



## The effects of climate change on a mega-diverse country: predicted shifts in mammalian species richness and turnover in continental Ecuador

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### ABSTRACT

Ecuador has some of the greatest biodiversity in the world, sheltering global biodiversity hotspots in lowland and mountain regions. Climate change will likely have a major effect on these regions, but the consequences for faunal diversity and conservation remain unclear. To address this issue, we used an ensemble of eight species distribution models to predict future shifts and identify areas of high changes in species richness and species turnover for 201 mammals. We projected the distributions using two different climate change scenarios at the 2050 horizon and contrasted two extreme dispersal scenarios (no dispersal vs. full dispersal). Our results showed extended distributional shifts all over the country. For most groups, our results predicted that the current diversity of mammals in Ecuador would decrease significantly under all climate change scenarios and dispersal assumptions. The Northern Andes and the Amazonian region would remain diversity hotspots but with a significant decrease in the number of species. All predictions, including the most conservative scenarios in terms of dispersal and climate change, predicted major changes in the distribution of mammalian species diversity in Ecuador. Primates might be the most severely affected because they would have fewer suitable areas, compared with other mammals. Our work emphasizes the need for sound conservation strategies in Ecuador to mitigate the effects of climate change.

Abstract in Spanish is available with online material.

*Key words:* climate change scenarios; CliMond; conservation assessment; ensemble forecasting; species range; species richness; species turnover.

CONTINENTAL ECUADOR COVERS A SMALL AREA OF 253,370 km<sup>2</sup>, YET IT SHELTERS A VAST DIVERSITY OF PLANTS AND ANIMALS. Biodiversity studies have reported 422 mammalian species in Ecuador (Tirira 2014), and continually add new species to this list. For example, the western Andes remain a *terra incognita* where new species and records are frequently reported, making Ecuador a mega-diverse country (Mittermeier *et al.* 1997). Such diversity is primarily related to the confluence of three biogeographic regions and their environmental variability (Dangles & Nowicki 2010): the Amazon basin, the Tumbes-Chocó-Magdalena region, and the Tropical Andes (Fig. 1A). Two of these regions are considered biodiversity hotspots due to their high density of endemic species and threats these species face (Mittermeier *et al.* 1999). Mammals, in particular, are highly threatened, with 26 percent of species classified as vulnerable, endangered, or critically endangered in continental Ecuador (Tirira 2011).

Habitat destruction and climate change pose serious threats to biodiversity in the region, with likely consequences for species ranges (Chen *et al.* 2011). Climate models predict temperature

increases between 2 and 7°C in tropical South America by the end of the 21st century (Urrutia & Vuille 2009). Both tropical and mountain regions are expected to show no-analog environmental conditions under climate change scenarios, including higher maximum temperatures (Bradley *et al.* 2006) and drier conditions (Lapola *et al.* 2009). Birds (Barbet-Massin *et al.* 2012, Tingley *et al.* 2012), nonvolant mammals (Levinsky *et al.* 2007) and amphibians (Pounds *et al.* 2006), among others, have already been shown to respond to climate change by shifting their ranges. With environmental gradients shifting geographically, species may move out of protected areas, causing the reserve network to become ineffective (Burns *et al.* 2003, Hannah *et al.* 2007). Changes in the distributions of species in mountain areas will likely be more complex than usually hypothesized at broad spatial scales. For example, the interactions between precipitation and temperature changes are not always in the same direction through the altitudinal gradient, producing pockets of downward shifts in distributions (Pounds *et al.* 1999, Jacobsen *et al.* 2014, Crespo-Pérez *et al.* 2015). This complexity highlights the importance of considering multiple abiotic factors at finer spatial scales (Tingley *et al.* 2012, Anderson 2013).

These factors taken together—Ecuador being in a mountainous region, harboring high biodiversity in a small area, and

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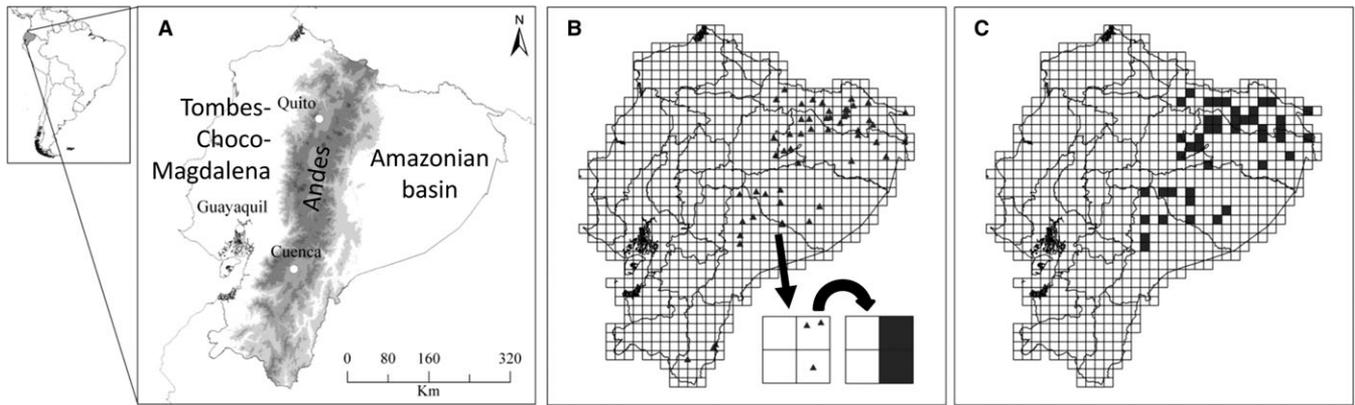


