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TITLE
Using species distributions models for designing conservation strategies of Tropical Andean biodiversity under climate change

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ABSTRACT

Biodiversity in the Tropical Andes is under continuous threat from anthropogenic activities. Projected changes in climate will likely exacerbate this situation. Using species distribution models, we assess possible future changes in the diversity and climatic niche size of an unprecedented number of species for the region. We modeled a broad range of taxa (11,012 species of birds and vascular plants), including both endemic and widespread species and provide a comprehensive estimation of climate change impacts on the Andes. We find that if no dispersal is assumed, by 2050s, more than 50% of the species studied are projected to undergo reductions of at least 45% in their climatic niche, whilst 10% of species could be extinct. Even assuming unlimited dispersal, most of the Andean endemics (comprising ~5% of our dataset) would become severely threatened (>50% climatic niche loss). While some areas appear to be climatically stable (e.g. Pichincha and Imbabura in Ecuador; and Nariño, Cauca, Valle del Cauca and Putumayo in Colombia) and hence depict little diversity loss and/or potential species gains, major negative impacts were also observed. Tropical high Andean grasslands (páramos and punas) and evergreen montane forests, two key ecosystems for the provision of environmental services in the region, are projected to experience negative changes in species richness and high rates of species turnover. Adapting to these impacts would require a landscape-network based approach to conservation, including protected areas, their buffer zones and corridors. A central aspect of such network is the implementation of an integrated landscape management approach based on sustainable management and restoration practices covering wider areas than currently contemplated.

Keywords: Andes, biodiversity, conservation, climate change, threats, climatic niche, maxent
1. Introduction

Despite ambitious goals to significantly reduce the rate of biodiversity loss by 2010 (CBD, 2007), biodiversity continues to be severely threatened (Ramirez-Villegas et al., 2012; Sachs et al., 2009). These threats include over exploitation of natural resources (e.g. water, agricultural soils), habitat loss and degradation, and invasive species (Butchart et al., 2010; Kim and Byrne, 2006). Biodiversity loss has been increasing since the second half of the 20th century, and is likely to continue into the future (Kim and Byrne, 2006; MEA, 2005). With climate change entailing likely increases in temperature and regional and seasonal changes in precipitation (Knutti and Sedlacek, 2013), ecosystems and their services are likely to suffer additional stresses (Chen et al., 2009; Feeley and Silman, 2010; Fuhrer, 2003; IPCC, 2007).

The Tropical Andes tops the list of worldwide hotspots for species diversity and endemism (Fjeldså et al., 1999; Gentry, 1995; Sklenár and Ramsay, 2001). For this reason, the region is considered a key priority for biodiversity conservation (Brooks et al., 2006; Myers et al., 2000). At the same time, the Tropical Andes have been identified as one of the most severely threatened natural areas globally (Jetz et al., 2007; Mittermeier et al., 1997). During the last century, concentration of human population and associated demands for goods and services in the inter-Andean valleys and the inner slopes of the Andean ridges, has transformed a significant portion of the natural landscape causing habitat loss and degradation followed by species extinction and disruption of ecosystem functions (e.g. water-flow regulation), especially in the Northern Andes (Bruinsma, 2003; Wassenaar et al., 2007; Armenteras et al., 2011; Rodriguez et al., 2013).
Resource-base over-exploitation of natural resources has led to a severe land degradation process (Podwojewski et al., 2002; Poulenard et al., 2001, 2004), increasing the pressure on the goods and services provided by these ecosystems (Rundel and Palma, 2000). In addition, the Andes are expected to undergo severe stresses over the next 100 years as a result of climate change (Beaumont et al., 2011; Malcolm et al., 2006).

Addressing potential impacts from climate change is important because the environmental impacts of human activities (Biesmeijer et al., 2006; MEA, 2005) could be exacerbated by the likely rapid changes in the climate system during the 21st century (IPCC, 2007; Knutti and Sedlacek, 2013). Warren et al. (2013) estimated that, in the absence of any climate change mitigation strategy, large range contractions for ca. 60% of plants and 35% of animals could be expected globally. Understanding and quantifying the extent at which climate change could threaten Andean species is therefore critical since many of the species in the region occur in low dense populations with narrow distribution patterns (i.e. endemics) with a high level of replacement within the environmental gradients. These characteristics make the Andean biota particularly sensitive to climate change disruptions.

Our primary objective was to assess the likely impacts of climate change on the distributions of vascular plant and bird species of the Tropical Andes. Using species distributions modelling techniques, we assessed the potential climatic niche of 11,012 species, and then projected them under the SRES-A2 emission scenario for two periods: 2020 and 2050. Future projected changes in species assemblages, including richness, turnover and range size were assessed. Lastly, the
projected impacts in selected groups of species of Andean origin were analysed. Finally, we discuss future strategies to reduce expected biodiversity loss.

2. Study area

The study area (Tropical Andes hereafter) comprises all interconnected areas above altitudes of 500 m within the countries of Venezuela, Colombia, Ecuador, Peru and Bolivia, plus the Sierra Nevada de Santa Marta in Colombia, delimited using data from the SRTM digital elevation model (Farr et al. 2007). Extending over 1.5 million km² from 11° N to 23° S, the Tropical Andes are the longest and widest mountain region in the tropics (Figure 1) (Clapperton, 1993; Fjeldså and Krabbe, 1990). The morphological and bioclimatic heterogeneity of the Andes have led to the formation of an enormous diversity of microhabitats favouring speciation (Mittermeier et al., 1997; Young et al., 2002). Moreover, their location between the lowlands of the Amazon, La Chiquitania and El Chaco to the east and the Chocó, Tumbes-Guayaquil and the arid systems of the Sechura Desert to the west, has created complex dynamics of species exchange and isolation (Bass et al., 2010; Young et al., 2002). The Tropical Andes harbours more than 45,000 vascular plant (20,000 endemics) and 3,400 vertebrate species (1,567 endemics) in just 1 percent of the Earth’s land mass (Lamoreux et al., 2006; Olson et al., 2001).

