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Research

Recalculating route: dispersal constraints will drive the redistribution of Amazon primates in the Anthropocene

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Climate change will redistribute the global biodiversity in the Anthropocene. As climates change, species might move from one place to another, due to local extinctions and colonization of new environments. However, the existence of permeable migratory routes precedes faunal migrations in fragmented landscapes. Here, we investigate how dispersal will affect the outcome of climate change on the distribution of Amazon's primate species.

We modeled the distribution of 80 Amazon primate species, using ecological niche models, and projected their potential distribution on scenarios of climate change. Then, we imposed landscape restrictions to primate dispersal, derived from a natural biogeographical barrier to primates (the main tributaries of the Amazon river) and an anthropogenic constraint to the migration of many canopy-dependent animals (deforested areas). We also highlighted potential conflict zones, i.e. regions of high migration potential but predicted to be deforested.

Species response to climate change varied across dispersal limitation scenarios. If species could occupy all newly suitable climate, almost 70% of species could expand ranges. Including dispersal barriers (natural and anthropogenic), however, led to range expansion in only less than 20% of the studied species. When species were not allowed to migrate, all of them lost an average of 90% of the suitable area, suggesting that climate may become unsuitable within their present distributions.

All Amazon primate species may need to move as climate changes to avoid deleterious effects of exposure to non-analog climates. The effect of climate change on the distribution of Amazon primates will ultimately depend on whether landscape permeability will allow climate-driven faunal migrations. The network of protected areas in the Amazon could work as 'stepping stones' but most are outside important migratory routes. Therefore, protecting important dispersal corridors is foremost to allow effective migrations of the Amazon fauna in face of climate change and deforestation.

Keywords: biodiversity distribution, climate change, climate-driven migration, deforestation, protected corridors

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Introduction

The geographical distributions of species are not static, shifting over time. Paleontological records abound with examples of range shifts, in which fossils are found where species do not occur nowadays (Davis and Shaw 2001, Gavin et al. 2014). Climate-driven range shifts result from the combination of local extinction on species range limits and colonization. Temperature increases are expected to result, for example, in poleward and upslope movements at the cooler extremes of species distributions and range contractions at the warmer extreme (Parmesan and Yohe 2003, Forero-Medina et al. 2011, Gavin et al. 2014). Therefore, species might be expected to move from one place to another, as the climate changes, thus maintaining their geographical ranges within preferred environmental conditions (Pecl et al. 2017).

As the climate changes, the optimal environmental conditions for survival of a given species will probably move from one place to another, yet some populations may be able to track such changes via dispersal across permeable landscapes (Corlett and Westcott 2013). Successful migrations will therefore depend on the species' ability to keep pace with climate change velocity and the existence of permeable migratory routes (Ackerly et al. 2010). However, habitat loss and fragmentation create landscape mosaics that affect species' movements and may ultimately prevent climate-driven dispersal, thus confining species to unsuitable climates (Gouveia et al. 2016). Therefore, migration towards suitable climates in the future will probably not be possible for several species (Schloss et al. 2012). As consequence, those species might have to cope with non-analog climates, i.e. conditions that exceed the amplitude, extremes and seasonality values to which species are adapted (Ribeiro et al. 2016).

For several animal groups, dispersal through landscape mosaics will likely determine the outcome of climate-driven migrations towards suitable environments in face of climate change (Hang et al. 2013, Gouveia et al. 2016). Amazonian primates are particularly vulnerable to climate change because they inhabit climate conditions close to their upper thermal physiological thresholds (Colwell et al. 2008, Dillon et al. 2010), which are highly preserved among lineages (Araújo et al. 2013). Even small increases in temperature may lead to deleterious effects on primate populations' fitness (Sesink Clee et al. 2015). Neotropical primates, in particular, are canopy-dependent and poor dispersers, not likely to be able to track their climatic niches if they encounter certain barriers, such as large patches of open habitat (Schloss et al. 2012). Thus, potential migratory routes as response to climate change may be disrupted by deforestation, restricting range shifts (Gouveia et al. 2016). Dispersal limitation combined with habitat loss, may limit climate-driven movements of tropical species to the upslope direction (Lawler et al. 2013), exposing Amazonian primates to non-analog climate conditions (Graham et al. 2016).

Although lack of empirical evidence is a major problem in climate change literature, effects on population structure (Sesink Clee et al. 2015), range size (Meyer et al. 2014), species' interactions (Wiederholt and Post 2010), exposition to novel parasites (Barrett et al. 2013), and climate–deforestation feedbacks (Struebig et al. 2015) have already been found in primates worldwide. Here, we evaluated how dispersal limitation by natural and anthropogenic barriers might affect the outcome of climate change on Amazon's primate distribution. To do so, we combined climate and deforestation forecasts into different dispersal scenarios, assuming species-specific dispersal constraints across rivers and deforested areas. Climate change forecasts were derived from projections of the International Panel on Climate Change (IPCC – AR5) and deforestation forecasts relied on prospects of human development and road expansion across the Amazon basin (Soares-Filho et al. 2006).