FIGURE 1. Study area and occurrence data aggregation strategy. (A) The study area showing the three main biogeographic regions and the Andean range; (B) Individual occurrence data were overlaid over an 18-km resolution grid; occurrences falling in the same grid cell were aggregated as a single occurrence, whereas cells containing no occurrence record for the focal species were subsequently considered in the random draw of background sites; (C) the same occurrence data shown in (B) but after aggregation at the resolution of the grid.

presenting a high habitat reduction rate—put its biodiversity at high risk under climate change scenarios. Studies related to climate change in the region have focused on the current status of glaciers and water availability (Buytaert & De Bièvre 2012, Rabatel *et al.* 2013, Michelutti *et al.* 2015), and on paleo changes in hydrology and climate in the Amazon (Cheng *et al.* 2013). One exception is Garavito *et al.* (2015), who investigated the effects of climate change on 129 tree species endemic to the upper mountains of the tropical Andes, and found that the risk of extinction of different species would increase an average of 18–20 percent. However, we lack information on the potential effects of climate change on mammal biodiversity in Ecuador.

We explored potential effects of climate change on the distribution of Ecuadorian mammals by comparing two different climate change scenarios for the year 2050. We aimed to analyze changes in species richness and turnover rates caused by future climate change. We used species distribution modeling with an ensemble forecasting strategy considering eight different modeling techniques and three levels of presumed species prevalence. We contrasted two extreme dispersal scenarios (no-dispersal vs. full dispersal) to calculate changes in species richness and species turnover over time, and analyzed the potential future impacts on mammalian species diversity in Ecuador. Our study analyzed the existing and potential effects of climate change on tropical mammals, and examined which species and areas would be more susceptible to climate change, to improve recommendations for the conservation and management of target species.

## METHODS

**SPECIES OCCURRENCE DATA.**—To forecast species distributions, we obtained occurrence records from the Mammalogy Section of the Museum of Zoology (QCAZ-M) at the *Pontificia Universidad Católica del Ecuador* and from the *Red Noctilio* database, which gathers information of mammal collections from 75 museums of natural history around the world (Tirira 2013).

We focused on the biodiversity of mammalian species in continental Ecuador. Our study area had a total of 9,183 available records with revised geographic coordinates for 236 species. However, 35 species had <10 records after spatial aggregation of the data (see below). We therefore modeled 201 species, representing 58 percent of the mammals known to occur in continental Ecuador, and including twelve orders and 37 families *sensu* Wilson and Reeder (2005).

**ENVIRONMENTAL DATA.**—We obtained climate variables from CliMond (Kriticos *et al.* 2011), a data base that was generated with input from WorldClim (Hijmans *et al.* 2005) and the Climatic Research Unit (CRU) datasets (New *et al.* 2002). CliMond includes basic climatological variables related to precipitation and temperature, as well as additional composite variables indicating humidity and productivity. CliMond was designed for large-scale studies, including variables that are widely recognized as limiting species distributions (Watling *et al.* 2012), and are relevant biologically for characterizing species ranges (Nix & Busby 1986). Since the release of CliMond, a new set of CRU simulations includes more recent climatological and socio-economic data, and describes four pathways of greenhouse gas emissions and atmospheric concentrations (Pachauri *et al.* 2014). Unfortunately, these updates were not available in CliMond at the time of our study and the latest database of WorldClim does not include radiation and moisture indices we considered important to characterize environmental gradients in Ecuador. The previous simulations remain valid and are supported by a recent study, which showed that the new models and those released in 2007 produce similar projected global temperature changes, and projection uncertainties have been similar over successive IPCC reports (Knutti & Sedláček 2013). We therefore decided to use CliMond for our projections.

Our climate change scenarios include socio-economic scenarios released in 2007 (Pachauri & Reisinger 2007). We divided the list of 35 CliMond bioclimatic variables into four groups: temperature (11 variables), precipitation, radiation, and moisture (8

variables in each group). We obtained the environmental variables at a resolution of 10-min (~18.6 km × 16.6 km on the equator). To minimize multicollinearity between predictors, we selected eight minimally correlated variables based on the following procedure. First, we carried out a Principal Component Analysis (PCA), which allowed us to select variables that represent the major axes of environmental gradients in the study region; the first three principal components summarized more than 80 percent of the total variance in the environmental data and, consequently, we retained these components. In the following steps, we tried to represent these axes by using the raw variables that (i) most influence each PCA axis, (ii) are minimally correlated between them (Pearson correlation <0.75), and (iii) represent the four environmental groups among CliMond variables. We selected these eight variables for the final analysis: BIO001—Annual mean temperature, BIO02—Mean diurnal temperature range, BIO03—Isothermality (diurnal/annual temperature range), BIO12—Annual precipitation, BIO18—Precipitation of warmest quarter, BIO20—Annual mean radiation, BIO23—Radiation seasonality, and BIO31—Moisture index seasonality.

Climate forecasts predict plausible future climates that result from a combination of a particular General Circulation Model (GCM) describing the physical processes, and a particular Special Report on Emissions Scenario (SRES) that describes the socio-economic processes. Here we considered two GCMs: CSIRO-MK (Centre for Australian Weather and Climate Research) and MIROC-H (Centre of Climate Research, Japan). Kriticos *et al.* (2011) argued that these two GCMs have a good representation of the observed climate at a regional scale. For each GCM, we chose two SRES families: A1 and A2. Family A1 assumes a world of very rapid economic growth, and family A2 assumes a world of slow economic growth. We did not consider conservative carbon emission scenarios because previous work suggested that they are no longer plausible (Kriticos *et al.* 2011). In fact, the latest CRU simulations showed that the conservative pathway is an unrealistic stringent mitigation scenario (Pachauri *et al.* 2014), where emissions would need to decline substantially in the very short term, including major coordination between multiple countries worldwide (Van Vuuren *et al.* 2011).