3. Methods

We modelled the climatic niches of 11,012 species (1,555 birds and 9,457 plants) using species distributions models. We modelled the climate-constrained present-day distributions of all species, and projected them onto two different future periods (2020s, 2050s) and two contrasting dispersal scenarios. The approach implemented here aims to evaluate the likely impacts of
climate change on the widest array possible of Andean plant and bird species by mid 2020s and mid 2050s and comprises the following six steps:

1. Assembling of species occurrence data
2. Generation of climate surfaces
3. Maximum entropy species distribution modeling
4. Analysis of projected climate change impacts on species assemblages
5. Delineation of conservation recommendations for the 2020s and 2050s

3.1 Species datasets

Presence data for 11,012 species (1,555 birds and 9,457 plants) were sourced from three databases. CONDESAN, the Centro de Datos para la Conservación de la Universidad Nacional Agraria La Molina (CDC-UNALM), and a previous global study (Warren et al., 2013) (W2013). From the three sources, we extracted all occurrences in the five tropical Andean countries (i.e. Venezuela, Colombia, Ecuador, Peru and Bolivia) of all vascular plant clades (Magnoliophyta, Pteridophyta, Pinophyta, Psilophyta, Cycadophyta, Gnetophyta, Lycopodiophyta) and bird (class Aves, phylum Chordata) species with at least one record within the study area (Figure 1B). By including these three sources of data we ensured the inclusion of common and widespread species (see Warren et al. 2013) as well as narrow-range Andean endemics and imperil species (also see Sect. 4.1 for details).

CONDESAN’s database consisted of data from multiple sources. Vascular plant specimen data were obtained from the Missouri Botanical Garden's Vascular Tropicos (VAST) nomenclatural database (Garden, 2004), the Herbarium of the National Science Institute in Colombia (ISN) and
the Catholic University Herbarium (QCA) in Ecuador. Bird species data were obtained from databases belonging to the Chicago Field Museum of Natural History, Academy of Natural Sciences of Philadelphia, California Academy of Sciences and the Berkeley Museum of Natural History and cross-checked with BirdLife International database (version 2012). Additional data were obtained from private databases (Juan Fernando Freile for Antpittas, Paul Hamec for *Dendroica cerulea*; Cal Dodson-Lorena Endara for orchid’s records and James Luteyn’s database stored at the New York Botanical Garden site for *Ericaceae*) and published literature (Casares et al., 2003; Renjifo et al., 2002; Schuchmann et al., 2001). The CDC-UNALM database was produced from the review of papers and reports during the last 25 years. It also comprises field reports obtained by its own research as well as data provided by other national (i.e. Peruvian) researchers. The W2013 database was originally sourced from the Global Biodiversity Information Facility (GBIF, available at [http://data.gbif.org](http://data.gbif.org)). Warren et al. (2013) thoroughly checked the GBIF plant and animal database for location errors following the methodology of Ramirez-Villegas et al. (2012), whereby the consistency of the location data is verified at both geographic (using coastal and country borders) and environmental (using outlier-removal tests) levels. We carefully checked bird species names using BirdLife’s taxonomy database as a reference. Plant taxonomy was verified using The Plant List ([http://www.theplantlist.org](http://www.theplantlist.org), see Warren et al., 2013).

### 3.2 Climate data

Current climate data were derived from WorldClim (Hijmans et al., 2005). WorldClim is a global gridded dataset of monthly climatological means of maximum, minimum and mean temperature and total precipitation developed through Thin Plate Spline interpolation of long-
term (i.e. 1950-2000) weather station records (Figure 1A). There is a generally dense distribution of weather stations across the core of our geographic analysis domain (Hijmans et al., 2005). Using the monthly WorldClim data we derived 10 ‘bioclimatic’ indices (Busby, 1991; Rivas-Martinez, 2004) (Table 1). These indices describe annual and seasonal trends and allow for an adequate characterization of the species bioclimatic niches. These indices are important limiting factors for growth and development of species, and have been used extensively for predicting species distributions using presence-only data (Elith et al., 2006; Graham et al., 2008; Warren et al., 2013). For the Andes, the 10 bioclimatic indices chosen cover aspects of both average and extreme conditions of a year. In addition, the use of the ombrothermal index allows for differentiating climate conditions between and across ecosystems (Rivas-Martinez, 2004).

We obtained future climate projections from the CMIP3 (Coupled Model Inter-comparison Project phase 3) web data portal (https://esg.llnl.gov:8443/index.jsp) (Meehl et al., 2007). We downloaded monthly time series of temperature and precipitation data for the baseline period (20th century) and projections of future climate for the 21st century for the SRES-A2 emission scenario for 24 different Intergovernmental Panel on Climate Change (IPCC) coupled GCMs (Table 2). We chose SRES-A2 because we considered the full-mitigation SRES-B1 unlikely, and because differences between SRES-A2 and SRES-A1B and SRES-A1FI by 2050s are negligible (Hawkins and Sutton, 2009). Based on the availability of maximum and minimum temperature data, we further selected a subset of nine GCMs (Table 2).
Using the complete GCM time series, for each of the GCMs, months and variables, we calculated the 30 year running average over the baseline period (1961-1990) and two future periods: 2020s (2010-2039) and 2050s (2040-2069), representing the early and mid-21st century. We then calculated the anomalies (deltas) of each GCM future scenario with respect to the baseline period (average 1961-1990 climate) for each month, variable and period.

Given the significant heterogeneity in Andean climates, coarse scale GCM grids fail to represent the diversity of niches where species are distributed, hence we increased the resolution of the GCM data by means of empirical downscaling with the delta method (Ramirez-Villegas and Jarvis, 2010). For each month, variable, and period, the respective set of GCM deltas was averaged (i.e. ensemble mean). Temperature anomalies were directly added, whilst precipitation anomalies were added as a relative factor to the value in WorldClim in order to avoid precipitation values below zero due to the differences between the GCM simulated and WorldClim observed baseline. For each of the future periods, we calculated the same bioclimatic indices as for current climate data (Table 1). This yielded climate scenarios for each of the future periods as an average trend of the set of available GCMs on the SRES-A2 emission scenario.

We used the ensemble mean (rather than individual GCMs) owing to processing and storage needs, and given the considerable number of species being modelled and the resolution at which the models were projected (2.5 arc-min).
3.3 Species distribution models (SDMs)

Species distributions were modelled using Maxent (Phillips et al., 2006; Phillips and Dudík, 2008), a robust bioclimatic envelope modelling techniques (Smith et al., 2013). We modelled only species with at least 10 distinct locations (Ramírez-Villegas et al., 2010; Wisz et al., 2008), as a compromise between model quality and sufficient coverage of limited-range species. Maxent models the climate-constrained distribution of a species using presence-only data and a set of environmental descriptors (Elith et al., 2010; Phillips et al., 2006). Maxent has been tested extensively and has been found to suitably perform as a state-of-the-art modelling technique both under current and future conditions (Costa et al., 2010; Phillips, 2008; Smith et al., 2013).

