 2008) and selecting linear, quadratic, and hinge features only.

We evaluated models by computing area under the curve values (AUC), running 10 bootstraps with 75 % of occurrence points for training and the remaining 25 % for testing for those species with more than 10 occurrence points, and jackknifing for species with <10 records (Pearson et al. 2007). However, models used in analyses were built with all available records to avoid biases in distribution models (Araújo et al. 2011). Models with AUC values <0.8 or that had large discrepancies with existing knowledge of their distribution were removed from the analyses, resulting in 156 species in the final dataset (Appendix 1).

To convert maps from suitability indices to presence/absence, we visually checked minimum training presence and 10th and 20th percentile omission thresholds. We found that the 20th percentile threshold consistently gave predictions that were in agreement with published range maps and expert opinion. While an expert informed approach was used recently to select thresholds in range-restricted Andean birds (e.g., Young et al. 2009), we emphasize that our results do not depend on threshold choice, since we were concerned with proportional changes through time (i.e., % change in range size) instead of absolute changes.

Because the three main cordilleras have very similar climates, models generated for a species that exists on one or two cordilleras often predict suitable habitat in the other cordilleras. As a result, species' distributions are often predicted considerably beyond their known range (Graham et al. 2010). To address that, we trimmed current distribution models to the regions (Fig. 1) where they have been reported or are presumed to occur based on published range maps (Hilty and Brown 1986; Hilty and Meyer de Schauensee 2003; Ridgely and Greenfield 2001; Ridgely et al. 1994, 1989) and based on distribution breaks observed after thresholding the distribution models following Graham et al. (2010). Trimming of models is important because it accounts for the role of history in shaping species distributions and improves estimates of change in

range size through time. We further restricted predictions for current and future distributions to areas where vegetation was untransformed using the GLC 2000 vegetation layer.

For future models, we adopted two possible dispersal scenarios: contiguous and no dispersal. In the contiguous dispersal scenario (CD), we assumed that species could disperse within the 11 main geographic regions where they had been recorded, but that movement among adjacent regions was only possible when the margins of current and future ranges were contiguous (i.e., at least current and future ranges for a species shared a corner). The rationale for this is that within regions, we do not expect to find any major barriers to dispersal, but current geographic barriers can be crossed only if they become climatically suitable. For example, a species currently inhabiting the Central Andes could not have a future distribution in the East Andes unless a bridge of suitable habitat between those two cordilleras was projected under future climates. In the no-dispersal scenario (ND), species future ranges were restricted to places that are predicted as suitable in the present. Therefore, for each species, we had twelve possible future distributions from the combination of GCMs (HadCM3, CSIRO, and CCCma), emissions scenarios (A2 and B2), and dispersal scenarios (CD and ND). To present our results, we averaged across the three GCMs to produce the following scenario-dispersal combinations: A2-CD, A2-ND, B2-CD, and B2-ND.

## Landscape and community analyses

To estimate changes in area and structure of species geographic ranges resulting from climate change, we identified habitat patches for each species. A habitat patch for any given species was defined as a group of untransformed (as established with the GLC 2000 landcover dataset) and climatically suitable cells that either shared an edge or a corner (i.e., an 8-cell neighborhood grouping rule). We computed the landscape statistics total area, mean patch area, and Euclidean distance to nearest patch for current and future predictions of species distributions using Fragstats 3.3 (McGarigal et al. 2002).

Species richness was reported as mean species richness (MSR) for each region, as computed by the formula $\sum_{j}^{3} \sum_{i=1}^{N} A_{ij}/A_t$, where $N$ is the total number of species in the region, $A_i$ is the area of species $i$ projected by model $j$ in the region, and $A_t$ is the total area of the region. Similarity between current and future avifaunas was measured on a cell-by-cell basis using the Jaccard's index of similarity $J = c/(a + b - c)$, where $c$ is the number of species present in a cell in the present and future, $a$ the number of species in the present, and $b$ the number of species in the

future. This index ranges from 0 to 1, higher values indicate greater community similarity between current and future predicted communities.