To process the environmental and occurrence data, we generated a regular grid of 18-km resolution for continental Ecuador (872 grid cells). We included the occurrence records of species distributed across the study area into the grid using a spatial aggregation strategy, which recorded any number of occurrences within a single grid cell as a presence record (Fig. 1B and C). This procedure eliminates pseudo-replication and brings environmental and occurrence data to the same resolution.

**MODELING METHODS.**—SDMs describe the relationship between species occurrences and environmental conditions (Elith & Leathwick 2009) to define suitable conditions for species (Anderson 2013). Some of them use presence-only data, while others require presence-absence data. Here we used presence-only records and generated background data to create a contrast between occupied

sites and the overall available environment. We randomly selected 200 background sites for each species across all available environments, excluding grid cells that were already marked as present. We selected background sites independently for each individual model run and species, to represent a subset of the environmental space where the species of interest has never been recorded. These background data served as pseudo-absences in the modeling efforts that required presence-absence data, as well as for the calculation of classification rates during model evaluation (see below). We used the R statistical software (v.2.15.3, R CORE TEAM 2012) to build and calibrate all models.

We used eight modeling methods based on logistic regression and machine learning approaches (Segurado & Araújo 2004, Elith *et al.* 2006, Phillips & Dudik 2008). Presence-only methods included BIOCLIM (Busby 1991), DOMAIN (Carpenter *et al.* 1993), and Mahalanobis distances (Farber & Kadmon 2003), which use presence records to describe the multivariate environmental space where a species is found, and the Maximum Entropy method (MaxEnt) which finds a distribution closest to uniform within the environmental space of occurrence sites (Phillips *et al.* 2006). Presence-absence methods included Generalized Linear Models (GLM) and Generalized Additive models (GAM), which are regression-based methods that model ecological relationships allowing for a binomial response (Austin 2002). We also included decision tree-based methods like classification trees (CART) and boosted regression trees (BTR), which identify environmental breaks that produce homogeneous groups in an iterative procedure (Friedman *et al.* 2000, Elith *et al.* 2008). These presence-absence methods allow us to change the expected species prevalence by using different weights on presences and background data, taking into account the uncertainty related to the expected species frequency when presence-only data are used (Meynard *et al.* 2013) and controlling for the effect of including a disproportionate number of absences when only a few presences are recorded. Here we used three levels of prevalence: 0.2, 0.5, and 0.8. This procedure resulted in 16 predicted probabilities of occurrence per species under current climatic conditions and under each climate change scenario.

We adopted a leave-one-out jackknife approach to calculate different classification success metrics for each model (Fielding & Bell 1997) because this is most appropriate for species with a small number of records. Notice that while presence records are fixed (*i.e.*, all available records are used) during this evaluation procedure, pseudo-absences were redrawn for each new jackknife iteration. We evaluated model projections by calculating sensitivity, specificity, the area under the receiver operating characteristic (ROC) curve (AUC), and the True Skill Statistic (TSS). In a ROC plot, the true positive rate (sensitivity) is plotted against the false positive rate (1-specificity) at all possible thresholds of presence-absence classification as the threshold varies from 0 to 1. We defined the area under this curve (AUC) as the probability at which presences and absences are accurately classified. Prediction accuracy is considered to be good for AUC values >0.8 (Fielding & Bell 1997). We also calculated the true skill statistic (TSS), which represents a better balance when species prevalence is very

high or very low (Allouche *et al.* 2006). We calculated this as  $TSS = \text{sensitivity} + \text{specificity} - 1$ , and it ranges from -1 (poor) to 1 (perfect classification). We considered values  $>0.6$  as appropriate (Coetzee *et al.* 2009).

To draw the consensus distribution for each species, we selected the five models that performed best in terms of AUC and TSS and then used these models to make a unique consensus prediction using a mean between predicted probabilities of occurrence (Marmion *et al.* 2009). This ensemble forecasting strategy has been recommended to take into account variability between models (Araújo & New 2007, Franklin 2009), and usually reduces uncertainty and increases accuracy by selecting the most consensual projections (Araújo *et al.* 2005, Coetzee *et al.* 2009). Because of the broad diversity of SDMs used here, the consensus predictions could contain a mixture of results from presence-only and presence-absence models, depending on model performance. Consensus predictions were then transformed to presence-absence (binary response) by using the threshold value that maximizes the sum of sensitivity plus specificity (Liu *et al.* 2005). The final projections of species distributions were based on the final runs of the models using all the occurrence data (Araújo *et al.* 2005).

For each climate change scenario, we calculated species richness per grid cell by stacking projections for individual species (Dubuis *et al.* 2011). Although this method may overestimate species richness in general, it has the advantage of allowing the analysis of species composition at the same time as species richness. Also, it may have higher correlations between observed and predicted values, as compared to a multiple regression approach where species richness would be modeled directly as the response variable (Dubuis *et al.* 2011). Since we were interested in analyzing changes in individual species ranges, as well as overall species compositional turnover across the study area, we adopted the stacking method. Some areas in Ecuador have not been surveyed thoroughly or even at all, so using the observed species richness as the response variable in a modeling effort will likely underestimate species richness in these areas (see Appendix S1 for more details).

For prediction into future scenarios, we adopted two extreme dispersal scenarios. The first was an unlimited dispersal scenario, whereby we assumed that species would track suitable climate over the entire study area. We also used a no-dispersal scenario (species would not be able to disperse at all), so that any future range will only include the overlap between the current potential range and the future potential range. Realistic future range shifts will likely fall between these extremes. We therefore represented a conservative and a pessimistic scenario in terms of area expansions and reductions, as well as in terms of compositional turnover.