Here, we followed a similar methodology to that employed by Warren et al. (2013), whereby default features optimised to broad species groups were used to construct Maxent models for each species (Phillips, 2008; Phillips et al., 2006; Phillips and Dudík, 2008). For each species we drew 10,000 pseudo-absences from the countries where the species was reported (according to our database). This was done to avoid over-fitting of the models whilst maintaining a good discrimination between presence and absence of the species (Isaac et al., 2009; VanDerWal et al., 2009).

Most niche modeling techniques are sensitive to the number of predictors used and Maxent is no exception (Braunisch et al., 2013; Dormann, 2007; Phillips, 2008). Excess predictors in a Maxent model can cause over-fitting and hence bias the responses under future scenarios by over-weighting certain drivers over others (Warren and Seifert, 2010). Hence, following Warren et al. (2013), we reduced the number of predictors in the Maxent model for species with low numbers.
of occurrences. For those species with \(< 40\) unique data points, a set of six climate predictors was used (i.e. \(P_1, P_4, P_{12}, P_{15}, I_0\) and \(I_{od2}\)), whilst for taxa with \(> 40\) unique data points, the complete set of 10 predictors (i.e. \(P_1, P_4, P_5, P_6, P_{12}, P_{15}, P_{16}, P_{17}, I_0\) and \(I_{od2}\)) was used. This choice was a compromise between having overly-complex Maxent models for species with low numbers of occurrences and having overly-simplistic models for species with very large numbers of occurrences.

Maxent models were fitted using cross-validation (10 iterations), each one randomly dropping 10-20\% input points. We then assessed the model skill using the Area under the ROC (Receiver Operating Characteristic) Curve of the test data (AUC\textsubscript{Test}), calculated as the average AUC\textsubscript{Test} of the 10 runs. Despite known limitations (Lobo et al., 2008; Warren et al., 2013), AUC\textsubscript{Test} is a useful metric for selecting Maxent models of appropriate complexity (Warren and Seifert, 2010) and is a widely used model accuracy and selection criterion (Braunisch et al., 2013; Graham et al., 2008; VanDerWal et al., 2009). The procedure applied here allowed us to discard species with models showing low predictive skill: only models with 10-fold average test AUC\textsubscript{Test} \(\geq 0.7\) were projected onto the future climatic periods.

We then projected the fitted models onto both the continuous WorldClim current climate surfaces and the downscaled surfaces of future climate conditions (2020s and 2050s). We then binned the probability distributions using the ‘prevalence threshold’ (Liu et al., 2005; 2013). This threshold is defined as the average probability over all input data points used to fit the model (i.e. training presence points). To reduce commission (i.e. straying too far from the actual niche of a taxon) or omission (i.e. missing major species populations due to lack of observations), the
current climate distributions of each species were further clipped within a 300 km buffer around the respective input occurrence points (also see Warren et al. 2013).

For future climatic scenarios, species distribution maps were first binned using the prevalence threshold, and then further limited using two assumptions about species’ dispersion mechanisms (Jarvis et al., 2008; Thomas et al., 2004; Thuiller et al., 2005): (1) no dispersal and (2) unlimited dispersal. For the no dispersal scenario, the projected future distributions were not allowed to stray away from the current-climate distribution. For the unlimited dispersal scenario, all future suitable areas outside the current-climate distribution were considered of the future distribution. This implies that a species can migrate and occupy any new site that becomes suitable under future climatic conditions. We acknowledge that unlimited dispersal is unrealistic (particularly for plants), but we use this scenario to illustrate the likely impacts of climate change on diversity even when the best possible conditions are assumed (e.g. through use of assisted migration, also see Sect. 5.3).

3.4 Assessment of climate change impacts in species assemblages

Species richness was calculated using the binned species distributions as the total number of species in a given site (i.e. pixel) and then used to calculate changes in species richness as the difference between future species richness and current species richness divided by current species richness. Additionally, we calculated the species turnover for the unlimited dispersal scenario (Broennimann et al., 2006). This index arises from a modification of the ‘classical’ species turnover (beta-diversity) indicators (Lennon et al., 2001; Whittaker, 1960) which are
computed in geographic space using a defined spatial neighbourhood (Broennimann et al., 2006)

$$\text{species turnover} = 100 \times \frac{\text{species gain} + \text{species loss}}{\text{initial species richness} + \text{species gain}}$$  \[\text{Equation 1}\]

This turnover index has a lower limit of zero when the ‘species gain’ and the ‘species loss’ are zero (both of which are very unlikely to happen with a large set of species), and an upper limit of 100, when the whole set of species changes from one time period to the other (i.e. either the species gain or loss equals the initial species richness and there is no loss or gain respectively).

3.5 Assessment of individual species responses to climate change

To estimate the sensitivity to climate change at the species level for both migration scenarios and periods, we intersected the current and future climatic niches and calculated the climatic niche persistence. This is defined as the percentage of area that remains suitable in relation to the total area in the current climatic niche (Loehle and LeBlanc, 1996; Peterson et al., 2001). Climatic niche loss and gain were first calculated as the percentage area predicted to become unsuitable or suitable respectively in the future climatic niche in relation to the total area in the current climatic niche (Broennimann et al., 2006). The species range change was then calculated as the difference between climatic niche gain and loss. This represents the percentage of range expansion or contraction in relation to the current climatic niche for each species under the future scenarios.

4. Results
4.1 Species datasets

Our final modelling dataset comprised 478,301 vascular plant occurrences for 9,457 species and 88,636 bird occurrences for 1,555 species (Figure 1B). The W2013 dataset provided the greatest proportion of occurrences, with 93% of all locality points used, and holding data for 9,371 vascular plants species and 1,429 birds. The database from CDC-UNALM provided 4.14% of the occurrence points used for 186 vascular plant and 1,316 bird species. CONDESAN’s dataset contributed 2.9% of the occurrences representing 501 birds and 237 vascular plants. Despite the majority of records were from the W2013, the CDC-UNALM and CONDESAN datasets provided critical occurrence data for rare, endemic and narrow-range species that were poorly (if at all) represented in the W2013 database (see e.g. Supplementary Figure S1 in Warren et al. 2013).

