

Vulnerability of the Colombian vascular plant flora to elevational upslope shifts in a warming world

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Running Title: Colombia's flora in a warming world

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Abstract

Aim: Colombia hosts approximately 10% of all plant species on Earth and is blessed with three Andean mountain ranges. Under climate warming, species face elevational upslope shifts leading to (1) lowland biotic attrition, (2) range shift gaps, (3) range contractions and (4) mountaintop extinctions. Here, we assess the vulnerability of the Colombian flora to these range-shift consequences.

Location: Continental Colombia.

Methods: Using altitudinal ranges of ~17,000 plant species and a re-distribution model based on the adiabatic lapse rate, we calculate the number of species affected by each consequence in Colombia's major bioregions considering different scenarios for lowland biotic attrition and mountaintop extinction. Finally, we calculate the geographic distances species would need to migrate in order to track their thermal niches and discuss the importance of Colombia's National Parks as refugia under climate warming.

Results: We find 43% (~7632 species) of the Colombian vascular plant flora vulnerable to one of the four consequences under 2 °C warming, and 90% (~15975) under 5 °C warming. Lowland biotic attrition and range shift gaps challenge the highest number of species in all bioregions, while the Amazon and Pacific uplands are particularly vulnerable to range contractions and mountaintop extinctions. We find several species with restricted altitudinal ranges may face geographical displacement of more than 500 km making them especially vulnerable, already under 2 °C warming.

Main Conclusions: The biodiversity of the Amazon and Pacific lowlands may suffer from biotic attrition, and its fate may depend on whether thermal niches of lowland species are truncated and whether migration rates can keep pace with warming. Considering that more than 50% of the total area of Colombia's National Parks are located in the lowlands, conservation strategies are needed that reduce the challenges for species during upslope migration, such as establishing protected migration corridors and reducing habitat fragmentation along the altitudinal gradient.

1 Introduction

Plant species are distributed heterogeneously in space, time and altitude (Schimper et al., 1903). Their current geographic and altitudinal distributions are the result of their evolutionary history, biotic interactions with other species, and their adaptation to environmental conditions such as precipitation regime and temperature (Salisbury, 1926; Schulze, 1982; Stahl et al., 2014).

- 5 Temperature is an important component of the ecological niche and related to the thermal requirements of plants, referred to as the thermal niche (Santiago et al., 2016). The thermal niches of tropical plants are directly related to their altitudinal ranges because in tropical latitudes the ambient temperature is mainly determined by the wet adiabatic lapse rate (i.e. air temperature decrease with increasing altitude).
- 10 Currently, tropical plants are exposed to climate warming (Colwell et al., 2008; Morueta-Holme et al., 2015; Duque et al., 2015). In order to track their thermal niches (a process called thermophilization), tropical plants would need to migrate 144 km pole-wards (Colwell et al., 2008), or 200 meters upward (Bush, 2002) for each warming degree. Thus, in the presence of mountains, it is more likely that species shift their altitudinal ranges upslope as has been demonstrated recently (Feeley et al., 2011; Feeley, 2012; Morueta-Holme et al., 2015; Feeley et al., 2013; Duque et al., 2015). Recent studies estimate an upslope migration rate of approximately 2 meters per year for the last twelve years in the Northern Andes (Feeley et al., 2011; Duque et al., 2015). Under climate warming, thermophilization challenges the establishment of cold-loving plants at lower altitudes and favors migration towards higher altitudes (Gottfried et al., 2012; Duque et al., 2015). If warming rates exceed species migration rates, thermophilization can cause migration-lags (Corlett & Westcott, 2013). Thus, thermophilization can increase mortality and cause potential declines in biodiversity during upslope migration. While thermophilization may cause drastic and idiosyncratic changes in the composition of plant communities, climate refugia may be particular important for the maintenance of biodiversity under climate warming (Morelli et al., 2016). Refugia are areas relatively buffered from contemporary climate change over time (Morelli et al., 2016).

- Colwell et al. (2008) have identified four major processes that emerge during upslope range shifts (hereafter called range-shift consequences): (1) Lowland biotic attrition, (2) range shift gaps, (3) range contraction, and (4) mountaintop extinction. Lowland biotic attrition refers to the decline of species richness in tropical lowlands caused by upward migration. Because there are no 'lower latitudes or altitudes' from where potential colonizers could immigrate (e.g. into the Amazon basin, Feeley & Silman, 2010) and because it is unlikely that all tropical lowland species have retained their adaptation to warmer tropical climates they may have experienced millions of years ago (Jaramillo et al., 2006, 2010), tropical lowlands are expected to suffer species losses. However, if tropical lowland species have retained their adaptations to tolerate warmer than today climates, then their thermal niches are truncated and species loss may be less severe (Feeley & Silman, 2010). Range shift gaps emerge when climate warming exceeds the migration rates of species (e.g. Corlett & Westcott, 2013). This challenges dispersal and establishment of species at higher altitudes. Range shift gaps especially occur for species with narrow altitudinal ranges that do not overlap between *pre* and *post* warming (Colwell et al., 2008). When species shift their elevational ranges upslope facing a fixed boundary (e.g. mountaintops, glaciers, or rocky terrain lacking soils) this leads to a contraction (i.e. reduction) of the species altitudinal range. If there is no adequate habitat or mountain area available at higher altitudes, species may suffer mountaintop extinction (Gottfried et al., 2012). Even more, range contraction increases the density of species and populations at the mountaintop that provide usually less area than the foothills or mountain ranges at intermediate altitudes (Körner, 2000). This may further challenge the maintenance of biodiversity, because more species would need to survive in less area with less resources. Thus species loss from area loss is inevitable (e.g. considering species-area relationships, Pereira et al., 2010). Finally, the four aforementioned consequences are expected to have more severe consequences in the tropics than at mid- or high latitudes, because tropical species have narrower thermal niches than extra-tropical species that are adapted to seasonal changes in temperature (Janzen, 1967; Ghalambor et al., 2006).

- 45 Colombia harbours in less than 0.7% of the global ice-free land area, approximately 10% of all plant species on Earth (i.e. 35000 - 40000 out of 350000 - 400000 species, Bernal González et al., 2016) with approx. 6383 endemic plant species (Bernal González et al., 2016). Thus, the four aforementioned consequences might not only have implication for the maintenance of biodiversity at the regional (e.g. Pauli et al., 2012) but also at the global scale. One reason of Colombia's extraordinary

biodiversity as compared to other bigger neotropical countries (e.g. Brazil, Mexico) may be due to the environmental heterogeneity caused by the presence of the three Andean mountain ranges. The Andes reach different heights in different regions of Colombia, but also cause marked differences in local and regional climates (e.g. precipitation rates and seasonality, Poveda et al., 2011) as well as evolutionary histories (Hoorn et al., 2010) and hence in biodiversity. Thus, the consequences of lowland biotic attrition, range shift gaps, range contraction, and mountaintop extinction can be expected to differ between Colombia's bioregions.

Here, we aim to evaluate the vulnerability of the Colombian vascular flora to elevational upslope shifts in (1) terms of number of species that could be affected by each of the four range-shift consequences as well (2) the number of altitudinal meters and the geographical distance under continuous warming up to 5°C warming. We do this at the national scale, but also for the major bioregions of Colombia that are divided by the three Andean mountain ranges effectively limiting species dispersal. With this, we hypothesize that bioregions are differently impacted by the four range-shift consequences due to their geographical characteristics. Specifically, we hypothesize that bioregions with a large proportion of lowland area such as Amazonia shall be impacted more severely by biotic attrition and range shift gaps than bioregions with less lowlands such as the inter-Andean valleys. This is, because lowland species in general exhibit narrower thermal niches than their Andean counterparts and thus a restricted altitudinal range (Janzen, 1967). We also predict that bioregions with higher mountains shall be less affected by range contractions and mountaintop extinction than bioregions delineated by mountains of less altitude, because species are not constrained in shifting their ranges upslope. In our analyses, we also consider the possibility that thermal niches of lowland species are truncated and that upslope range shifts are constrained either by the maximum altitude of the region or the maximum altitude available for plants to grown under current climate. Finally, we provide a map of future migration hotspots and discuss the implications of species geographical displacement and the distribution of National Natural Parks for conserving Colombia's biodiverse flora under climate warming.