**RANGE SHIFTS UNDER CLIMATE CHANGE.**—We used the consensus forecast to estimate the climatically suitable space for current and future distributions for each species from predicted binary responses. We then calculated the percentage of area gained or lost for each species, the number of species predicted to occur in

each grid cell, the difference in species richness and the compositional turnover between now and 2050. We calculated the Species Temporal Turnover (STT) for each grid cell as  $STT = 100 \times (L+G)/(SR+G)$ ; where STT is the species temporal turnover, L is the number of species lost in each grid cell, G is the number of species gained and SR is the current species richness of the target grid cell (Thuiller *et al.* 2005). A turnover value of 0 indicates that the assemblage of species is predicted to remain the same in the future, and a value of 100 percent indicates that the assemblage of species is completely different. Notice that turnover can be high in regions where species are lost as well as in places where species are gained.

## RESULTS

Most variability between predictions of species richness came from the particular GCM used rather than from the SRES scenario, although the general geographic trends in species diversity remained the same across scenarios (see Appendix S2). The combination of MIROC with A1B produced the most conservative climate scenario (*i.e.*, the one that predicts the least changes in species richness and turnover) and the combination of CSIRO with A2 produced the most pessimistic scenario. For simplicity, here we focus on these two extreme scenarios for 2050 to analyze shifts in diversity. Supplementary materials S2 and S3 contain further comparisons between different combinations of GCM x SRES.

All scenarios predicted that climate change will have effects on species richness distribution patterns. First, we found that species richness per grid cell would generally decrease (Fig. 2). Currently, mammal species richness is concentrated in the northern tropical Andes of Ecuador and in the western Amazon basin (Fig. 2A), representing the greatest species richness (123 species) recorded anywhere within the drainage. Under all scenarios (Fig. 2B–E) this maximum richness is expected to drop by 2050 (compare in Fig. 2, red and light orange areas for example). As expected, the no-dispersal scenario (lower row in Fig. 2) produces a more-pessimistic prediction than the full-dispersal scenario (upper row in Fig. 2), with large reductions in species richness all over Ecuador. Hotspots move little from their present locations, although the models predict a slight shift to the southeast for the Amazon basin and to the north for the Andes, due to individual species shifting in the same direction. This shift is logically seen for the full-dispersal scenario but not for the no-dispersal scenario.

As previously noted, these changes reflect extreme-case scenarios (Fig. 3, see also Appendix S2 and S3). For example, the climate scenario CSIRO-A2, which represents the most pessimistic extreme, predicts a maximum species richness per grid cell by 2050 of 75 species under the full-dispersal scenario and 58 under the no-dispersal scenario (Fig. 3C and E), whereas MIROC-A1B predicts 92 and 77 species, respectively (Fig. 3B and D). Half of grid cells have fewer than 40 and 30 species for MIROC-A1B and CSIRO-A2 respectively under the full-dispersal scenario (Fig. 3B and D), but species richness in the same grid

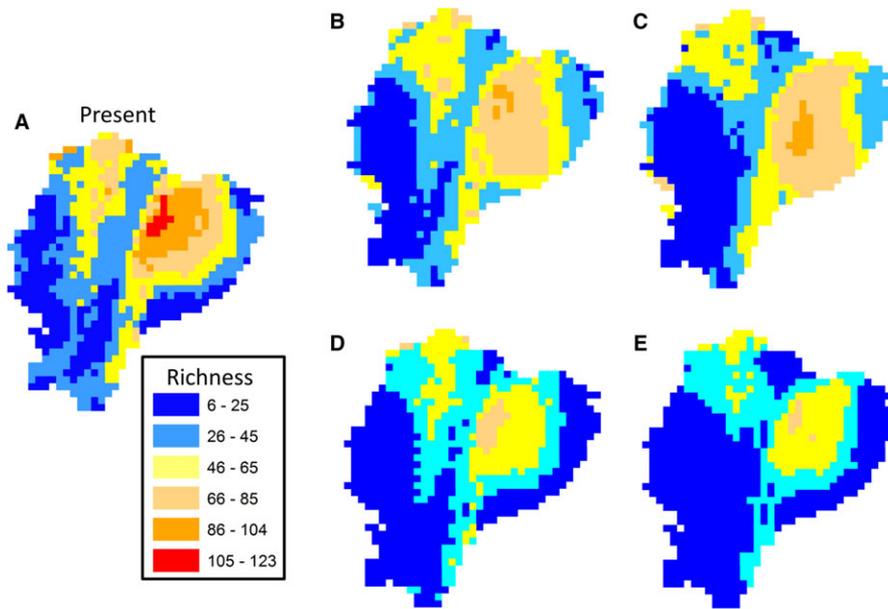


FIGURE 2. Comparison of species richness: (A) under current conditions; 2050 conditions for (B) MIROC—A1B, full dispersal hypothesis; (C) CSIRO—A2, full dispersal hypothesis; (D) MIROC—A1B, no dispersal hypothesis; and (E) CSIRO—A2, no dispersal hypothesis. Shown color codes at the left lower corner are the same for all maps.

cells would drop to 20 and 15 species, respectively, under the no-dispersal scenario (Fig. 3C and E).

Comparing the difference in species richness and species turnover between full-dispersal and no-dispersal scenarios provides complementary information on the potential changes in diversity (Fig. 4). For both scenarios, when the difference in species richness is large, the turnover rate is also large, independently of whether this represents species losses or gains. Notably, some of the areas that are predicted to gain species under the full-dispersal scenario are also predicted to suffer the highest compositional turnover.

Concerning range shifts for individual species, changes in suitable area will likely be important within Ecuador. Roughly 35 percent of the species would lose some area of their range in the country under the full-dispersal hypothesis and the MIROC-A1B scenario, and 30 percent of the species would lose more than half of their current potential range in Ecuador (Fig. 5). Under the most pessimistic scenario (CSIRO-A2), 40 percent of species would lose more than half of their range under full dispersal.