4.2 Performance of species distribution models

Almost half of the plant (48%) and bird species (44%) had an average test AUC > 0.9, suggesting a good aptitude of the models to discriminate the species’ fundamental climatic niche. The average test AUC of all plant species was 0.874 (median = 0.894, SD = 0.088), while that of bird species was 0.872 (median = 0.889, SD = 0.076) (Figure 2). Cross-validated runs indicated that variability of AUC ranged from 0 to 13.7% for training-sets and from 0 to 38.8% for evaluation sets. Relatively unstable test statistics were found for species with very low number of data points (high variability in AUC across repetitions), both in training and test sets.
Maxent models performance as measured by the average AUC was relatively similar for birds (BD) and vascular plants (VP), on average (Figure 2). Average training VP AUC ranged from 0.433 to 0.999, whilst test AUC varied from 0.28 to 0.999. In a few cases (< 500 for plants and < 50 for birds) the AUC statistic fell below the 0.7 threshold for model quality, probably owing to a combination of a limited number of species records and an asymmetric spatial distribution (i.e. high spatial autocorrelation). Less than 1% of the whole set of plant and bird species had an AUC value equal to or worse than random discrimination of presences and absences (AUC ≤ 0.5). All species with average test AUC below 0.7 were removed from any further analyses (see Sect. 3.3.1). Based on a sufficiently high AUC (i.e. > 0.7), a total of 9,062 vascular plant and 1,456 bird species (95.7 and 96.6% respectively) were used in all following analyses.

4.3 Shifts in species richness and community turnover

Current species richness ranged from 0 to 452 species for birds and from 0 to 1,535 species for vascular plants per pixel of 25 km² (Figure 3). The highest concentration of plants is located on the outer slopes of the Western and Eastern Andean chain, between 1,500 to 3,000 m in altitude, primarily in the Andes of Colombia, Ecuador and Venezuela as well as on the inner slopes of the Central Chain of Colombia (upper Magdalena river basin) (Figure 3A). Diversity of birds is particularly high throughout the Peruvian Andes, in the montane forests along the Eastern ridge (Range = 141-452), and in the montane forests of the north-western chain of Ecuador (Figure 3B).
Patterns of changes in species richness show important differences depending on the dispersal thresholds and the period analysed (2020 or 2050). The unlimited dispersal scenario projects an upslope migration of both plant and bird species suggesting important changes in the configuration of the diversity patterns of Andean biota. On the other hand, the no-dispersal scenarios show a significant reduction in species richness for both plant and bird species with major changes by 2050. The maximum richness values in the no dispersal scenario by 2050 period are 1,244 for plant species (mean = 163 ± 178) and 295 for birds (mean = 29 ± 36) per 25 km² pixel (Figure 4). Areas showing the largest decreases in species richness are located along the montane forests of the Eastern Andes of Bolivia and Peru between 500 and 1,200 m, on the outer slopes of the Eastern Andean foothills in Colombia and Ecuador, and on the Pacific slope of Northern Ecuador and southern Colombia (Figure 4). Conversely, the areas with minor changes are the highlands of Peru and Bolivia (Altiplano) and the pacific slope of the Peruvian Andes.

Negative changes in species richness are also observed even when unlimited dispersal is considered. Loss of diversity is observed from north to south of the Andes, although some particular areas are worthy of more attention; areas below altitudes of 1,500 m in the east Peruvian Andean mountains (i.e. central and eastern Huanuco, Pasco and Junin) seem to be severely impacted (>60% loss in species richness), and the same pattern is observed in the border between Ecuador and Peru, and in Nariño, Valle del Cauca, and Putumayo in Colombia. These
changes may be attributed to the eastern margins of the mountain chain being less climatically
suitable in warmer climates.

The projected changes in community turnover are concentrated to a large extent in the High
Andes of Bolivia and Peru, as well as in the foothills of the Sierra de la Macarena, Sierra Nevada
de Santa Marta and around the Magdalena river basin in Colombia. Significant shifts are also
evident in the Venezuelan Andes along the Merida chain (Figure 5).

4.4 Individual species responses

Increases are projected in average climatic niche size for all species under the unlimited dispersal
assumptions for the 2020s period (Figure 6A). As expected, more severe impacts are projected
for the 2050s, and this is reflected in a less pronounced increase of range size in the unlimited
dispersal scenario and a stronger decrease in the non-dispersal scenario (Figure 6A, B).
Considering an unlimited dispersal scenario, the rates of climatic niche expansion seem to be
high, with most of the species being highly favoured or barely affected by climate change if
migration in fact occurs and other non-abiotic factors remain stable (e.g. land-use patterns, pests
and diseases), particularly for birds. Some 45% (n=655) of bird and 41% (n=3,715) of vascular
plant species modelled are likely to experience an increase in their climatic niches of 100% or
more by 2050s (Figure 6A). By contrast, only a limited proportion of species (< 10 %) is
expected to experience no increase or a net loss in their climatic niche size. Our estimates indicate that even assuming unlimited dispersal some species are expected to undergo range contraction (even to the extent of extinction), thus highlighting specific sensitivities to climate change.

In a no dispersal scenario, the differences between periods become more evident (Figure 6B). Whilst by 2020s the maximum changes in range size are reductions of 50% and 80% for birds and vascular plants, respectively, by the 2050s, species within both groups are projected to experience 100% range reduction, indicating likely extinctions for a vast number of species.

To illustrate species-specific responses under future climate, we further selected and analysed two contrasting genera for each species group (plants and birds). These genera were selected because they are of relatively recent origin (during the Pleistocene, ca. 1 to 3 million years ago), include species that are endemic to the Andes, and are classified vulnerable or critically endangered by IUCN (Table 3 and 4). Many of the species of the genera *Grallaria* and *Eriocnemis* (class: *Aves*) are projected to expand their niche by more than 100% if dispersal was assumed. In particular, the species *E. cupreovenitris* and *E. nigrivestis* were found to increase their niche considerably by 2020 and 2050. In the case of no-dispersal, however, these species depict range contractions of 69 and 65% (respectively) by 2050. Similar responses were found for most species of the genus *Grallaria*, notably *G. alleni*, *G. aplotona*, *G. gigantea*, and *G.*
hypoleuca, for which range contractions of 59, 83, 54, and 63 % are projected by 2050s (no dispersal), respectively (Table 3).