2 Methods

2.1 Data

For our analysis, we use the Colombian plant catalog ("Catálogo de plantas y líquenes de Colombia", Bernal González et al., 2016), which provides the following information for more than 26500 vascular, non-vascular plants and lichens native to Colombia: species name including family membership, occurrence in departments and bioregions as well as the minimum and maximum altitude each species has been observed. In order to avoid biases in our analyses due to the ample occurrence of some taxons along the altitudinal gradient, we removed all bryophytes and lichens from the database using the Integrated Taxonomic Information System (ITIS, 2017). Then, we removed all species without altitudinal range and generated species presence/absence matrices for departments and bioregions. Finally, we removed all species which do not occur in any department or bioregion, which resulted in a data matrix consisting of 17751 species.

In order to consider dispersal barriers as imposed by the Andes, we modified the bioregions provided in the Colombian plant catalog. To do so, we subdivided the Andes bioregion and aggregated the respective parts of it to the other bioregions. This spatial redistribution of the Andes bioregions was done based upon the geographic distribution of the major watersheds of Colombia (Salazar Holguín & IDEAM, 2016). Hence, we generated six new bioregions or basins (i.e. Amazonia, Orinoquia, Pacific, Caribbean, Cauca Valley, Magdalena Valley, see also Appendix Fig. A1) and adjusted the species assignment to these new bioregions based on the presence absence matrices of bioregions and departments. All these adjustments were done using QGIS, Version 2.18.7 (QGIS Development Team, 2009) and the R package 'raster' (Hijmans, 2016).

2.2 Range shift model

To simulate the altitudinal re-distribution of the Colombian flora under climate warming, we developed a general and simple range shift model based upon the adiabatic lapse rate and the current altitudinal ranges provided in the Colombian plant catalog

(Eq.1,2). This model predicts altitudinal range shifts from warming assuming a temperature decrease of 0.55 °C for 100 meters altitude increase as reported for the Northern Andes (Bush, 2002) and that species will track their thermal niche. In other words, we quantify the vulnerability of Colombian vascular plants in terms of range shift consequences emerging from this assumed dispersal effort of 181.81 meters per degree warming.

$$5 \quad Elev.Min(E, c) = Elev.Min(E, c_0) + (181.81 * c) \quad (1)$$

$$Elev.Max(E, c) = Elev.Max(E, c_0) + (181.81 * c) \quad (2)$$

Where:

Elev.Min: Minimum elevation of specie E.

Elev.Max: Maximum elevation of specie E.

10 c_0 : Current temperature in °C.

c : Warming in °C

This simple model further assumes (1) all terrestrial area of Colombia will experience a temperature increase in equal rate and form, (2) all plant species do track their thermal niches under warming (i.e. migrate 181.81 meters/°C) and (3) the altitudinal ranges provided in the Colombian plant catalog are reliable. If we assume that thermal niches of lowland species are truncated, a correction of the lower elevational range limit is necessary. To do so, we implemented a modified correction for truncated niches as proposed by Feeley & Silman (2010). This correction uses temperature, but can equally applied in a similar manner for altitudinal range limits since relative values of temperature and altitude are transferrable using the adiabatic lapse rate. Correcting for truncated niches resamples for all lowland species the minimum altitudinal range based upon the altitudinal ranges of upland species. We modified this resampling procedure only resampling the lower range limits of species which have an altitudinal range smaller than the mean altitudinal range of their sampled upland counterparts. In other words we consider only lowland species to have truncated niches, which have in average smaller ranges than their upland counterparts, thus being more conservative in correcting for truncated niches than Feeley & Silman (2010). We used an altitude of 500 m.a.s.l to separate lowlands from uplands.

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2.3 Simulation scenarios

In order to simulate species altitudinal range shifts accounting for the possibility of truncated niches of lowland species and different altitudinal limits constraining upward range shifts, we develop four different simulation scenarios: (S1) Currently observed species altitudinal ranges are a complete representation of species realized thermal niches, (S2) the current altitudinal ranges of lowland species (i.e. their thermal niches) are truncated, (S3) mountaintop extinction occurs when future species altitudinal ranges lie completely above the maximum altitude of the Andes in each bioregion and (S4) mountaintop extinction occurs when future species altitudinal ranges lie above the maximum altitude of species currently present in each bioregion. This latter scenario is based on the fact that the rate of soil development does lack behind the rate of climate change. Each scenario is simulated under continuous warming from 0 °C to 5 °C. We used 2°C and 5°C warming as references since temperature rise until 2100 probably will lie within these limits (IPCC, 2015).

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2.4 Range-shift consequences

We calculated the number of species affected by each range shift consequence (Eq.3) summing up the species affected in each bioregion (R). Whether a species is affected (i.e 1) or not (i.e. 0) depends on its condition (γ), which varies depending on the process as provided in Equation 4-7.

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$$NSA(R, c) = \sum_{E=1}^{\tau} \gamma(E, R, c) \quad (3)$$

Where:

NSA : Number of species affected.

γ : Species condition.

R : One of the 6 bioregions.

5 c : Warming in °C.

τ : Number of species currently registered in bioregion R .

The number of species affected by range shift gaps is calculated as the sum of all species, for which the minimum elevation in a warmer climate $Elev.Min(E, c)$ is greater than the current maximum elevation $Elev.Max(E, c_0)$ (Eq.4). To calculate the magnitude of range shift gaps per degree warming, we also calculated the number of meters each species is affected using $Elev.Min(E, c) - Elev.Max(E, c_0)$.

$$\gamma(E) = \begin{cases} 1 : Elev.Min(E, c) > Elev.Max(E, c_0) \\ 0 : Elev.Min(E, c) \leq Elev.Max(E, c_0) \end{cases} \quad (4)$$

The number of species affected by range contraction is calculated as the sum of all species (Eq. 5), for which the maximum elevation in a warmer climate $Elev.Max(E, c)$ exceeds the upper elevation limit that is the maximum elevation of the Andean chain $Lim.Max$ (under S3) or the maximum elevation of the highest occurring species in the respective bioregion $Lim.Max$ (under S4) while its minimum elevation $Elev.Min(E, c)$ remains below these limits. To calculate the magnitude of range contraction per degree warming, we calculated the number of meters each species is affected by range contraction using $Elev.Max(E, c) - Lim.Max$.

$$\gamma(E, R) = \begin{cases} 1 : (Elev.Max(E, c) > Lim.Max(R) > 0) \wedge (Elev.Min(E, c) < Lim.Max(R)) \\ 0 : Elev.Max(E, c) \leq Lim.Max(R) \end{cases} \quad (5)$$

20 The number of species affected by mountaintop extinction is calculated as the sum of all species, for which the minimum elevation in a warmer climate $Elev.Min(E, c)$ exceeds the maximum limit established under S3 or S4 (Eq. 6). To calculate the magnitude of potential mountaintop extinction under different degrees of warming, we also calculated the number of meter each species is affected using $Elev.Min(E, c) - Lim.Max(R)$.

$$\gamma(E, R) = \begin{cases} 1 : (Elev.Min(E, c) > Lim.Max(R)) \\ 0 : Elev.Min(E, c) \leq Lim.Max(R) \end{cases} \quad (6)$$

25 We calculated the number of species affected by lowland biotic attrition as the sum of all species, for which the current minimum elevation $Elev.min(E, c_0)$ lies below 500 m.a.s.l. and for which the minimum elevation in a warming climate $Elev.min(E, c)$ exceeds the 500 m.a.s.l. lowland limit definition Lim , (Eq.7). To calculate the magnitude of biotic attrition under different degrees of warming we also calculated the number of meter each species is affected using $Elev.min(E, c) - Lim$. Strictly speaking, not species are affected by lowland biotic attrition but the lowlands of the respective bioregions, which suffer species loss because of emigration. For convenience of presenting the results we use these two aspects interchangeable.

$$\gamma(E, R) = \begin{cases} 1 : (Elev.Min(E, c_0) < Lim(R) > 0) \wedge (Elev.Min(E, c) > Lim(R)) \\ 0 : (Elev.Min(E, c_0) < Lim(R) > 0) \wedge (Elev.Min(E, c) < Lim(R)) \end{cases} \quad (7)$$

In order to identify the regions most strongly affected by each of the four consequences, we not only quantify the number of species affected, but also the magnitude (i.e. as numbers of meters) species are challenged under continuous warming. To do so, we provide linear regressions for the average number of meters over degree warming using the slope and intercept of the

regression line as indicator for magnitude (Fig. 3). The slope would indicate the strength (or magnitude) by which warming results in an average species upslope shift, while the intercept indicates the warming, from which on a process 'kicks in'. For biotic attrition and range shift gaps we used the scenarios S1 and S2, for range contraction and mountaintop extinction the scenarios S3 and S4.