When analyzing the percentage of area change for individual species in six different mammal groups, we found that the majority of species (58%) would reduce their potential distribution area, even when allowing full dispersal (Fig. 6). Primates and bats would be most affected; about 30 percent of primate species and 23 percent of bat species would experience severe reductions ( $\geq 50\%$ ) of their potential distribution ranges followed by rodents, carnivores, and species classified as 'others'. Those three groups would be equally affected (18% of species in each group will lose more than 50% of their potential distribution). The group least

influenced by future climate change is the ungulates (<14% of species will lose more than 50% of their potential distribution). The model predicted that twelve species would lose almost all their area at the 2050 horizon under both climate change scenarios; most of them are bats (*Chiroderma salvini*, *Platyrrhinus brachycephalus*, *Rhinophylla alethina*, *Sturnira ludovici*, *Sturnira magna*, *Trachops cirrhosus*, and *Tadarida brasiliensis*). Eight species in four taxa could double their potential distribution range; most of them are rodents (e.g., *Akodon aerosus*, *Scolomys melanops*, and *Dactylomys dactylinus*).

In general, the models predicted that species would lose a greater percentage of their potential distribution range under the less conservative climate change scenario (CSIRO-A2), while the 67 percent of species that would experience an increase in their potential distribution area would also gain a greater percentage of area under this scenario. For example, the giant otter, *Pteronura brasiliensis* (Carnivora) is expected to increase its potential distribution area by 150 percent at the horizon 2050 under the MIROC-A1B scenario, and by >160 percent for the CSIRO-A2 scenario. The same happens with other species like *Anoura cultrata* (Chiroptera) and *Coendou rothschildi* (Rodentia), which are expected to increase their potential distribution area by 134 and 117, and >160 percent each, for the MIROC-A1B and CSIRO-A2 scenarios, respectively. In total, 17 species would be able to increase their suitable area by more than 80 percent, assuming full dispersal.

Finally, the frequency of species and percentage of area lost in the future due to climate change (Fig. 7) is expected to result in a decrease in the number of species as the area lost increases. A large number of species will lose more than 80 percent of their potential distribution range.