Similar responses are reported for the plant genera Polylepis and Gynoxis. Species such as P. lanuginosa and P. tomentela showed significant increases in range size in both future scenarios (unlimited migration), but rather large decreases in range size under no-migration assumptions. By contrast, some species of these genera (e.g. P. incana, P. reticulate, G. buxifolia, and G. caracensis) report range contractions for both dispersal scenarios and periods (Table 4). These species that respond negatively even under when unlimited dispersal is allowed can be considered of very high sensitivity, and perhaps also be prioritised for further research to understand such sensitivities.

5. Discussion

5.1 Changes in species distribution patterns

Our results suggest that impacts of climate change over the Andean biota could be extremely severe. This finding is in agreement with previous studies for the Andean region (Feeley and Silman, 2010; Feeley et al., 2011ab; Tovar et al., 2013), other tropical areas (Hole et al., 2009; Miles et al., 2004; Still et al., 1999), or globally (Warren et al., 2013). The effects of climate change on the Tropical Andes can be synthesized at two different levels: the extent of the whole Tropical Andes (regional level), and at the species level. At the regional level, the inner and outer Andean foothills (800 – 1,500 meters) are likely to be the most affected due to a high amount of species loss. In addition, the spatial patterns of species turnover demonstrate a bimodal response. First, an upslope shift of several species from mid elevations to the high
Andes is expected. Second, a large west and southward displacement of species from the upper areas of the northern portion of the study area (i.e. Merida, Perijá and Santa Marta) towards lower latitudes and a significant climatic niche reduction of mountain-top endemics is also projected.

The areas that would be most affected by high absolute species turnover rates and the subsequent change in the composition of communities are the montane dry forest, the Santa Marta massif, the Mérida ridge, the inner slopes of the Central and Eastern ridges of the Colombian Andes and the Altiplano of Peru and Bolivia (> 3,800 meters).

At the species level, the biophysical impacts of exposure to climate change are projected to be highly variable. In this study, the two contrasting dispersal scenarios show extremes of a spectrum of projected responses by species to climate change. For plants, it is likely that the true response lies nearer the no-dispersion scenario (see also Feeley et al., 2011a), whereas for birds the response may in some cases resemble that of the full-dispersion scenario. Overall, we report that plant species may be more negatively affected in both magnitude and direction of range change impacts than birds in both periods. The same pattern holds for both migration scenarios, probably due to a greater proportion of endemic and narrow-range plant species and/or the presence of isolated (meta) populations (Figure 6A) (also see Ramirez-Villegas et al. 2012), and perhaps to some extent also due to incompleteness of samples for some species. Yet species interactions might have a prominent role in this point. For example, species interactions can slow climate tracking and produce more extinctions than predicted by climatic niche models only (Urban et al. 2013); or on the contrary, broad-ranging animals might transport seeds enabling
long-distance dispersal, as documented before during the last de-glaciation period, in which trees
dispersed at rates of 100-1000 m year\(^{-1}\) (Clark, 1998).

The projected alteration of the spatial distribution patterns of Andean assemblages (Feeley and Silman, 2010; Feeley et al., 2011a; Jetz et al., 2007) suggest the appearance of novel communities adapted to non-analogous climatic conditions, which could affect the functioning of Andean ecosystems (Williams and Jackson, 2007). Many shrubby and epiphyte species (e.g. Solanaceae, Bromeliaceae) depend on their specialized symbiotic interactions with animals for seed dispersion and pollination. Climate change effects on these organisms could cause spatial, temporal, or physiological asynchronies between mutualistic species, producing changes in community composition and structure (Zavaleta et al., 2003).

Our estimates are thus useful in gauging general trends and possible impacts, although it is very likely that individual responses at the species or community level will be determined by species’ ecological traits (i.e. dispersal capacity), species interactions (i.e. competition) and/or by their physiological response to stresses, leading (in some cases) to different outcomes. If species are sufficiently mobile they may be able to track the geographic displacement of their climatic niches, or if species are capable of rapid evolutionary change or have a wide range of abiotic tolerances, they may adjust to changing ecological conditions and landscapes (Broennimann et al., 2006). According to Travis (2003) and Opdam and Wascher (2004), the exact nature of a species’ response to different rates of climate change depends upon colonization ability and how much of a generalist the species is. For species with lower colonization ability and for specialist species, the threshold occurs at a lower climate change signal. In a human dominated world,
however, natural or semi-natural ecosystems are embedded in tracts of unsuitable landscape, and populations of species restricted to those habitat types are spatially dissected. By consequence, what is ascribed as a shifting species range is in fact the complex result of extinction of (meta) populations at the warm range limit (that surpasses thresholds of species adaptability), and colonization and growth of (meta) populations into regions that newly came within the cold range limit (that enters the range of species adaptability). Hence, for understanding the potential risks of climate change to a species, we must consider the dynamics of the populations constituting the geographical range in connection to the spatial features of the landscapes across the range (also see Sect. 5.3). Human land-use may be especially important in the Andes where anthropogenic activities above tree line and in the piedmont may create a hard barrier to upward migrations, imperilling Andean biodiversity (Feeley et al. 2010; 2011a); therefore, the incorporation of a coupled model that integrates climate change scenarios together with land cover change dynamics is a priority task to analyse specific responses of the Andean biota to these drivers of change.

5.2 Species extinction risks

Climatic fluctuations during the Pliocene-Pleistocene period strongly influenced the origin and spatial arrangement of the majority of Andean species used in this study (Luteyn, 2002; Young et al., 2002; García-Moreno et al. 1999). During periods of intense climatic change in the Pleistocene, epiphyte-laden evergreen vegetation remained only where conditions remained stable, suggesting that ecologically stable areas may have existed during the glaciations as small pockets within surrounding drier pieces of montane forest (Fjeldså, 1995; Roy et al., 1997; Arctander and Fjeldså, 1997). As a consequence, many of these surviving species present in
these ecosystems are endemic, with narrow habitat tolerances in conjunction with a restricted distribution range (Kattan et al., 2004). These patterns and conditions constitute a perfect scenario to promote higher rates of species loss and turnover under projected climate anomalies such as those projected in the present study.

In this context, reductions in the size of the climatic niche such as those herein projected imply that a number of species may become restricted to a few sites. Species with small range sizes are vulnerable to smaller stochastic events as these could affect a larger proportion of the species’ total population, especially in fragmented landscapes (With and King, 1999). As a result of this, extinction risks will likely intensify for a large portion of the taxa analysed here, particularly at long lead times (2050s in this study). Our study, as many others, assumes that species will die out within regions that are predicted to become climatically unsuitable for them (Ohlemüller et al., 2006), and takes no account of species- or population-level adaptive responses that may reduce negative effects (see e.g. Harte et al., 2004). Despite that, our results may be conservative given that we (1) did not include habitat loss data for the Tropical Andes in the analysis (Leisher et al., 2013; Ramirez-Villegas et al., 2012), (2) did not consider potential impacts of changing interannual variability (e.g. frequency or intensity of drought or heat waves) in our models, and (3) did not model any secondary effects such as pests, diseases or important species-level interactions required for survival. Furthermore, the rather low generation times of many vascular plants and some bird species will probably preclude adaptation rates from keeping pace with human induced climate change.