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2.5 Geographical redistribution

To provide a geographical perspective about the magnitude and direction of potential species migrations due to climate warming, we develop a species migration map based upon the range shift model. First, we identify current coarse scale species distributions based upon altitudinal ranges, bioregions and departments. For this we used the information of the Colombian plant catalog, a map of Colombia's departments and bioregions (Fig. A1), as well as a digital elevation model (Jarvis et al., 2008) with a spatial resolution of 30 arc seconds. From this, we derived the geographical centroids (i.e. midpoints of separated species distributions) of potential current species occurrences. Second, we derived these local geographical centroids under 2°C warming based upon the predicted future altitudinal ranges and calculated from this potential geographic displacement distances for each species. Even though the resulting species displacements are not based on actual species range maps, they nevertheless provide a robust estimate of expected displacement distances and directions. All calculations and spatial analysis were done using the R software for statistical computing (R Core Team, 2016) and the 'raster' package (Hijmans, 2016).

3 Results

At the national scale 7595 (42.8%) plant species were at least affected by one of the four consequences under 2°C warming, and 15897 (89.5%) under 5°C warming. Furthermore, 57 (0.3%) were affected by two processes at the same time (i.e. range shift gaps and range contraction or range contraction and mountaintop extinction) under 2°C warming, and 913 (5.1%) under 5°C warming. Considering the "worst case" scenarios (S1, S4), 5240 (29.5%) species were challenged by range shift gaps (S1), 2457 (13.9%) by lowland biotic attrition (S1), 983 (5.5%) by range contraction (S4) and 15 (0.1%) by mountaintop extinction under moderate 2°C warming, while 10087 (56.8%) by range shift gaps, 9734 (54.8%) by biotic attrition, 2623 (14.8%) by range contraction, and 308 (1.7%) by mountaintop extinction under 5°C warming.

At the scale of bioregions, we found Amazonia with 5017 species the most affected bioregion, followed by the Pacific region (3896 species), the Magdalena valley (3554 species), Orinoquia (3151 species), and the Caribbean (3022 species) under 2°C warming. The Cauca valley is the least affected regions, where 2807 species are affected. Under 5°C warming 10474 species are affected in Amazonia, 10305 in the Pacific region, 9690 in the Magdalena valley, 8294 in the Cauca valley, 8091 in Orinoquia and 7968 in the Caribbean. In the following we provide more detailed results for each range-shift consequence:

3.1 Biotic attrition

Under 2°C warming we found 2457 species emigrating from the lowlands to the uplands within the different bioregions. Under the S1 scenario, this corresponds to a rate of lowland biotic attrition between 18.5% and 28% depending on the bioregion (Fig. 1a). If we consider that the realized thermal niches of lowland species are truncated (i.e. S2 scenario) this translates into biotic attrition between 11.2 (~865 species) and 19.7% (~1125 species) (Fig. 1b). Based on our predictions under the S1 scenario, a warming greater than ~2.7 °C will lead to 100% lowland biotic attrition in all Colombian lowlands, suggesting a severe to complete lowland biodiversity loss. When correcting for truncated niches of lowland species (S2), 11.1% (~1158) of all lowland species will be affected by biotic attrition under 2°C, and 61.2% (~4727) under 5°C warming. Among the different bioregions, the lowlands of the Amazon and Pacific bioregions were most affected by biotic attrition, and the Caribbean the least affected (Fig. 1a, Fig. 1b). It is worth noting here, that the order with which bioregions are impacted doesn't remain the same between S1 and S2, indicating that the correction for truncated niches differently affects the bioregions (Fig. 1a, Fig. 1b). While Amazonian species richness suffers most from biotic attrition under the S1 scenario, it is among the least affected under

the S2 scenario considering a warming of 2°C. For Amazonia, the magnitude in terms of altitudinal range shifts in meters is slightly smaller as compared to other bioregions, especially in the S2 scenario. This means that Amazonian species challenged by biotic attrition need to shift the ranges in average slightly less upslope than species of other regions challenged by biotic attrition (Fig. 3a,b).

5 3.2 Range shift gaps

With the majority of species challenged (~29.5% in S1), range shift gaps emerges as the range-shift consequence with the highest impact in all regions. This has to do with the restricted altitudinal range of the majority of species considered in this study (Appendix Fig. A2). For example 16.7% of all species have an altitudinal range less than 200 meters. Under 2°C warming, this species in average face range shift gaps of approximately 200 altitudinal meters (Fig. 2c) in the different bioregions, which can also be derived from Eq.1,2. If we correct for truncated niches (S2), the impact of range shift gaps is reduced, since less species exhibit restricted altitudinal ranges. Under the S1 scenario, Amazonian species are the most affected as compared to the other bioregions (Fig. 1c), however when considering truncated niches no big differences emerge among bioregions (Fig. 1d), except a steep increase of species affected in Amazonia from 4.5°C warming on. Interestingly, considering the magnitude of range shift gaps in mean altitudinal meters over species, Amazonia switches from most affected (S1) to the least affected (S2), as compared to the other bioregions among which no big difference emerge (Fig. 3c,d). This probably has to do with the strong increase in the number of species affected from 4.5°C warming on, however of those species a considerable amount exhibit only small range shift gaps (Fig. A2).

3.3 Range contraction

Overall, a smaller proportion of species is affected by range contraction and mountaintop extinction compared to the aforementioned processes considering the different bioregions as well as the different scenarios. Under 2°C warming 897 (S3) and 983 (S4) species are challenged, while under 5°C warming 2065 (S3) and 2.623 species are challenged (S4) (Fig. 1e,f). Most of these species can be found in Amazonia and the Pacific bioregion, indicating a smaller altitudinal extent of these regions compared to others. Interestingly, we do not find major differences between the S3 and S4 scenario, except for the Caribbean. Even though bioregions may differ in the maximum altitude of mountains and thus the availability of refugia under climate warming, one may consider the Andes as sufficiently high to enable upslope migration, and this considering the absolute altitude of the Andes (S3) as well as the highest occurrences plants grow currently (S4). Considering the magnitude of range contraction, shows that species in the Amazon and Pacific suffer more range contraction already from little warming on, as compared to the other bioregion under the S3 and S4 scenario. Under the S3 scenario, Caribbean species ‘only’ suffer range contraction from ~2°C warming on, whereas this particularity disappears under the S4 scenario.

30 3.4 Mountaintop extinction

The uplands of the Amazon and Pacific bioregions are sensitive to mountaintop extinction with 238 species in the Amazon and 69 in the Pacific (S3, 5°C warming), whereas the other bioregions show only few species vulnerable to mountaintop extinction. This results seems to be robust without major changes considering the S3 or S4 scenario (Fig. 1g,h). In average the magnitude of mountaintop extinction (i.e. species shifting their ranges “above the mountaintop”) is higher in these two bioregions than in the others (Fig. 2g,h). Interestingly, bioregions are affected very differently when considering the magnitude of mountaintop extinction (Fig. 2g,h), consistent with the results of range contractions. For example, the Caribbean seems the least vulnerable bioregion to mountaintop extinction under the S3 scenario. Considering that the maximum altitude of the Andes in the Amazon (3978 m.a.s.l) and Pacific (4597 m.a.s.l) is lower compared to those of the other bioregions (5140 - 5453 meters) confirms our hypothesis that these regions are more vulnerable to mountaintop extinctions.