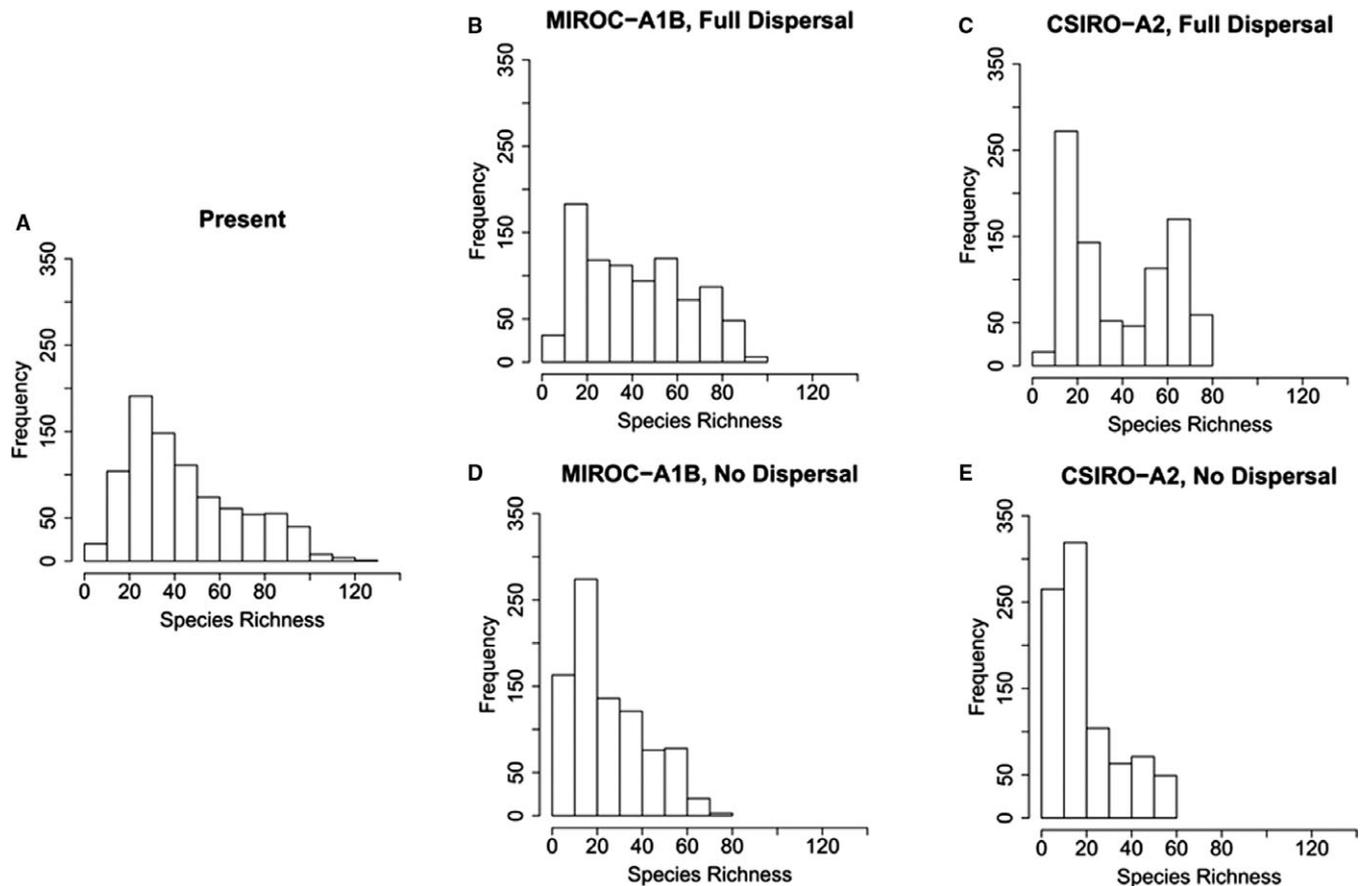


FIGURE 3. Histograms showing the distribution of species richness (frequency of species per grid cell) for current conditions, as well as for the two extreme scenarios and the two dispersal hypothesis: (B) and (D) correspond to MIROC-A1B, which is the most conservative scenario, whereas (C) and (E) correspond to CSIRO-A2, which is the most pessimistic scenario. The upper row (B and C) represents full dispersal scenarios, while the lower row (D and E) represents no-dispersal scenarios.

## DISCUSSION

**GENERAL DISTRIBUTION CHANGES.**—Species richness obtained from current models is expected to decrease in all climate change scenarios and dispersal assumptions, even under a full-dispersal scenario where species would be perfectly capable of tracking their preferred environments. Our results show that, although the no-dispersal scenario produces more important changes in species richness, spatial patterns of shifts remain similar across all models. As an example, the no-dispersal scenario predicted richness patterns similar to those obtained with a full-dispersal scenario (Fig. 2). Regions such as the Northern Andes and Amazonia would remain hotspots, but with fewer species. Amazonia would also present a low species turnover, probably because both climatic models (CSIRO and MIROC) predicted the entire country to become warmer, but with a slight increase in precipitation in the east. Shifts in precipitation patterns could affect potential species distributions in tropical forests more than changes in temperature (Condit 1998), and precipitation would explain a greater proportion of range limit movements than temperature in some

areas (Tingley *et al.* 2012). Understanding this precipitation-richness relationship therefore remains pivotal to forecasting the potential effects of climate change in the area.

**PREDICTIONS FOR DIFFERENT GROUPS AND SPECIES.**—Since our modeling effort is based on presence-only data and we do not have an independent dataset to evaluate model results, our projections must be interpreted with caution. For example, some grid cells have been better surveyed than others across Ecuador, and we do not have an independent estimate of sampling effort. This means that some of the background data might include sites where the target species is actually present but has not been recorded. However, we designed our pseudo-absence selection strategy to minimize the effect that a wrong absence could have in modeled distributions because (1) background data were randomly selected and changed from one model and species to the next; (2) the calculation of classification metrics was iterated over the equivalent number of presences during the jackknife procedure and for each model and species, randomly selecting new sites at each iteration; (3) the weighting scheme when using

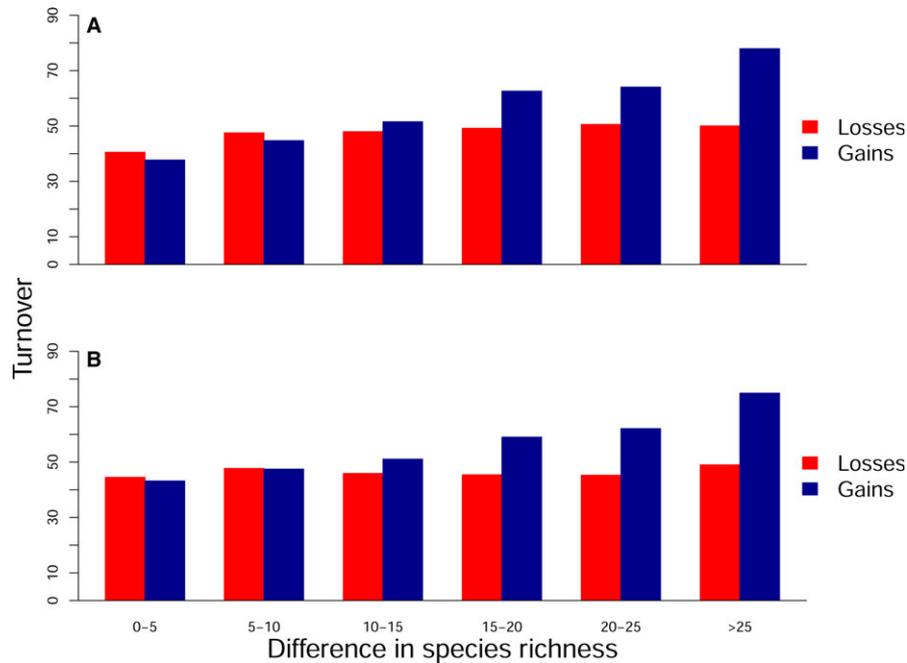


FIGURE 4. A comparison between ranges of difference species richness (losses and gains) and the average of turnover for each of those ranges in 2050 for (A) Scenario MIROC– A1B; and (B) CSIRO– A2.

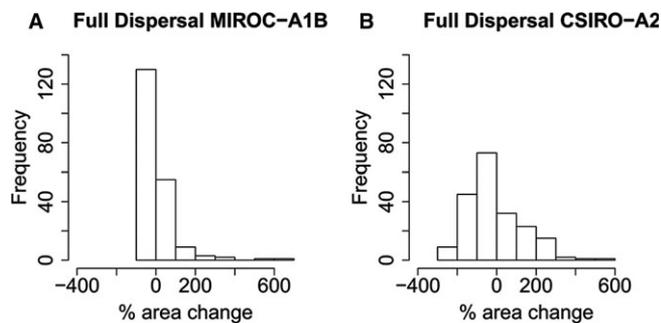


FIGURE 5. Change in species suitable area within Ecuador expressed in terms of a percentage of the current potential range in the country with respect to future projections. (A) MIROC-A1B; (B) CSIRO-A2, both represent a full dispersal hypothesis.