## Representation of species in protected areas

We gathered geographic information on the coverage of PAs in the country from a recent assessment by Vásquez and Serrano (2009). In Colombia, there are at least 34 types of PAs, which we divided into two major groups: strict and non-strict PAs. Strict PAs are defined as those meeting IUCN protected area management categories I–IV (Dudley 2008), where extraction activities are not allowed and protection is enforced at a national government level. These are mainly National Parks, Sanctuaries, and National Reserves. Non-strict PAs include areas where extraction activities are regulated but not forbidden, and include National Protective Forests Reserves, Indian Reservations and regional and private reserves. Private reserves were not included in Vásquez and Serrano (2009); however, coordinates and area were available for 49 % of them. This information was used to create polygons as circles centered at the reserve coordinates with the same area.

Given that the resolution of our models was close to 1 km², which is larger than many of the reserves in our dataset, we computed the percentage of area protected per individual cell. This allowed us to compute protected area per species as:

$$\sum_{i=1}^{N} X_i p_i$$

where $N$ is the total number of cells in the study area, $X_i$ is an indicator of whether the species is present ($X = 1$) or absent ($X = 0$) in cell $i$, and $p_i$ is the percentage of area protected in cell $i$. This procedure eliminates the arbitrariness in choosing a threshold to decide whether a cell is protected or not (Araújo et al. 2011). We computed this value for all species in both present and future climate-dispersal scenarios.

Ideally, targets for species representation should be established based on species' biology (e.g., area necessary for a viable population). However, such detailed biological information is not available for species in our study area. Therefore, we chose three different targets based on IUCN thresholds of area of occupancy in criterion B2 to consider a species as either Vulnerable (2,000 km²), Endangered (500 km²), or Critically Endangered (10 km²; IUCN 2001). The rationale for choosing these targets is that they would protect the totality of the range of a species that would qualify as threatened under criterion B2. For those species that had range sizes smaller than any of the targets, the maximum target was the current species' range size.

## Results

### Changes in species ranges

Our models project a variety of potential responses to climate change, ranging from the complete loss of suitable habitat to a threefold increase in suitable habitat (Appendix 1). Nonetheless, most species are projected to have smaller ranges (median change: −33 to −43 %; Fig. 2a), reduced distribution patch sizes (median change: −14 to −26 %; Fig. 2c), and increased distance between distribution patches (median change: 9–10 %; Fig. 2d). Projections of future range sizes for most species (73–85 %) for any given climate-dispersal scenario produced by the three GCMs had high coefficient of variation (>10 %; Fig. 2b), reflecting disagreement in projected climate change in the region, particularly for precipitation-related variables (Appendix 2). Importantly, suitable habitat for 18 (12 %) species is projected to disappear completely in Colombia under some of the scenarios considered (Table 1). For 12 of these species, no suitable habitat is predicted outside of Colombia, 8 of them being restricted to the isolated Sierra Nevada de Santa Marta.

We found that global threat status (BirdLife International 2008) was a poor predictor of decrease in range size. There were no significant differences among IUCN threat categories in the proportion of predicted change in range size under any of the future scenarios considered (Kruskal–Wallis test, $p > 0.05$ for all future scenarios). Furthermore, we found no significant differences between threatened (CR, EN, and VU) and non-threatened species (NT and LC) in their predicted change in range size for any of the future scenarios (Wilcoxon test, $p > 0.05$ for all future scenarios). The relationship between IUCN category and the proportion of predicted change in range size was robust to the statistical approach taken (Appendix 3).