40 Figure 2 shows that 739 species could be challenged simultaneously by range shift gaps and range contraction (S3, 5°C) and 302 species could be challenged by range shift gaps and mountaintop extinction. In both aspects, again, more species are affected in the Amazon and Pacific bioregion, showing a consistent trend with continuous warming (Fig. 3).

3.5 Hotspots of species geographical redistribution

Figure 4a shows where plants would migrate to (or ‘arrive’ given the assumptions of our model) under 2°C warming and therefore presents a potential for the geographic re-distribution of plant species across Colombia. Major migration hotspots emerge at the foothills of the Andes, especially at the Eastern flank of the Eastern chain and the western flank of the Western chain. Furthermore, this analysis indicates the National Parks of “El Cocuy”, “Tamá”, “Pisba”, “Sierra de la Macarena”, “Serrania de los Churumbelos”, “Alto fragua Indasi”, “Las Hermosas”, “Los Farallones de Cali” and “Los Katios” as important refugia, also for arriving immigrants. We found that plants would need to migrate in average 212 (+/- 181) km under 2°C warming to reach places that provide their realized thermal niche in the future. Interestingly, there are only few places in the vast extensions of Amazonia (e.g. la Serrania de Chribiquete, Fig. 3a) where plants would find appropriate refugia under climate warming. This reinforces the importance of understanding truncated thermal niches, since this map has been derived under the S1 scenario.

4 Discussion

Based on our model simulations we found that (1) a significant proportion of the Colombian vascular flora could be affected at least by one of the four range-shift consequences, (2) the Amazon and Pacific uplands are prone to mountaintop extinction, (3) most species are challenged by range shift gaps, and (4) Amazonia might suffer the highest species loss among bioregions, which however depends on whether niches of lowland species are truncated or not. And finally (5) 198 lowland species might be challenged by geographical displacement of more than 500 km, which is unlikely to be compensated by contemporary natural migration rates.

Plants species have shifted their altitudinal ranges since millions of years (Bush, 2002; Marchant et al., 2001), however contemporary rates of warming are unprecedented, challenging species migration and causing migration lags (Corlett & Westcott, 2013). Over the last decades, altitudinal range shifts due to thermophilization have been reported of $\sim 2.5 \text{ m} * \text{y}^{-1}$ for juvenile tree species of tropical montane forest in the Peruvian Andes (Feeley et al., 2011), of $\sim 1.92 \text{ m} * \text{y}^{-1}$ for vegetation zones at the Chimborazo (Morueta-Holme et al., 2015) and $\sim 2.0 \text{ m} * \text{y}^{-1}$ for adult tree species in Colombian montane forest (Duque et al., 2015). If we assume a warming of 2°C until 2100, species are challenged with approx. 4 m altitudinal range shift per year, which is higher than contemporary observed migration rates, thus challenging species altitudinal upslope shifts (Chen et al., 2011; Brodie et al., 2016). Thus, species may not only be challenged by the four range shift challenges as assessed in this study, but may also face other challenges imposed by migration rates surpassing their migration capacities (Corlett & Westcott, 2013). Then, phenotypic plasticity (Jump & Peñuelas, 2005) and evolutive changes (Burger & Lynch, 1995) become important to ensure adaptation and thermophilization; otherwise local extinctions may become inevitable.

Except for the Amazon and Pacific bioregions, we found the Andes sufficiently high to provide refugia for most Colombian vascular plant species under the S3 and S4 scenario. Nevertheless, we found that 1.7% (~ 301 species) - 14.8% (~ 2627 species) (S4, 5°C warming) of the Colombian vascular flora could be affected by range contractions (Fig. 1e,f). These range contractions are further exacerbated because of the geometry of mountaintops, where available area decreases proportionally more than at lower altitudes (e.g. Körner, 2000). Less area implies less resources, and for example soil formation rates may lack behind rates of warming and species migrations. It is also likely that water availability decreases with climate change in mountain areas (e.g. melting of glaciers) affecting plant establishment and constraining upslope shifts (Pauli et al., 2012). These factors cannot be considered by our simple model, and may lead to increased population densities and competition, affecting population sizes and complicating the survival of some species (Olsen & Klanderud, 2014). On the other hand, mountains provide a diversity of microclimates within little area resulting from subtle changes in aspect, exposition, wind exposure and soil characteristics (e.g. Dobrowski, 2011). For example there is no data available of how altitudinal ranges may change with latitude or between the eastern and western slopes of the Andes. This small-scale variability is neither considered here nor reflected in the altitudinal ranges of the Colombian plant catalog. Hence species may encounter so called cryptic or micro-refugia (Dobrowski, 2011) that are difficult to consider in broad scale assessments, especially in tropical mountains lacking data about species paleo-altitudinal

ranges (Lenoir & Svenning, 2015). In other words, there is a multitude of additional processes, especially biotic interactions (Roux et al., 2012; Alexander et al., 2015), that may increase or decrease the probability of mountaintop extinctions.

We found between 10% (~ 1751 species, S1, 2°C warming) to 57% (~10118 species, S2, 5°C warming) of the Colombian vascular flora could be challenged by range shift gaps, which affects predominantly species with restricted altitudinal ranges (Fig.A2). Whether or not a species is sensitive to range shift gaps depends on its migration capacity, which in turn depends on species functional traits, such as dispersal type (e.g. wind or animal dispersed), seed size, seed spread rate, reproductive rate, or requirements for establishment (Angert et al., 2011). Despite species migration could alleviate the risk of range shift gaps, migration is constrained by landscape fragmentation. Hence the occurrence of range shift gaps may interact with forest fragmentation at lower altitudes (e.g. Kattan & Alvarez-Lopez, 1996). Considering that the Andes are highly transformed with the highest population density in Colombia (Etter & van Wyngaarden, 2000), range shift gaps could even reach the potential as predicted by our model and impede species to reach the future thermal niches.

Our results suggest that Amazonian biodiversity may suffer most from biotic attrition, especially from ~ 2.7°C warming on (Fig. 1a). However when correcting for niche truncation (Fig. 1b) there is no big difference compared to the other bioregions. Nevertheless we predict a biodiversity loss from the Amazonian lowlands of 28% (~1733) under 2°C warming and 100%(6209) under 5°C warming without correcting for truncated niches, and 11% (~682) under 2°C warming and 66% (4093) under 5°C warming with truncated niche correction. Feeley & Silman (2010) predicted under 5°C warming a almost 100% biodiversity loss for Amazonian lowland forests, and more than 50-70% when considering truncated niches. Even though using different species data (i.e. realized thermal niches vs. altitudinal ranges), geographical extents (Amazon basin vs. Colombian Amazon) and methodologies for correcting truncated niches (i.e. see Methods Section), both analysis obtain similar estimates. Hence, studying truncated thermal niches of lowland species is important to better understand the fate of Amazonian biodiversity under climate warming (Corlett, 2011) and correcting for truncated niches becomes a delicate methodological issue. We followed the method proposed by Feeley & Silman (2010), however with the small difference that we did not assume a niche truncation for all lowland species, but only for those which have in average smaller altitudinal ranges compared to their upland counterparts, avoiding the problem of generating smaller than observed contemporary altitudinal ranges negatively impacting lowland biodiversity. While Feeley & Silman (2010) propose that lowland species may have retained their ancestors' ability to tolerate higher than contemporary temperatures, it is unclear whether this is actually the case and whether the current warming rate will allow sufficient time for plants to adapt or acclimate (Thomas et al., 2004; Walther et al., 2002). In a physiological study based on experimental warming of branches and leaves of tropical trees, Doughty (2011) showed that prolonged exposure to 2°C warming can already cause irreversible damage to the photosynthetic machinery. Unfortunately experimental and physiological studies about species thermal tolerances are rare and the impacts of warming on tropical lowland forests are little understood (Corlett, 2011).