presence-absence methods will control the relative influence of pseudo-absences with respect to the available occurrences; (4) the ensemble forecasting strategy adopted here will consider only the best models and will tend to capture the consensus between them (Araújo *et al.* 2005, Coetzee *et al.* 2009); and (5) we used a combination of presence-only and presence-absence models to draw the consensus projections. All of this makes it extremely unlikely that a particular pseudo-absence has a major influence on the final projections of species distributions. Moreover, a preliminary comparison of the richness patterns in well-sampled areas suggests that our predictions are a good first approximation of reality (see Appendix S1). Gathering more extensive biodiversity data across highly diverse and vulnerable regions such as those

represented in Ecuador should be of high priority to preserve global diversity. However, in the absence of better data, the modeling approach presented here represents a systematic method to fill in knowledge gaps and prepare for the future.

Coastal regions and mid-elevation Andean slopes have historically been the most disturbed by human activities in Ecuador. According to Tirira (2011), species like *Tremarctos ornatus* (Carnivora) in the Andes and *Ateles fusciceps* (Primates) in the coastal region are critically endangered species mainly because of habitat fragmentation. Our results showed that *Ateles fusciceps* would lose 62 percent of its current range due to climate change. Given the magnitude of these potential changes, it would be advisable to incorporate both habitat fragmentation and vulnerability to climate change when evaluating species threats (Bomhard *et al.* 2005).

Primates assessed here might be the most severely affected group because they would have fewer suitable areas as compared to other mammals. In contrast, the models predicted that carnivores and ungulates would be less affected by changes. These orders are the least dispersal-limited and the distances they need to disperse might be shorter, relative to the distances required for species of other orders (Schloss *et al.* 2012). The assumption of no-dispersal could be more appropriate for conservation assessments since many other factors affect dispersal abilities of species and most of the reductions in range for mammals are due to dispersal limitations rather than a reduction in the area that is climatically suitable.

CONSERVATION ISSUES.—With the full-dispersal scenario, we expect species to be able to colonize new suitable sites, but in reality

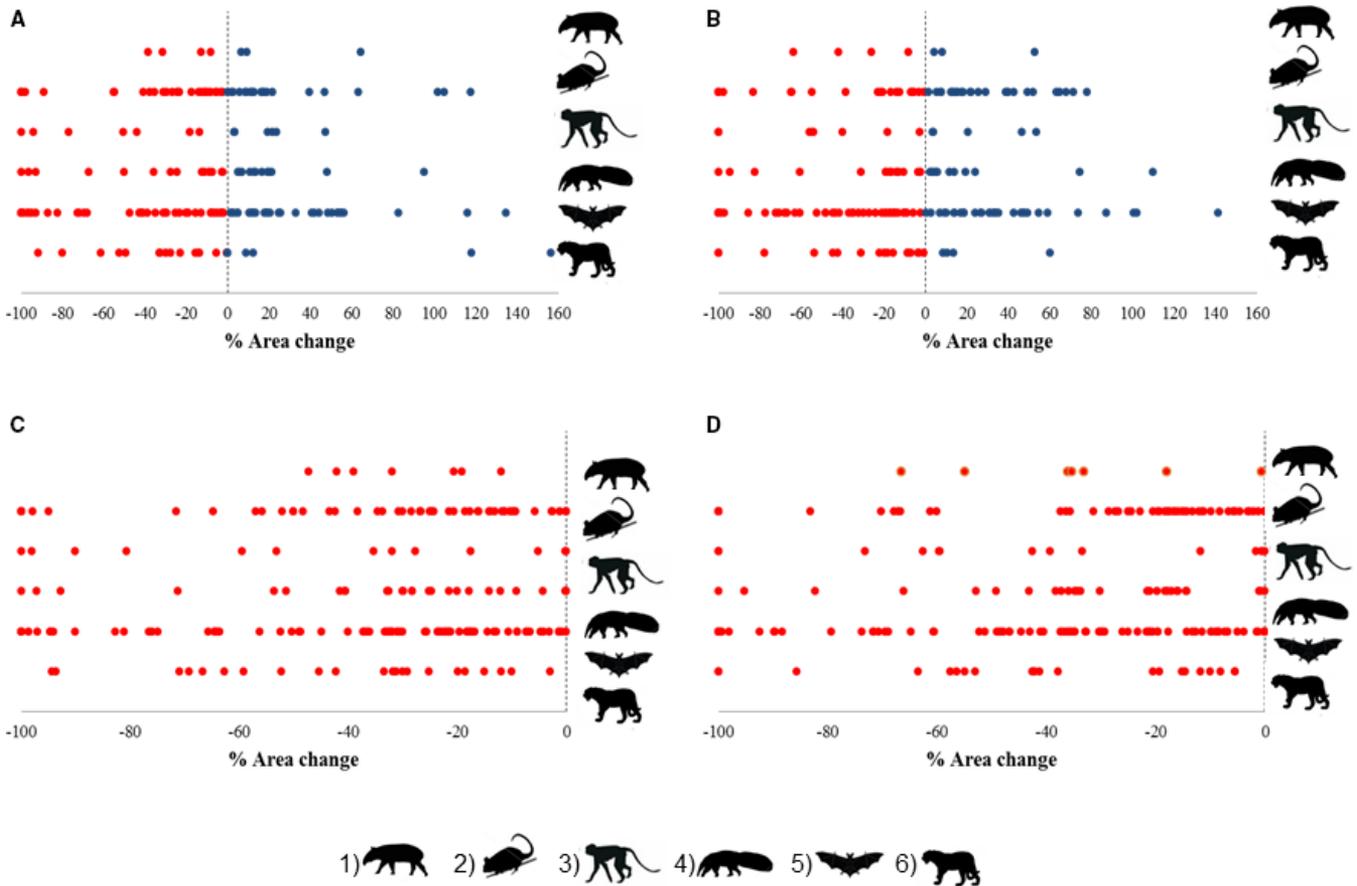


FIGURE 6. Percentage of area change for each species divided in six groups of mammals (each point represents one species): (1) ungulates, (2) rodents, (3) primates, (4) bats, (5) carnivores, and (6) others. Comparison under future conditions for 2050 for conservative and pessimistic scenarios. MIROC—A1B (A and C) and CSIRO—A2 (B and D) under the full dispersal hypothesis (A and B) and no-dispersal scenario (C and D).