### Community-level patterns

Our models suggest that climate change may alter current patterns of species richness and composition across the country (Fig. 3; Table 2). Middle elevations (1,000–3,000 m) are projected to have the largest declines in mean species richness (MSR) and the lowest similarity with current community composition. In the worst-case scenario (A2-ND), up to 44 % of current MSR is projected to be lost from middle elevations, whereas in the best case (B2-CD), a loss of 32 % is projected. At a subregional scale, the Catatumbo region, San Lucas, and Santa Marta mountains exhibited the highest MSR losses as well as the smallest similarity with current community composition. A number of gains in species richness are projected to occur in the highlands of the three main cordilleras and the
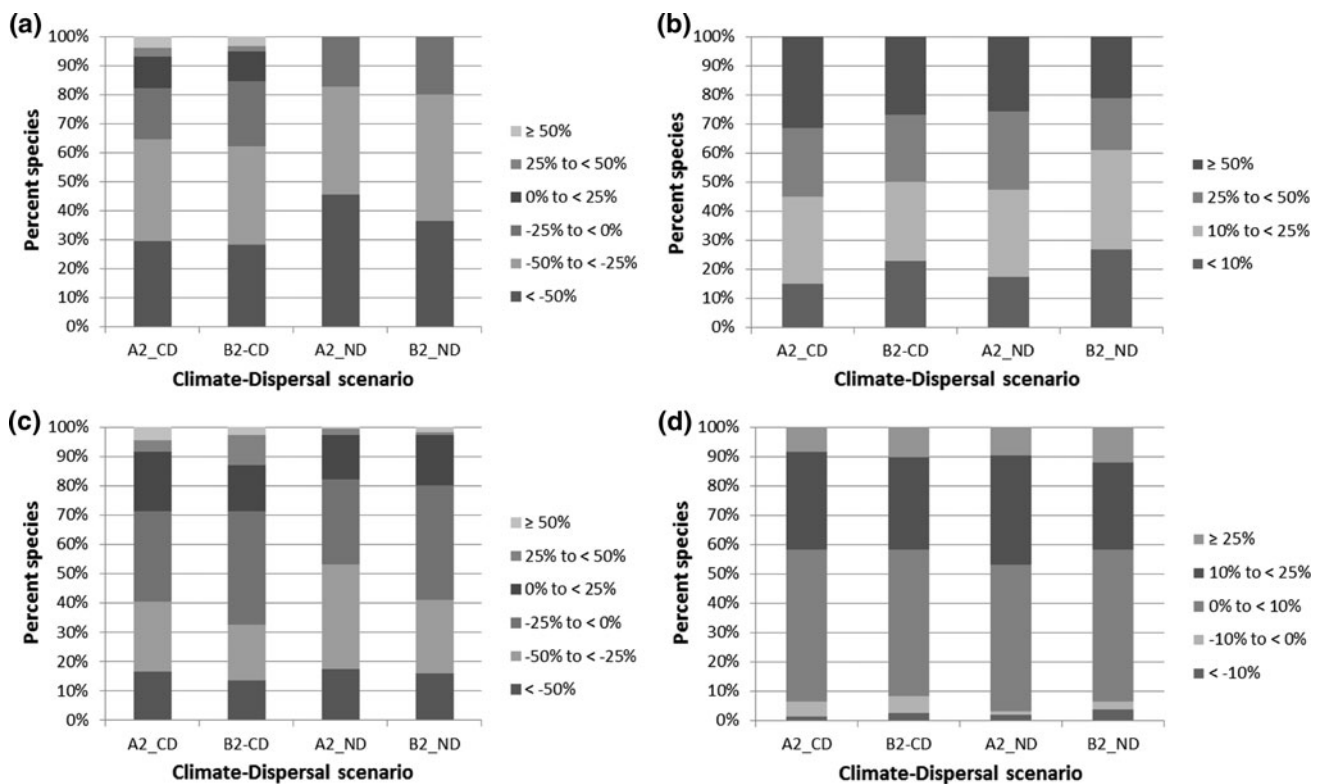
**Fig. 2** Average projected changes in landscape metrics of species distributions under climate change scenarios (A2 and B2) and dispersal assumptions (*CD* contiguous dispersal, *ND* no dispersal): **a** range size, **b** coefficient of variation of future range size projected by the 3 GCMs used, **c** mean distribution patch area and **d** mean distance to nearest distribution patch

**Table 1** Species whose climate envelope is projected to disappear by year 2050. Global status is based on BirdLife International (2008) and No. scenarios is the number of GCMs-climate-dispersal models projecting disappearance of climate envelope within and outside the study region (reported in parentheses for non-country endemics)