Our analyses suggest the Andes as efficient refugia under warming because they allow species to maintain their thermal niches. This is especially true for species occurring along the altitudinal gradient or nearby mountain ranges (e.g. the inter-andean valleys, the eastern piedemonte). However, species situated far from the mountain ranges (e.g. the Caribbean coast, the Amazon and Orinoco lowlands) may face migration challenges to track their thermal requirements because of the geographical distance. Geographical displacement may exceed a mean distance of 500 kilometers for up to 1.807 species, and even 1000 km for 4 species. Species facing long geographical displacement to track their often narrow thermal niches (Fig. 3b) are particularly vulnerable to local extinction. We found *Diplostephium ritterbushii* Cuatrec., *Jalcophila ecuadorensis* M.O.Dillon Sagást., *Loricaria colombiana* Cuatrec., *Myrosmodes ustulatum* (Schltr.) Garay., *Aciachne flagellifera* Laegaard., *Lachemilla rupestris* (Kunth) Rothm. to exhibit this vulnerability, none of those evaluated by the IUCN red list.

Chiribiquete National Park, the largest of Colombia's National Parks, emerges as important refugia for several Amazonian lowland species (Fig. 3a). Analyzing the altitudinal distribution of Colombia's continental National Parks, we found 14 National Parks are completely located in the lowlands below 500 m.a.s.l in the bioregions of Amazonia, the Caribbean, Orinoquia and the Pacific bioregion (Table. A1). These 14 parks represent 53.5% of the total area of Colombia's National Parks and according to our analysis are vulnerable to significant biodiversity loss. Thirteen national parks have part of their area in the lowlands

but extend to higher altitudes and represent 29% of the area covered by Colombia's National Parks. These parks are located in Amazonia, the Andes, Caribbean, Orinoquia and Pacific bioregions. Finally, 22 National Parks are located completely over 500 m.a.s.l, in all bioregions and represent 18% of the total National Parks area (See Table A1). Considering that the majority of National Parks area is located below 500 m.a.s.l challenges the role of some Parks as refugia under climate warming because they may suffer significant biotic attrition and their range shift gaps while species are shifting their ranges upslope. In this case management plans establishing migration corridors and reducing forest fragmentation, especially in Amazonia, Orinoquia and the Pacific lowlands, and between National Parks are becoming crucial. Parks extending over a large altitudinal gradient (e.g. Sierra Nevada de Santa Marta, Sierra Nevada de Cocuy, Farallones de Cali, and Sumapaz) will become highly important as refugia and the conservation of Colombia's future biodiversity.

We provided a comprehensive assessment of the vulnerability of the Colombian flora with more than 17.000 species to climate warming considering the available altitudinal ranges, dispersal limitations as imposed by the Andes and different scenarios for the lowlands and the mountaintops. We were able to identify the Andes as efficient refugia for species under climate warming and the Amazon and Pacific bioregion as particular vulnerable to biodiversity loss from mountaintop extinction and biotic attrition. The latter, however depends on the degree of thermal niche truncation of lowland species, which requires further ecophysiological and paleoecological research. We identified lowland species that would face tremendous geographical displacement as well as National Parks that lack appropriate refugia making them particularly vulnerable to climate warming. The implications of our findings suggest to complement the existing system of National Parks with conservation corridors that reduce dispersal barriers (such as agro-industrial monocultures) and forest fragmentation permitting species migration in the lowlands and altitudinal upslope shifts in the Andes.

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Data Accessibility

Data and analysis scripts are made accessible (upon acceptance) in the github repository, under the following link:

Authorship

BR conceived the idea. DPM did all data assembling and statistical analysis and wrote the first draft of the manuscript. BR and
5 DPM contributed equally improving the manuscript to its final version. DPM made accessible all data and scripts used in this study

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Figures

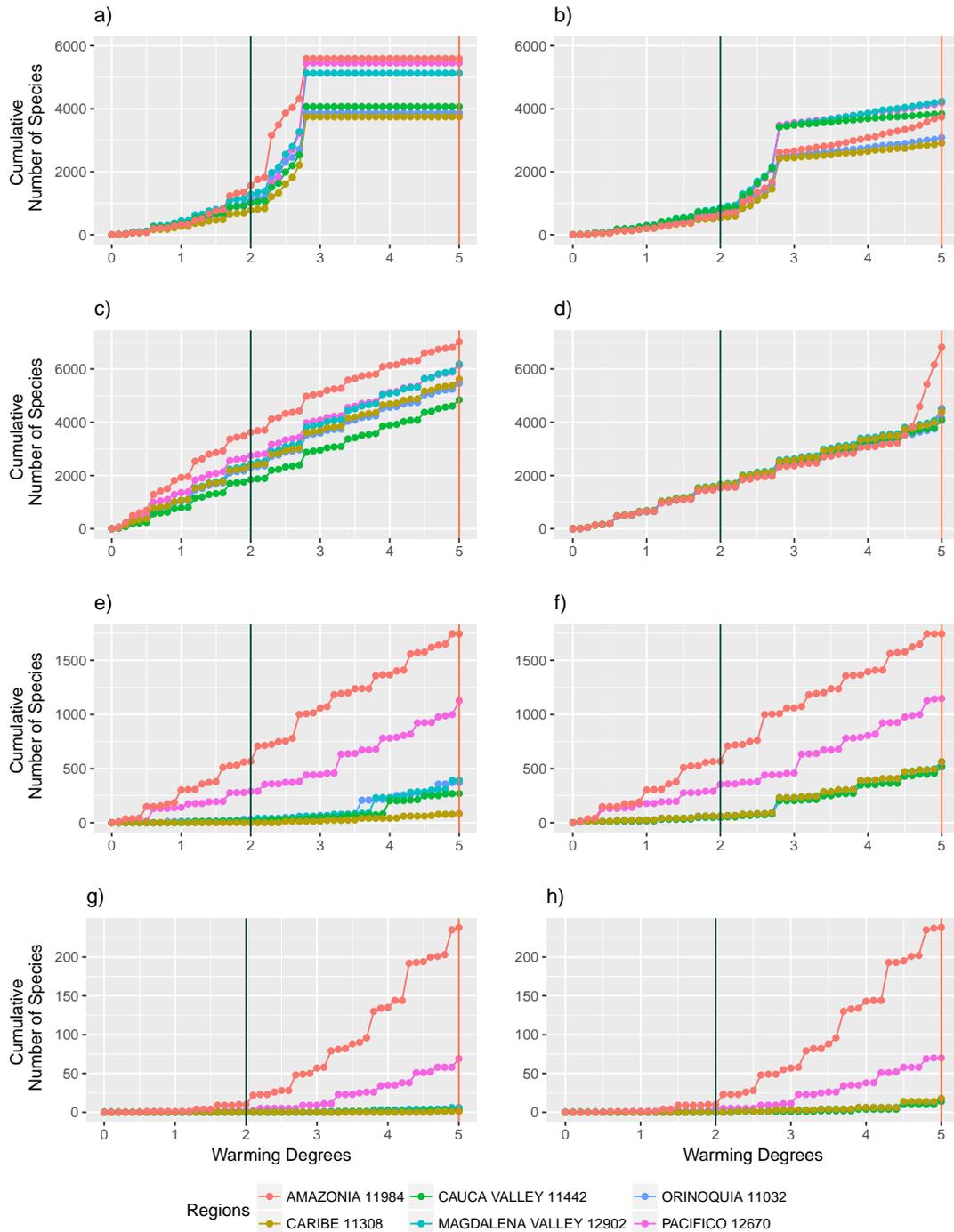


Figure 1. Cumulative number of species affected by: a) Lowland biotic attrition under the S1 scenario. b) Lowland biotic attrition under the S2 scenario. c) Range Shift Gaps under S1. d) Range Shift Gaps under S2. e) Range Contraction under S3. f) Range Contraction under S4. g) Mountaintop extinction under S3. h) Mountaintop extinction under S4. The total number of species for each region as recorded in the Colombian Plant Catalog is provided in the legend.