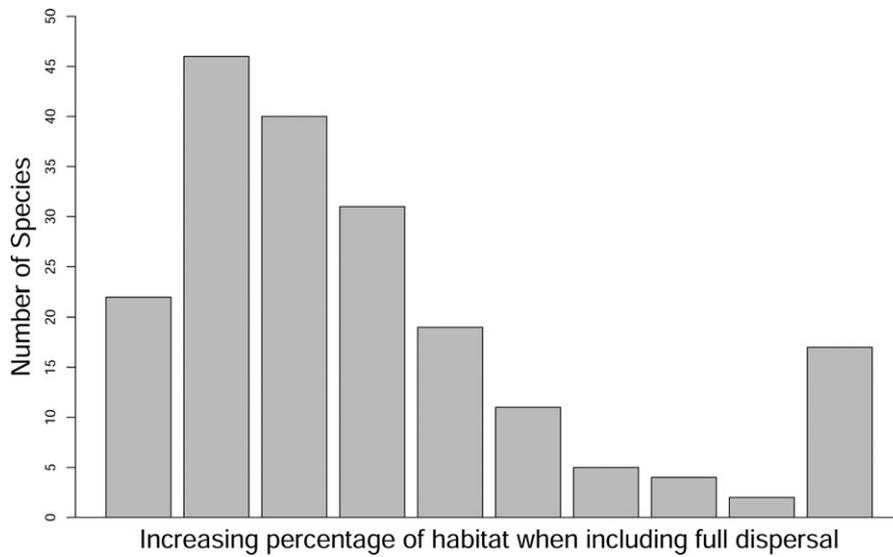


FIGURE 7. Histogram of percent of habitat lost per species under a full dispersal MIROC— A1B scenario.

some species may not be able to shift their ranges fast enough to track their suitable climates. Primates, for example, are more dispersal-limited than other taxa and may need to expand their ranges over longer distances to reach suitable climates (Schloss *et al.* 2012). In fact, survival of species in the future would depend on their abilities to track changes in suitable climates relative to the velocity at which climate changes in space (Loarie *et al.* 2009). For example, in some locations in Amazonia, average dispersal velocity for a subset of mammal species is about 1 km/yr, but the average velocity of climate change experienced can be as high as 8 km/yr (Schloss *et al.* 2012). In tropical regions, species generally have more restricted physiological tolerances and are expected to be more sensitive to climate change (Deutsch *et al.* 2008). The inability to keep pace with climate change may be due to narrower climatic niches of tropical species (Schloss *et al.* 2012). We predict an important loss of species in the Ecuadorian Andes, since some species living in this region could already be near their critical thermal maximum. Other approaches have documented a rapid loss of climatically suitable space for species of different taxa, and greater shifts are restricted to the mountains (Parmesan 2006, Tingley *et al.* 2012). According to Janzen (1967), tropical mountain passes should act as effective dispersal barriers. Also, dispersal ability of mammals could be higher or lower, depending on the species and the degree of fragmentation of their habitat.

Habitat loss and fragmentation are among the most important threats to global diversity (Laurance & Cochrane 2001), making it important to evaluate the synergistic effects of climate change and habitat fragmentation (Drake *et al.* 2005, Mantyka-Pringle *et al.* 2012). In Ecuador, deforestation rate is of 77,647 ha per year. The coast is the most disturbed area and has only 28 percent of the original forest cover remaining. Amazonia still has 89 percent of its original vegetative cover. The coast has an annual rate change of  $-2.49$  percent, while the Tropical Andes has a  $-1$  percent, and Amazonia a  $-0.3$  percent (MAE 2012). Therefore, to ensure mammal species survival into the near future, it is necessary to include the effects of habitat loss and dispersal limitations.

## CONCLUSIONS

A combination of distribution modeling techniques can be a useful methodology for data exploration to identify potential knowledge gaps, provide direction to fieldwork design, and guide conservation assessments incorporating climate change impacts on species' potential distribution (Elith *et al.* 2006, Hernandez *et al.* 2006). Although species distribution modeling is widely used for conservation planning, it is also necessary to continue collecting data on species for reliable assessments of the effects of climate on biodiversity and for the formation of sound management policies. SDMs ignore many potentially important ecological processes, such as biological interactions and dispersal mechanisms. Given the constraints of these models, results need to be taken with caution. However, their consistency across model types and extreme dispersal scenarios in this study provide

a strong indication of potentially important shifts in diversity in this megadiverse area. Our results show that even under conservative climate change and full-dispersal scenarios, diversity patterns in Ecuadorian mammals are likely to undergo considerable changes. Future research should therefore aim at understanding how these effects of climate change will interact with habitat degradation, and reinforce conservation efforts that take these effects into account.

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## DATA AVAILABILITY

Data available in the Dryad Repository: <http://dx.doi.org/10.5061/dryad.4v52c> (Iturralde-Pólit *et al.* 2017).

## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Richness and predictive success.

APPENDIX S2. Geographic distribution and sources of uncertainties.

APPENDIX S3. Consistency of diversity projections under different climate change scenarios over time and space.

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