| Species | Region | Country endemic | Global status | No. scenarios |
|---|---|---|---|---|
| *Anisognathus melanogenys* | Santa Marta | Yes | LC | 8 |
| *Atlapetes melanocephalus* | Santa Marta | Yes | LC | 6 |
| *Attila torridus* | Colombia-Ecuador border | No | VU | 12 (0) |
| *Basileuterus conspicillatus* | Santa Marta | Yes | NT | 8 |
| *Campephilus gayaquilensis* | Colombia-Ecuador border | No | NT | 8 (0) |
| *Coeligena phalerata* | Santa Marta | Yes | LC | 8 |
| *Goldmania violiceps* | Darien and N Choco | No | LC | 4 (2) |
| *Grallaria bangsi* | Santa Marta | Yes | VU | 6 |
| *Heliodoxa gularis* | Colombia-Ecuador border | No | NT | 8 (8) |
| *Heliangelus strophianus* | Colombia-Ecuador border | No | LC | 8 (0) |
| *Lipaugus weberi* | N Central Andes | Yes | EN | 4 |
| *Myadestes coloratus* | Darién | No | LC | 6 (6) |
| *Myioborus flavivertex* | Santa Marta | Yes | LC | 4 |
| *Ortalis erythroptera* | Colombia-Ecuador border | No | VU | 12 (0) |
| *Pipreola chlorolepidota* | Colombia-Ecuador border | No | NT | 6 (2) |
| *Pyrrhura viridicata* | Santa Marta | Yes | EN | 12 |
| *Synallaxis fuscorufa* | Santa Marta | Yes | VU | 2 |
| *Xenornis setifrons* | Darién | No | VU | 2 (0) |
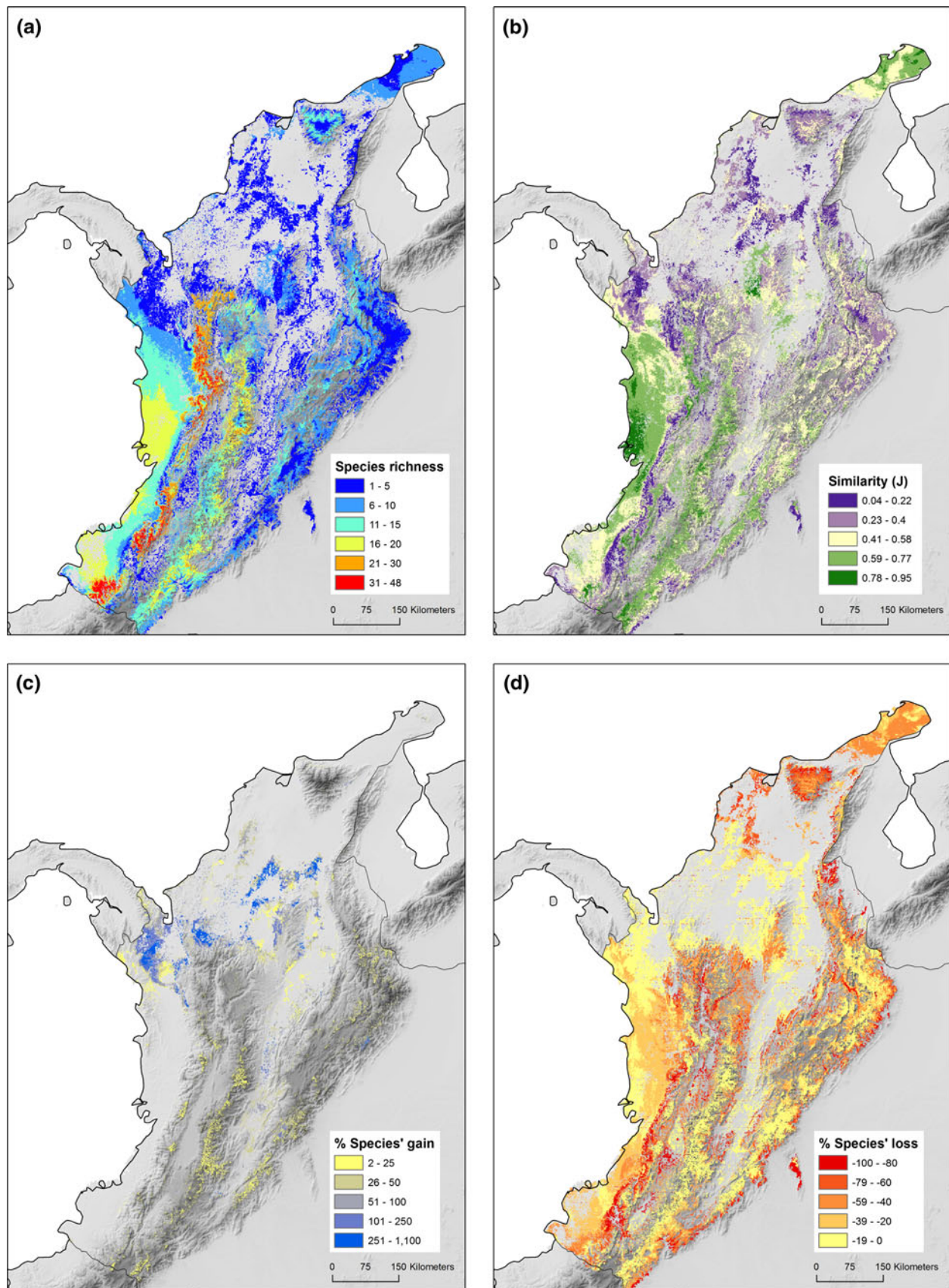
◄ **Fig. 3** Current and future patterns of species richness, under climate scenario A2 and contiguous dispersal: **a** current richness of threatened and range-restricted birds. **b** Projected Jaccard similarity of current and future communities, **c** percent of species' gains relative to current richness and **d** predicted percent of species' losses relative to current richness