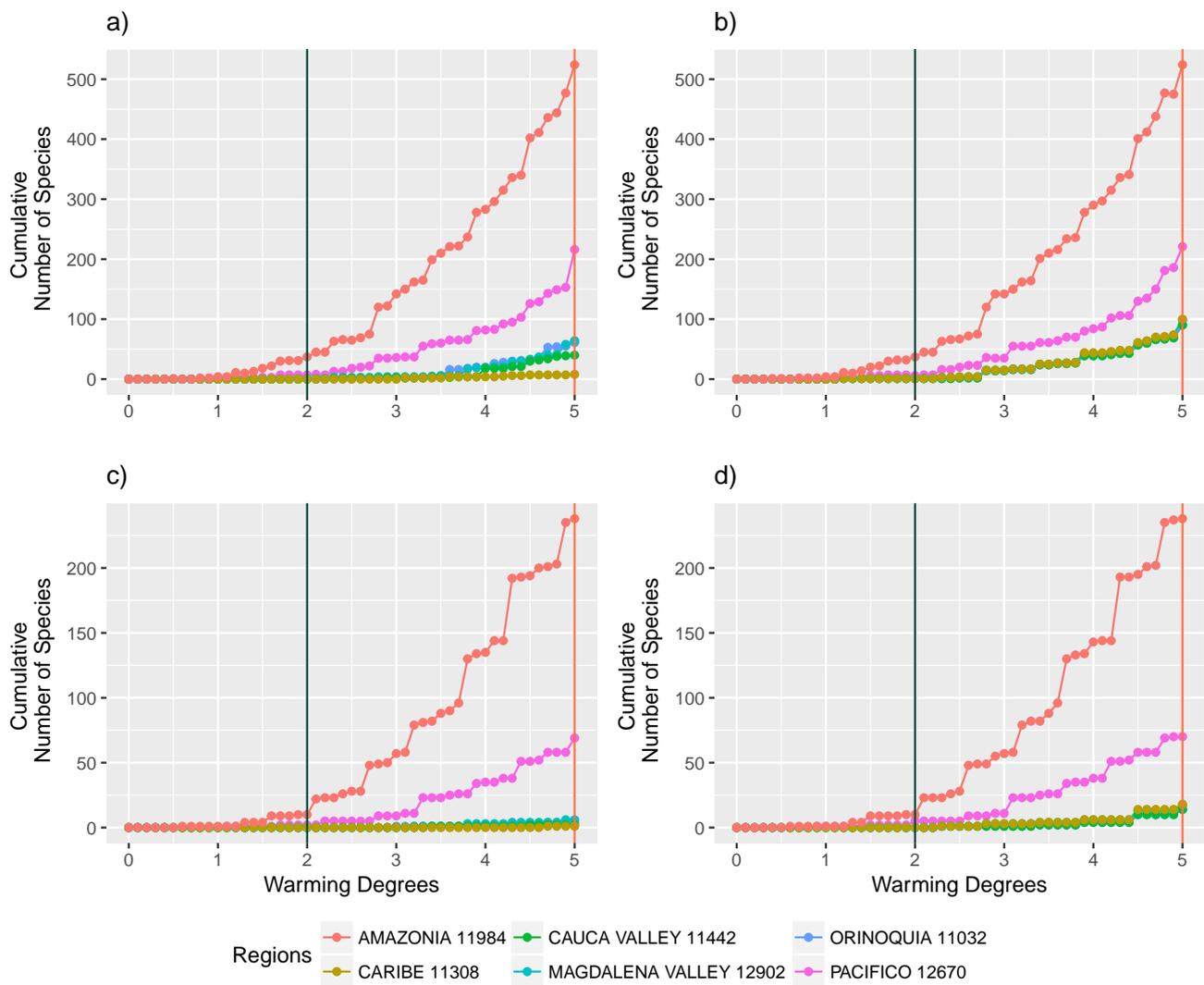


Figure 2. Cumulative number of species affected by: a) Range shift Gaps and Range Contraction under S1. b) Range Shift Gaps and Range Contraction under S2. c) Range shift gaps and mountaintop extinction under S3. d) Range shift gaps and mountaintop extinction under S4. The total number of species for each region as recorded in the Colombian Plant Catalog is provided in the legend.

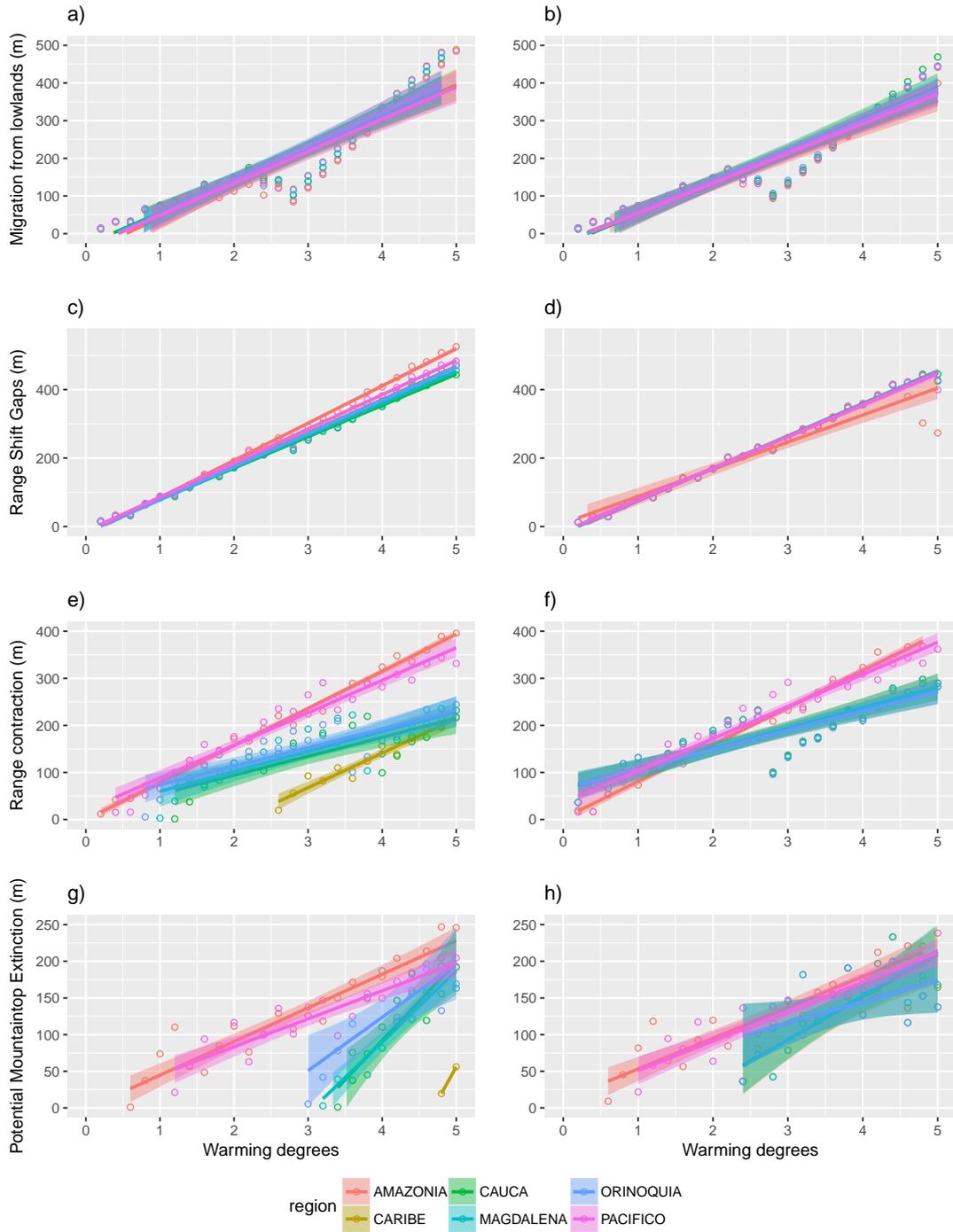


Figure 3. Average number of meters species will be affected in each bioregion: a) Lowland biotic attrition under S1. b) Lowland biotic attrition under S2. c) Range shift gaps under S1. d) Range shift gaps under S2. e) Range contraction under S3. f) Range contraction under S4. g) Mountaintop extinction under S3. h) Mountaintop extinction under S4. Confidence intervals of 95%