5.3 Management and conservation implications
In conservation planning, irreplaceability (commonly measured as singularity) and vulnerability (measured through threat processes) are among the most important dimensions to analyse (Brooks et al., 2006). Several authors have depicted the Tropical Andes as being within the most vulnerable regions with high irreplaceability (Brooks et al., 2006; Kattan et al., 2004; Mittermeier et al., 1997), placing the region extremely important for conservation action.

The question of whether the current protected area system is sufficient given the challenges of climate change is a critical one. A regional analysis by Ramirez-Villegas et al. (2012) showed that 8 out of 16 conservation areas in South America are in the Andean highlands. According to the present study, negatively impacted areas (orange to red areas in Figure 4) could lose up to 60% of species richness and suffer up to 100% changes in community makeup, thus, affecting ecosystem functioning as well as ecosystem services to human society (Gamfeldt et al., 2008). There is no question that these projected impacts will affect conservation planning during the 21st century, and hence further research should focus on developing a better understanding of conservation effectiveness under future climates for the Andes (Araujo et al., 2004). Tropical mountain systems such as the Andes are highly variable in climate, and therefore, offer a wide range of adaptation pathways for species, further increasing their value for conservation. The herein projected changes in range sizes, species richness and community composition are useful metrics in evaluating tools for conservation, such as for adjusting extinction risk assessments, delimitation of priority conservation areas and conservation targets within protected areas.

Using these results to identify priority areas at a medium to large scale could be particularly useful, given that diversity cannot always be easily captured in a single site-specific targeting of
conservation in the Andes, requiring instead, conservation actions spread throughout entire biomes (Fjeldså et al., 2005; Ramirez-Villegas et al., 2012). In this context, based on Opdam and Wascher (2004) we propose three major components for a conservation strategy in a warmer Tropical Andes. Firstly, a focus on landscape conditions for biodiversity, where populations potentially can respond to large-scale changes and disturbances. These conditions should allow populations to respond to large-scale disturbances. If species distributions patterns change more dynamically in space and time, local conservation management for single species will be less effective. Secondly, we propose to shift in strategy from protected areas towards landscape networks including protected areas, connecting zones and intermediate landscapes. Thirdly, we propose a shift from a defensive conservation strategy towards a landscape development strategy. A static approach of establishing isolated reserves surrounded by a highly unnatural landscape is not an effective strategy under a climate change scenario. Given the intense land use changes in the Andes, the sensitivity of Andean species to climatic changes, and the fact we are globally already committed to at least +2 °C warming, we must accept that conservation of biodiversity is only effective if we dynamically integrate it in the development of the entire landscape, based on coalitions with other functions such as the identification of key areas for provision of ecosystem services, heterogeneity, and landscape permeability (Brooks et al., 2006).

Regional policy and planning should aim at improving landscape connectivity. Amongst the most evident conservation planning strategies is the establishment of reserves. Particularly under climate change, the inclusion of new areas seems to be a relevant, albeit challenging, task (Hannah et al., 2007). Land tenure issues, poverty, development gaps between rural and urban areas, the demand for natural resources, and an economic model oriented toward extraction (e.g.
mining) make the establishment of new conservation areas difficult in the Andes. In the absence of such possibilities, the appropriate articulation of national reserves with other conservation sub-systems such as protective forests, indigenous territories, civil society reserves, and sub-national protected areas could be an appropriate mechanism of action. In addition, significant attention should be paid to the design (or adjustment) of the Andean protected area system. We recommend the following criteria be taken into account:

- Maintain the connectivity across the elevation, moisture and edaphic gradient (Killeen and Solórzano, 2008). These gradients are critical for maintaining beta diversity and response capacity (Thuiller et al., 2008).

- Incorporate ecotone diversity in the design of conservation areas. The landscapes within these areas are characterized by habitat mosaics that reflect differences in soil humidity, productivity, among others. These mosaics are occupied by species assembled in communities that reflect the presence of micro-environmental constraints in an area where climate stress is the overriding macro-environmental characteristic. These populations may have genetic traits distinct from core populations pre-adapting them to the physiological stress of climate change (Killen and Solórzano 2008). In the Tropical Andes the preservation of the ecotone between the montane forest and grasslands ecosystems is a fundamental adaptation measure to buffer the massive upward displacement of species ranges in response to increased warming (Feeley et al. 2011b).

- The identification of climatically stable areas as potential biological refugia through bioclimatic envelope model (see e.g. dark green areas in Figure 4 combined with dark areas in Figure 3) which could act as connectors and/or corridors between current and future areas of high biodiversity (Vos et al., 2008).
Improvement of landscape connectivity through the creation of biological corridors is probably the most frequent recommendation in the scientific literature (Heller and Zavaleta, 2009). We suggest an optimisation of spatial configuration of such corridors and an assessment of the risks of these turning into channels for disease transmission and/or movement of invasive species. In addition to these, a better land use planning through better and targeted government-level policies is warranted in order to reduce the risks of deforestation, loss of pollination services and genetic erosion in the agricultural frontier, while at the same time bolstering the dispersion and population breeding between (and within) remaining habitat patches (Opdam and Wascher, 2004).

5.4 Final remarks

Several sources of uncertainty may influence the results we provide here. These include the primary biodiversity data, the climate data and the climate envelope modeling (Braunisch et al., 2013; Pearson et al., 2006; Ramirez-Villegas and Challinor, 2012). Although these uncertainties are carried into the analysis, we argue that our results provide important insight on a globally important biodiversity hotspot. Importantly, our results agree and partly complement with previous regional and global studies (see Warren et al. 2013; Still et al., 1999; Thomas et al., 2004; Feeley and Silman, 2010). Improvement to our modeling approach for future studies may be warranted through achieving better spatial representativeness of both species and climate observations, the use of abundance data (in addition to presence-only data), better constraining species migration patterns, the inclusion of changes interannual variability and their effects on species distributions, the use of higher resolution climate models that resolve local climatic
change patterns in a more detailed manner, as well as a detailed assessment of relevant local processes driving extinctions.