southern parts of the Caribbean and Magdalena valley under contiguous dispersal scenarios. However, these gains will only result in a net increase in MSR in the highlands of the East Andes (Table 2).

Changes in protected areas

Estimates of representation afforded by PAs in Colombia were highly dependent on target choice, with 96.2 % of species currently meeting the 10-km² target but only 45.5 % meeting the 2,000-km² target (Table 3). Only 2 species (*Attila torridus* and *Ortalis erythroptera*) were identified as complete gaps (i.e., not currently represented in PAs). Under future scenarios, representation of species in PAs is projected to decrease. Using a 10-km² target, on average 94.7 ± 1.0 % (mean ± SD) species met their representation target in future scenarios, whereas targets for only 30.4 ± 3.9 % were met using a 2,000-km² target. The number of complete gaps is also projected to increase, though that is largely driven by the fact that their climatic range is predicted to disappear. If species whose climatic range is projected to disappear in the future were excluded from the representativeness analysis, then portions of species ranges would be expected to occur in PAs under all future climate and dispersal scenarios considered, except for *Attila torridus*, *Basileuterus conspicillatus*, and *Ortalis erythroptera*.

Non-strict PAs play a significant role for bird protection under changing climate, especially for the 2,000-km² target. Using a 10-km² target, non-strict areas only add 1.3 % completely represented species to strict PAs under current climate. However, using a 2,000-km² target, non-strict PAs contribute 14.1 % completely represented species. These areas also buffer some of the projected effects of climate change by increasing representation of species in PAs on average by 5.6 ± 1.2 % using a 10-km² target and up to 14.5 ± 2.2 % using the 2,000-km² target. *Lipaugus weberi* and *Tachornis furcata* are currently represented only in non-strict PAs.

**Discussion**

We used SDMs to project the distribution of threatened and range-restricted bird species of Colombia under future climate conditions. These models were used to estimate potential changes in range size, community patterns

(richness and composition), and representation in PAs. We found that range sizes of many species may shift and decrease with climate change and, as a consequence, species representation in reserves may decrease on average. This study is, to our knowledge, the most extensive assessment on the projected impacts of climate change on species of conservation concern for any country in South America.

Distribution changes

Although we found a range of responses of species to climate change, on average species were projected to have smaller and more fragmented geographic ranges as a consequence of distributional shifts induced by climate change. Changes in species range size and structure of the magnitude we identified are likely to have profound consequences for the viability of range-restricted and threatened bird species of Colombia (Keith et al. 2008). Further, our projection that suitable habitat for 4–9 % of the species evaluated may completely disappear in Colombia under 2050 climate scenarios is worrisome, although it is within the range found by Thomas et al. (2004) for Mexican birds and Malcolm et al. (2006) for the tropical Andes hotspot.

Most of the species whose climate envelope is projected to disappear in this study (Table 1) are confined to isolated mountains or regions isolated by geographic barriers (e.g., Sierra Nevada de Santa Marta, Darien). Therefore, dispersal of these species to other climatically suitable areas is unlikely. Although some populations are currently being monitored by monitoring programs (e.g., ProAves' banding program, Christmas Bird Counts), the status and trends of most populations remain unknown. Our results indicate that there were no significant differences between IUCN threat status and predicted change in range size and that many of the species we predicted to have a large range size decline are currently classified as low concern. Therefore, future assessments of extinction risk using IUCN categories in the country should take into account the threat of climate change.