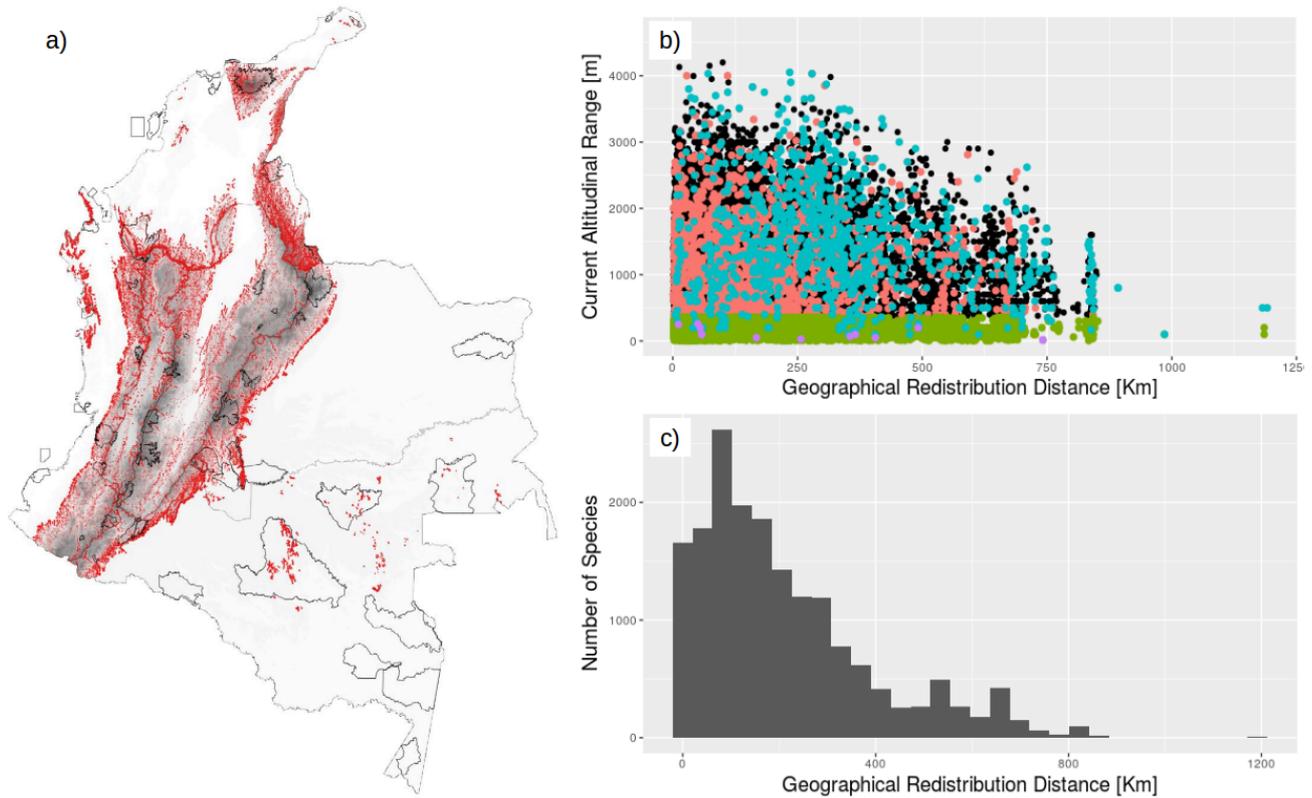


Figure 4. Geographical redistribution of the Colombia vascular Flora. a) Future migration hotspots, red points show the predicted places where species would arrive under a 2°C warming. Black polygons show the National Parks of Colombia and grey polygons denote the biogeographic regions. Grey shading shows the Colombian topography. b) Geographical redistribution distance vs. altitudinal range of Colombian vascular plant species. In orange: species affected by lowland biotic attrition. In blue: species affected by range shift gaps. In green: species affected by range contraction. In purple: species affected by mountaintop extinction. The six species on the extreme right (i.e. *Diplostephium ritterbushii*, *Jalcophila ecuadorensis*, *Loricaria colombiana*, *Myrosmodes ustulata*, *Myrosmodes ustulatum*, *Aciachne flagellifera*, *Lachemilla rupestris*) are particularly vulnerable because of their small altitudinal range and their enormous displacement distance for conserving their thermal niche. c) Histogram of the geographical redistribution distances of Colombian vascular plant species under 2°C warming.

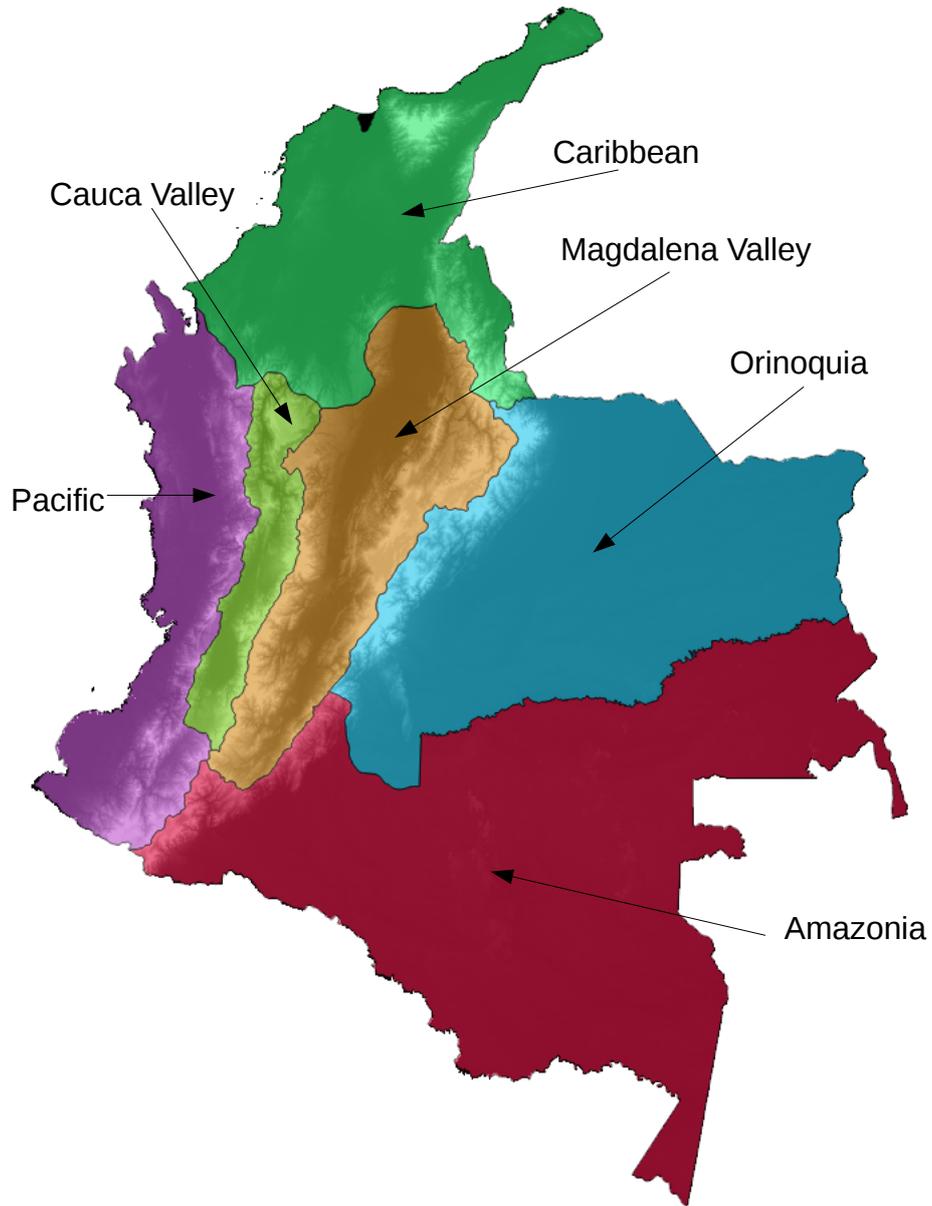


Figure A1. Modified bioregions of Colombia as used in this study.