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References


With, K.A., King, A.W., 1999. Extinction Thresholds for Species in Fractal Landscapes

### Table 1 List of bioclimatic variables used in the modeling

<table>
<thead>
<tr>
<th>ID</th>
<th>Variable name</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>Annual mean temperature</td>
<td>°C</td>
</tr>
<tr>
<td>P4</td>
<td>Temperature seasonality (standard deviation)</td>
<td>°C</td>
</tr>
<tr>
<td>P5</td>
<td>Maximum temperature of warmest month</td>
<td>°C</td>
</tr>
<tr>
<td>P6</td>
<td>Minimum temperature of coldest month</td>
<td>°C</td>
</tr>
<tr>
<td>P12</td>
<td>Annual precipitation</td>
<td>mm</td>
</tr>
<tr>
<td>P15</td>
<td>Precipitation seasonality (coefficient of variation)</td>
<td>%</td>
</tr>
<tr>
<td>P16</td>
<td>Precipitation of Wettest quarter</td>
<td>mm</td>
</tr>
<tr>
<td>P17</td>
<td>Precipitation of Driest quarter</td>
<td>mm</td>
</tr>
<tr>
<td>Io</td>
<td>Ombrothermic index</td>
<td>mm °C⁻¹</td>
</tr>
<tr>
<td>Iod2</td>
<td>Ombrothermic index of the driest 2-months of the driest quarter</td>
<td>mm °C⁻¹</td>
</tr>
</tbody>
</table>
### Table 2: List of all and available GCMs and principal characteristics (resolutions)

<table>
<thead>
<tr>
<th>Model</th>
<th>Country</th>
<th>Atmosphere**</th>
<th>Ocean**</th>
<th>A2*</th>
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<tbody>
<tr>
<td>BCCR-BCM2.0</td>
<td>Norway</td>
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</tr>
<tr>
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<td>1.85x1.85, L29</td>
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</tr>
<tr>
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<td>Canada</td>
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<td>1.4x0.94, L29</td>
<td></td>
</tr>
<tr>
<td>CNRM-CM3</td>
<td>France</td>
<td>T63 (2.8x2.8), L45</td>
<td>1.875x(0.5-2), L31</td>
<td></td>
</tr>
<tr>
<td>CSIRO-Mk3.0</td>
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<td>T63, L18</td>
<td>1.875x0.84, L31</td>
<td>A</td>
</tr>
<tr>
<td>CSIRO-Mk3.5</td>
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<td>T63, L18</td>
<td>1.875x0.84, L31</td>
<td>A</td>
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<td>1.0x(1/3-1), L50</td>
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<tr>
<td>GISS-AOM</td>
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<td>5x4, L13</td>
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<td>GISS-MODEL-ER</td>
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<td>5x4, L13</td>
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<td>IAP-FGOALS1.0-G</td>
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<td>2.8x2.8, L26</td>
<td>1x1, L16</td>
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<tr>
<td>INGV-ECHAM4</td>
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<td>2x(0.5-2), L31</td>
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<td>INM-CM3.0</td>
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<td>5x4, L21</td>
<td>2.5x2, L33</td>
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<tr>
<td>IPSL-CM4</td>
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<td>2x(1-2), L30</td>
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<tr>
<td>MIROC3.2-HIRES</td>
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<td>MIROC3.2-MEDRES</td>
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<td>1.4x(0.5-1.4), L43</td>
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<td>MIUB-ECHO-G</td>
<td>Germany/Korea</td>
<td>T30, L19</td>
<td>T42, L20</td>
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<tr>
<td>MPI-ECHAM5</td>
<td>Germany</td>
<td>T63, L32</td>
<td>1x1, L41</td>
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<tr>
<td>MRI-CGCM2.3.2A</td>
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<td>T42, L30</td>
<td>2.5x(0.5-2.0)</td>
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<tr>
<td>NCAR-CCSM3.0</td>
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<td>T85L26, 1.4x1.4</td>
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<td>NCAR-PCM1</td>
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<td>1x(0.27-1), L40</td>
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<td>UKMO-HADCM3</td>
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<td>1.25x1.25, L20</td>
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<tr>
<td>UKMO-HADGEM1</td>
<td>UK</td>
<td>1.875x1.25, L38</td>
<td>1.25x1.25, L20</td>
<td></td>
</tr>
</tbody>
</table>

*A: Monthly maximum and minimum temperature available **Horizontal (T) resolution indicates number of cells in which the globe was divided. Vertical (L) resolution indicates the number of layers in which the atmosphere was divided. When a model is developed with different latitudinal and longitudinal resolutions, the respective cell sizes (LonxLat) in degrees are provided instead of a unique value.*
Table 3 Change in distributional range for the Andean bird genera *Eriocnemis* and *Grallaria*.