Community effects

Community composition is projected to change dramatically, particularly in the mountains, where some regions may lose up to 84 % of their current species richness and have a similarity with current communities as low as 30 % (Table 3). These changes may result in communities that have no current analog, which could have significant implications for species interactions (Stralberg et al. 2009). For instance, some species might experience ecological release, whereas the populations of others might be suppressed or even excluded. In the Andes, there is substantial evidence that competition plays an important role in

**Table 2** Changes in mean species richness and mean community similarity across regions under climate change scenarios (A2 and B2) and dispersal assumptions (*CD* contiguous dispersal, *ND* no dispersal)

| Location | Area (km$^2$) | Mean species richness | | | | | Mean similarity | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Current | A2-CD | B2-CD | A2-ND | B2-ND | A2-CD | B2-CD | A2-ND | B2-ND |
| Caribe | 119,374 | 1.4 | −7 | −11 | −45 | −45 | 0.4 | 0.4 | 0.5 | 0.5 |
| Catatumbo | 9,647 | 0.2 | −76 | −79 | −84 | −84 | 0.3 | 0.3 | 0.3 | 0.3 |
| Chocó | 90,244 | 8.5 | −24 | −23 | −36 | −34 | 0.5 | 0.5 | 0.6 | 0.6 |
| Cauca Valley | 7,394 | 0.6 | −54 | −61 | −60 | −65 | 0.5 | 0.5 | 0.5 | 0.5 |
| Magdalena Valley | 64,031 | 1.1 | −7 | −15 | −42 | −44 | 0.4 | 0.5 | 0.6 | 0.6 |
| **Lowlands** | **282,892** | **3.5** | **−20** | **−20** | **−38** | **−37** | **0.5** | **0.5** | **0.6** | **0.6** |
| West Andes (W slope) | 16,603 | 12.0 | −35 | −33 | −42 | −39 | 0.5 | 0.5 | 0.5 | 0.5 |
| West Andes (E slope) | 12,122 | 9.3 | −34 | −34 | −43 | −41 | 0.4 | 0.5 | 0.5 | 0.5 |
| Central Andes (W slope) | 27,654 | 5.1 | −36 | −34 | −45 | −42 | 0.5 | 0.5 | 0.5 | 0.5 |
| Central Andes (E slope) | 29,712 | 6.1 | −30 | −29 | −41 | −39 | 0.5 | 0.5 | 0.5 | 0.6 |
| East Andes (W slope) | 39,843 | 3.4 | −31 | −27 | −47 | −42 | 0.5 | 0.5 | 0.5 | 0.6 |
| East Andes (E slope) | 39,883 | 4.5 | −33 | −28 | −45 | −40 | 0.5 | 0.5 | 0.5 | 0.6 |
| San Lucas | 1,732 | 2.2 | −39 | −42 | −56 | −57 | 0.4 | 0.4 | 0.4 | 0.4 |
| Macarena | 1,161 | 0.6 | −83 | −73 | −83 | −73 | 0.3 | 0.3 | 0.3 | 0.3 |
| Santa Marta Mts. | 4,666 | 6.1 | −65 | −51 | −68 | −54 | 0.3 | 0.4 | 0.3 | 0.4 |
| **Mid-elevations** | **171,112** | **5.7** | **−34** | **−32** | **−44** | **−41** | **0.5** | **0.5** | **0.5** | **0.5** |
| West Andes | 594 | 20.2 | −26 | −27 | −34 | −33 | 0.6 | 0.6 | 0.6 | 0.6 |
| Central Andes | 13,182 | 8.9 | −6 | −5 | −21 | −19 | 0.7 | 0.7 | 0.8 | 0.8 |
| East Andes | 14,007 | 4.0 | −9 | 6 | −44 | −31 | 0.4 | 0.5 | 0.5 | 0.6 |
| Santa Marta Mts. | 1,299 | 5.8 | −52 | −46 | −58 | −53 | 0.4 | 0.4 | 0.4 | 0.4 |
| **Highlands** | **29,063** | **6.7** | **−10** | **−5** | **−30** | **−25** | **0.5** | **0.6** | **0.6** | **0.7** |