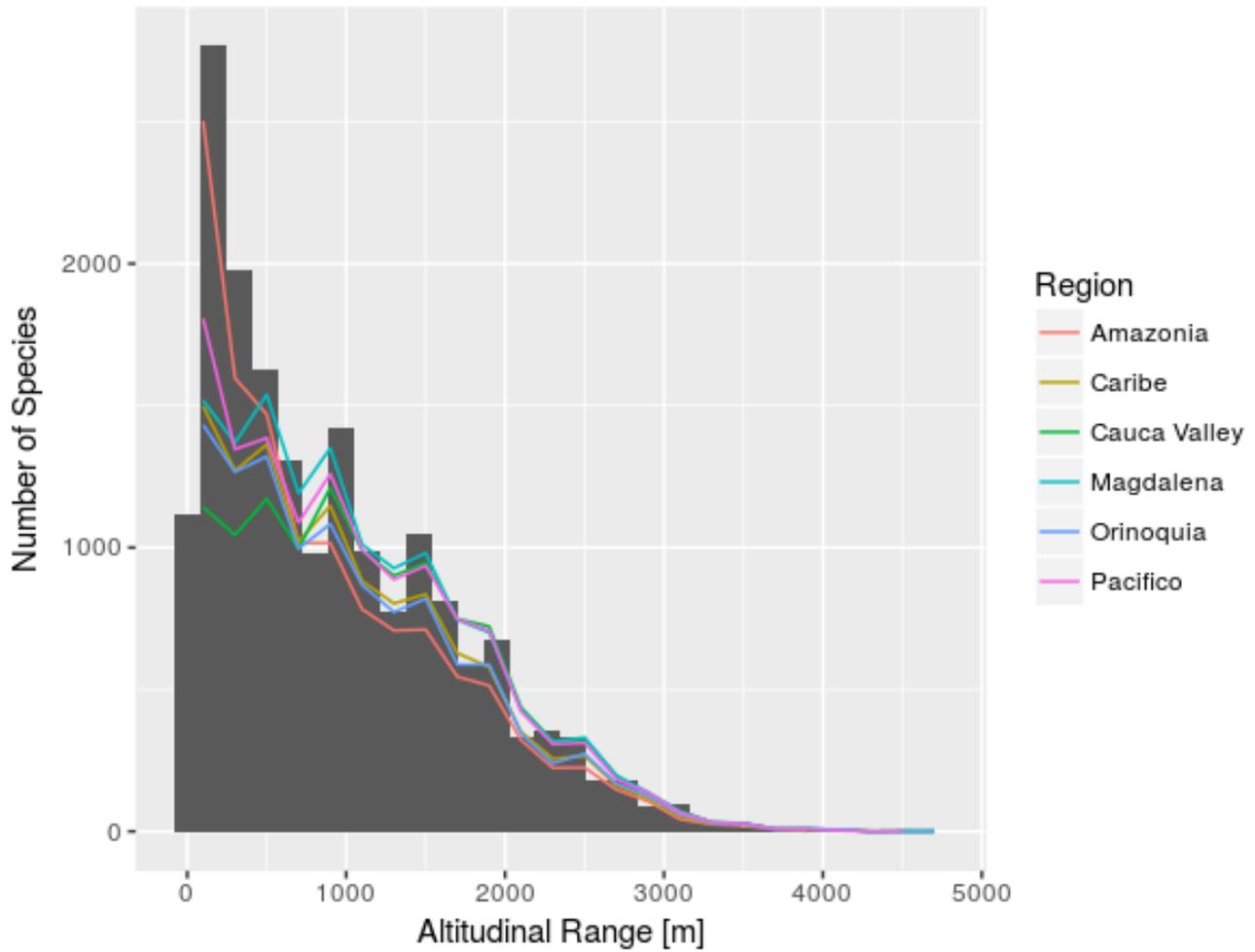


Figure A2. Altitudinal Range distribution of Colombia's vascular plants (in grey). For each one of the bioregions in different colors.

Table A1: Altitudinal ranges of National Natural Parks of Colombia made from the information available on the website of National Natural Parks Agency.

National Park	Minimum elevation	Maximum elevation	Extension (km^2)	Region
Yaigojé Apaporis	100	120	1500	Amazonia
Serranía de los Churumbelos	400	3000	971.89	Amazonia
Río Pure	0	340	9998.80	Amazonia
Reserva Nacional Natural Puinawai	96	100	10925	Amazonia
Reserva Nacional Natural Nukak	200	200	8.55	Amazonia
La Paya	200	200	4220	Amazonia
Cahuinarí	120	120	5755	Amazonia
Alto Fragua Indi Wasi	900	3275	680	Amazonia
Santuario de Flora Plantas Medicinales Orito Ingi	700	3300	102.04	Amazonia
Amacayacu	100	330	2935	Amazonia
Serranía de Chiribiquete	200	1000	12800	Amazonia
Santuario de Flora y Fauna Iguaque	2400	3800	69.23	Andes
El Cocuy	600	5330	3060	Andes
Tamá	350	3450	480	Andes
Serranía de Los Yariguíes	700	3400	509.63	Andes
Pisba	2000	3800	450	Andes
Catatumbo Barí	200	1800	1581.25	Andes
Santuario de Flora y Fauna Guanentá Alto Río Fonce	2000	4000	104.29	Andes
Área Natural Única Los Estoraques	1450	1800	6.4062	Andes
Tatamá	2000	4200	519	Andes
Selva de Florencia	850	2400	100.19	Andes
Nevado del Huila	2600	5780	1580	Andes
Las Orquídeas	350	3400	320	Andes
Complejo Volcanico Doña Juana – Casca-bel	1100	4500	658.58	Andes
Las Hermosas Gloria Valencia de Castaño	1600	4500	1250	Andes
Puracé	2500	5000	830	Andes
Santuario de Fauna y Flora Otún Quim-baya	1750	2276	4.89	Andes
Los Nevados	2600	5321	583	Andes
Santuario de Flora y Fauna Galeras	1950	4276	82.4	Andes
Cueva de los Guácharos	800	4020	71.3493	Andes
Santuario de Flora y Fauna Los Colorados	230	230	10	Caribe
Santuario de Flora y Fauna El Corchal “El Mono Hernández”	0	2	38.5	Caribe
Santuario de Flora y Fauna Ciénaga Grande de Santa Marta	200	1800	1581.25	Caribe
Paramillo	700	3300	4600	Caribe
Sierra Nevada de Santa Marta	0	5775	3830	Caribe
Macuira	85	867	250	Caribe
Santuario de Fauna y Flora Los Flamencos	100	330	5480	Caribe
Tayrona	0	900	150	Caribe

Chingaza	800	4020	766	Orinoquia
Sierra de la Macarena	200	400	6292	Orinoquia
Cordillera de Los Picachos	450	3800	4477.4	Orinoquia
El Tuparro	100	330	5480	Orinoquia
Tinigua	200	500	2080	Orinoquia
Sumapaz	700	4375	2231.79	Orinoquia
Utría	0	1400	543.8	Pacifico
Sanquianga	0	20	800	Pacifico
Munchique	600	3100	440	Pacifico
Los Katíos	2	600	720	Pacifico
Farallones de Cali	200	4100	1964.2	Pacifico