<table>
<thead>
<tr>
<th>Species</th>
<th>IUCN 2010 category¹</th>
<th>Endemic to Andes²</th>
<th>Elevation range (m)³</th>
<th>Range change (%) ³</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2020</td>
</tr>
<tr>
<td><em>Eriocnemis alinae</em></td>
<td>LC</td>
<td>-</td>
<td>2300-2800</td>
<td>-16.8</td>
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<tr>
<td><em>Eriocnemis cupreoventris</em></td>
<td>NT</td>
<td>-</td>
<td>1950-3000</td>
<td>149.4</td>
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<tr>
<td><em>Eriocnemis derbyi</em></td>
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<tr>
<td><em>Eriocnemis luciani</em></td>
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<td><em>Eriocnemis mosquera</em></td>
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<tr>
<td><em>Eriocnemis nigrivestis</em></td>
<td>CR</td>
<td>EC</td>
<td>1700-3500</td>
<td>261.4</td>
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<tr>
<td><em>Eriocnemis vestita</em></td>
<td>LC</td>
<td>-</td>
<td>2800-3500</td>
<td>8.4</td>
</tr>
<tr>
<td><em>Grallaria allenii</em></td>
<td>VU</td>
<td>B1a+b(i,i,ii,iii)</td>
<td>1800-2500</td>
<td>46.7</td>
</tr>
<tr>
<td><em>Grallaria erythroleuca</em></td>
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<td>PE</td>
<td>2150-3000</td>
<td>38.8</td>
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<tr>
<td><em>Grallaria flavotincta</em></td>
<td>LC</td>
<td>-</td>
<td>1300-2350</td>
<td>50.9</td>
</tr>
<tr>
<td><em>Grallaria gigantea</em></td>
<td>VU</td>
<td>B1a+b(i,i,ii,iii)</td>
<td>1200-2600</td>
<td>&gt; 500</td>
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<tr>
<td><em>Grallaria guatimalensis</em></td>
<td>LC</td>
<td>-</td>
<td>200-3000</td>
<td>10.0</td>
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<tr>
<td><em>Grallaria haplonota</em></td>
<td>LC</td>
<td>-</td>
<td>700-2000</td>
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<tr>
<td><em>Grallaria hypoleuca</em></td>
<td>LC</td>
<td>-</td>
<td>1400-2300</td>
<td>170.3</td>
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<tr>
<td><em>Grallaria mchalis</em></td>
<td>LC</td>
<td>-</td>
<td>1900-3150</td>
<td>73.1</td>
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<tr>
<td><em>Grallaria quitensis</em></td>
<td>LC</td>
<td>-</td>
<td>2200-4500</td>
<td>-8.4</td>
</tr>
<tr>
<td><em>Grallaria ruficapilla</em></td>
<td>LC</td>
<td>-</td>
<td>1200-3600</td>
<td>28.6</td>
</tr>
<tr>
<td><em>Grallaria rufocinerea</em></td>
<td>VU</td>
<td>B1a+b(i,i,ii,iii)</td>
<td>2200-3150</td>
<td>11.1</td>
</tr>
<tr>
<td><em>Grallaria rufula</em></td>
<td>LC</td>
<td>-</td>
<td>2300-3650</td>
<td>30.8</td>
</tr>
<tr>
<td><em>Grallaria squamigera</em></td>
<td>LC</td>
<td>-</td>
<td>2000-3800</td>
<td>5.6</td>
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<tr>
<td><em>Grallaria watkinsi</em></td>
<td>LC</td>
<td>-</td>
<td>600-1700</td>
<td>43.6</td>
</tr>
</tbody>
</table>

¹ Status of the species according to the IUCN red list of threatened species: LC: least concern, NT: near-threatened, VU: vulnerable, EN: endangered, CR: critically endangered. Additional criteria as in http://www.iucnredlist.org/static/categories_criteria_3_1

² Country where endemic, if endemic to the Andes. EC: Ecuador, PE: Peru, BO: Bolivia

³ Range change under different periods and for two dispersal scenarios. Full: unlimited dispersal, Null: no dispersal

Species in **bold** depict range contractions (either by 2020 or 2050) regardless of migration assumptions.
Table 4 Change in distributional range for the Andean plant genera *Gynoxis* and *Polylepis*.

<table>
<thead>
<tr>
<th>Species</th>
<th>IUCN 2010 category</th>
<th>Endemic to Andes</th>
<th>Elevation range (m)</th>
<th>Range Change (%)</th>
<th>2020</th>
<th>Null</th>
<th>2050</th>
<th>Null</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Gynoxis acostae</em></td>
<td>LC</td>
<td>EC</td>
<td>2700-4300</td>
<td>&gt; 500</td>
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<td>&gt; 500</td>
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<tr>
<td><em>Gynoxis asterotricha</em></td>
<td>n/a</td>
<td>-</td>
<td>3100-4100</td>
<td>&gt; 500</td>
<td>-21.0</td>
<td>&gt; 500</td>
<td>-65.5</td>
<td></td>
</tr>
<tr>
<td><em>Gynoxis baccharoides</em></td>
<td>VU D(ii)</td>
<td>-</td>
<td>3300-4200</td>
<td>233.3</td>
<td>-41.4</td>
<td>109.6</td>
<td>-69.2</td>
<td></td>
</tr>
<tr>
<td><em>Gynoxis buxifolia</em></td>
<td>n/a</td>
<td>-</td>
<td>2500-4100</td>
<td>-12.8</td>
<td>-21.9</td>
<td>-52.1</td>
<td>-56.9</td>
<td></td>
</tr>
<tr>
<td><em>Gynoxis caracensis</em></td>
<td>LC</td>
<td>PE</td>
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<td>EC</td>
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<td>-21.7</td>
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<td>EC</td>
<td>2900-4286</td>
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1 Status of the species according to the IUCN red list of threatened species: LC: least concern, NT: near-threatened, VU: vulnerable, EN: endangered, CR: critically endangered. Additional criteria as in [http://www.iucnredlist.org/static/categories_criteria_3_1](http://www.iucnredlist.org/static/categories_criteria_3_1)

2 Country where endemic, if endemic to the Andes. EC: Ecuador, PE: Peru, BO: Bolivia

3 Range change under different periods and for two dispersal scenarios. Full: unlimited dispersal, Null: no dispersal

Species in **bold** depict range contractions (either by 2020 or 2050) regardless of migration assumptions.
**FIGURE CAPTIONS**

**Figure 1** Study area. A. Elevation (in meters) across the tropical Andes countries overlaid with locations of weather stations in WorldClim; B. Number of modelling occurrences in 0.5 degree cells and key sites with high projected impacts (mentioned throughout the text).

**Figure 2** Evaluation of Maxent models. Distribution of the Area under the ROC Curve (AUC) for A. All vascular plants; B. All birds. Training AUC values are plotted for training (grey bars) and test (black bars) sets. AUC values of individual species are averages of 10 cross-validated runs with 10-20% of the input points drawn randomly.

**Figure 3** Modeled current species richness for A. Vascular plants and B. birds in the Tropical Andes as derived by the sum of binned species distributions models. Values are counts of species occurring in a 25 km² pixel.

**Figure 4** Spatial patterns of changes in species richness for birds and vascular plants under both migration scenarios and time periods. Values are percentage change in species richness from the present-day value shown in Figure 3.

**Figure 5** Species turnover for birds and vascular plants, for both periods. Community turnover can only be calculated for scenarios that somehow assume migration as this calculation requires that species can move to more suitable environments whenever possible. Values are percentages of change in community turnover as calculated by Eq. 1 (see Sect. 3.4 for details).

**Figure 6** Climate change impacts on individual species. Change in range size for birds (white bars) and vascular plants (grey bars) for A. Unlimited dispersal and B. No dispersal, for the SRES-A2 emission scenario and both periods (2020s and 2050s) (outliers have been removed from the plot for easier visualization). Box plots were constructed with n=1,456 and n=9,062 for birds and vascular plants, respectively.