Values of mean species richness under future climate scenarios are given as percent change from current values. Mean values for each altitudinal band are in boldface

**Table 3** Average percentage of species represented in protected areas across GCMs for climate change scenarios (A2 and B2) and dispersal assumptions (CD contiguous dispersal, ND no dispersal)

| | All protected areas | | | | | Strictly protected areas | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Current | A2-CD | A2-ND | B2-CD | B2-ND | Current | A2-CD | A2-ND | B2-CD | B2-ND |
| *Target* 10 km$^2$ | | | | | | | | | | |
| Target met | 96.2 | 95.5 | 93.6 | 95.5 | 94.2 | 94.9 | 90.4 | 87.2 | 91.7 | 88.5 |
| Partial gaps[a] | 2.6 | 1.9 | 3.8 | 3.2 | 4.5 | 2.6 | 6.4 | 9.0 | 6.4 | 9.0 |
| *Target* 500 km$^2$ | | | | | | | | | | |
| Target met | 78.8 | 69.9 | 61.5 | 70.5 | 64.1 | 67.9 | 58.3 | 46.2 | 60.3 | 47.4 |
| Partial gaps | 19.9 | 27.6 | 35.9 | 28.2 | 34.6 | 29.5 | 38.5 | 50.0 | 37.8 | 50.0 |
| *Target* 2,000 km$^2$ | | | | | | | | | | |
| Target met | 45.5 | 32.7 | 26.3 | 34.6 | 28.2 | 31.4 | 19.2 | 14.7 | 17.9 | 14.7 |
| Partial gap | 53.2 | 64.7 | 71.2 | 64.1 | 70.5 | 66.0 | 77.6 | 81.4 | 80.1 | 82.7 |
| Total gaps | 1.3 | 2.6 | 2.6 | 1.3 | 1.3 | 2.6 | 3.2 | 3.8 | 1.9 | 2.6 |

[a] Partial gaps are species that occur in protected areas but do not meet representation targets

restricting ranges of species along elevation gradients (Anderson et al. 2002; Remsen and Cardiff 1990; Terborgh and Weske 1975; but see Cadena and Loiselle 2007).

Nonetheless, it is uncertain what effect the rearrangement of communities could have on species persistence and current methodological advancements in the modeling of

species distributions using community information (i.e., Latimer et al. 2009), as well as research on species ecology, are needed to address this issue properly.

## Protected areas

Estimates of representativeness of PAs across time were highly dependent on the target used. When a small representation target was used (10-km$^2$), representation of species in PAs was close to complete with only two species absent from PAs. Results using this target resemble the representativeness estimate of Franco et al. (2007) who found that 83 % of the species for the Colombian Andes were protected in reserves. Our higher estimate of representation based on the 10-km$^2$ target is likely a consequence of the use of a more complete protected area layer and the use of SDMs which may make up for the lack of sampling in some PAs. However, when a larger representation target was used (2,000-km$^2$), the number of completely represented species was only 45.5 %. These results suggest that only 45.5 % species are protected beyond the minimum threshold to assess a species as Vulnerable on the basis of area of occupancy.

Our models project on average a 1.5–33.1 % decrease in the number of species meeting their targets under 2050 climate scenarios, depending on the target considered. With the exception of the 10-km$^2$ target, this decrease in representativeness is much higher than what has been found for other regions. For example, Hannah et al. (2007) reported a 10.1 % decrease in the number of species of mammals and birds in Mexico meeting a target of either 100 km$^2$ or 10 % of current range, whichever was larger. This result is somewhat surprising, given that the coverage of PAs in Colombia is much higher than in Mexico (24.0 vs. 9.4 % of total country area). In fact, representativeness is projected to decline even more (5.7–46.9 %) if only strict PAs are considered. These results suggest that non-strict PAs may act as an important buffer of the effects of climate change on species' representation in PAs and that overall, the reserve system is only sufficient to meet the bare minimum representation targets of threatened and endemic birds under a changing climate.

## Caveats

We relied on species distribution models to explore the influence of climate change on species distributions. This modeling approach is limited in that, as opposed to mechanistic approaches, it cannot establish causal relationships between species occurrences and climate, but it also does not consider explicitly other important factors shaping species distributions such as species interactions or population processes. Furthermore, projections of species distributions into future climate present the additional challenge of inferring occurrence in areas with combinations of climate and species composition for which we have no current analog (Elith et al. 2010). In spite of these shortcomings, SDMs have been found useful to unravel general trends in species distributions over short (Green et al. 2008) and large spans of time (Cordellier and Pfenninger 2009), and paleoecological evidence suggests that range shifts in response to climate change have been largely independent in the past (Huntley and Webb 1989; Coope 2004). Thus, the quantitative estimates found in this study should not be taken as factual predictions but instead as baseline estimates on the expected trends and relative magnitudes that species ranges, community composition, and protected areas representativeness may follow under climate change.

Successful implementation of SDMs to model future distributions is in itself subject to several uncertainties. Point locality data, current climate interpolations, future climate projections, statistical modeling methods, and dispersal assumptions have all associated uncertainties that will ultimately affect the quantitative estimates of distribution models (Beaumont et al. 2007; Heikkinen et al. 2006). In order to reduce uncertainty in our results, we georeferenced our point locality data to the highest possible accuracy and discarded species with low data quality, used climate layers from three GCMs to reflect the range of climatic conditions expected under climate change, and chose a robust modeling method (Elith et al. 2006). We also adopted two dispersal scenarios (no dispersal and contiguous dispersal) which are representative of the impact of differing dispersal abilities on species ranges under climate change. Nonetheless, there were some limitations in the data that we were unable to address. We generally had low sample sizes, partly due to the lack of sampling but also because of the inherent rarity and restricted distribution of many of the species included in our study. Climate interpolations for parts of the study region (e.g., Chocó) rely on a sparse network of weather stations which may induce errors in the estimation of species' climatic envelopes and future climate surfaces are still at a too coarse resolution for topographically complex areas such as the Andes. Furthermore, as many as 21 GCMs were produced for the AR4, and hence, we explored only partially the full extent of uncertainty in future climate reflected in those climate models in our study.

If we take an optimistic view, our results may have overestimated changes in species distributions. First, species may be tolerant to a broader range of climate conditions than can be inferred based on their current distribution (Brommer et al. 2008; Ghalambor et al. 2007). Second, species may be able to adapt to new climate conditions (e.g., Balanya et al. 2006; Byars et al. 2007). Currently, the

extent to which species are able to adapt to new climate conditions is controversial with some arguing that species are unlikely to evolve quickly enough to persist in new conditions. On the contrary, a pessimistic view of our results would argue that reduction of species' ranges could happen at a faster pace than projected by this study. As species populations become fragmented and their habitat deteriorates as a result of climate and land-use change, population sizes may decline and as a result population viability might decrease (Keith et al. 2008; Thuiller et al. 2008). Further, species may have decreased fitness as the environment they currently live in deteriorates with climate change (Thuiller et al. 2008). Finally, considering that deforestation greatly exceeds reforestation rates in Colombia (Dávalos et al. 2011; IDEAM 2010), future range sizes might shrink even faster than projected by this study.

## Recommendations

Although there are several limitations in modeling future species distributions and thus our quantitative results should be interpreted with caution, our results identify which species may be affected by climate change and highlight isolated mountains as areas that should receive conservation attention. Based on these results, we emphasize the need for (1) monitoring populations of birds for which future suitable climate is predicted to completely disappear, particularly those restricted to isolated mountains; (2) conducting field surveys, especially aimed toward species known in few locations, to improve distribution models; (3) including predictions of the effect of climate change on species distribution as part of IUCN assessments of species extinction risk (several guidelines to this purpose already exist (e.g., IUCN SPSC 2010; Akçakaya et al. 2006) and (4) identifying sites that would complement the current protected area network to meet species representation targets. For this last point, methods that make use of optimization algorithms and that explicitly include species' dispersal abilities (Klein et al. 2009; Phillips et al. 2008; Williams et al. 2005) are particularly promising because they may be more likely to identify sites that can ensure species persistence and representation over time while minimizing costs. Our success in mitigating the effect of climate change on bird populations will require consideration of these research and conservation needs.

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