Methods

Distribution data

The Amazon is the largest block of tropical forest in the world and it encompasses ten South American countries (Brazil, Colombia, Peru, Ecuador, Venezuela, Bolivia, Guyana, French Guyana and Suriname). The Amazon also concentrates a high number of species that are vulnerable to climate change (Pacifici et al. 2015). We defined the species endemic to the Amazon as those whose known distribution fell completely within the territory of the PanAmazonia (Fig. 1), plus a 200 km buffer to account for border uncertainty. Range maps were downloaded from the International Union for Conservation of Nature and Natural Resources (IUCN) database (<www.iucnredlist.org>, date of access: 15 November 2017). Identifying endemics based on range maps is useful for macroecological purposes as it overcomes some species-specific data deficiencies (Young et al. 2009, Swenson et al. 2012), especially because some of the areas that concentrate the highest number of species vulnerable to climate change are also data-deficient, such as the Amazon (Pacifici et al. 2015, 2018). A total of 80 primate species were considered endemic to the Amazon. Endemic species richness was concentrated south of the Amazon river and follows a west–east gradient, from the Andes mountains downstream (Fig. 1).

Species' distribution modeling

The potential distribution of the studied primate species was modeled according to the relationship between the points sampled within the known distribution and their corresponding climate variables (Supplementary material Appendix 1 Fig. A1). Such models were then projected into future climate change scenarios (up to year 2050) to predict climate-driven shifts in species' distribution. Although useful for assessing the effects of climate change on species potential distribution (Faleiro et al. 2013, Sales et al. 2017b) such approach is prone to positional errors, which might ultimately affect the predictive performance of species'

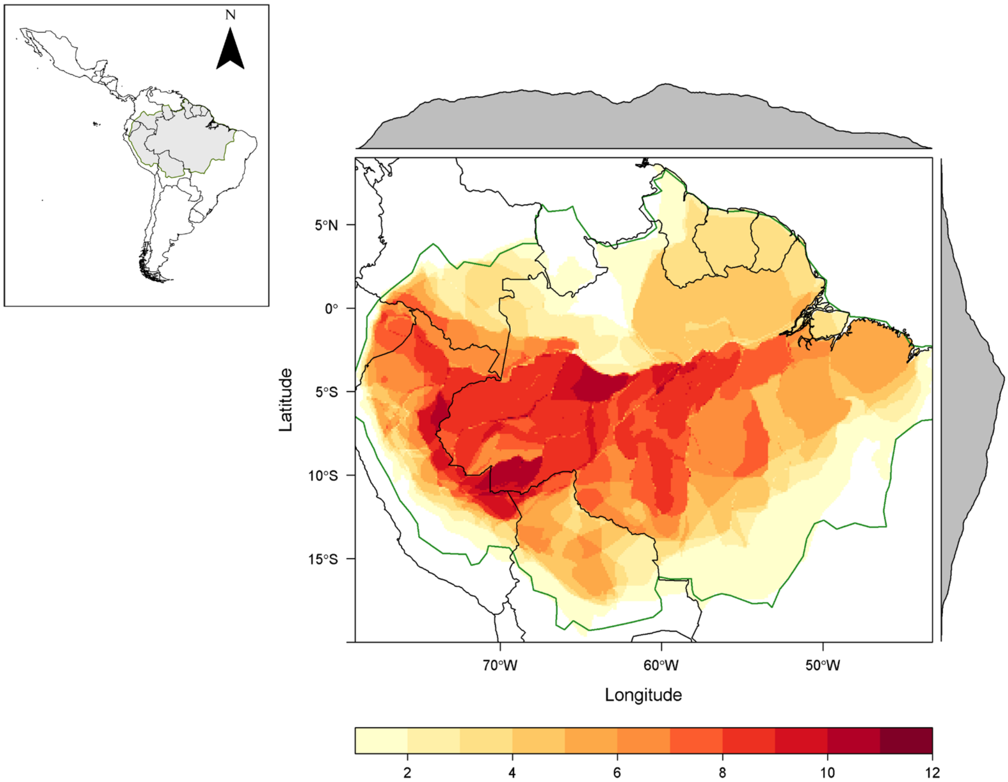

Figure 1. Current species richness of Amazon primates. The green polygon indicates the limits of PanAmazonia, which covers the Amazon biome across ten countries. Darker red color indicates higher species richness, while pale yellow color is for low species richness. Grey filled curves represent the richness distribution along latitude and longitude axis. The upper left panel indicates the PanAmazonia in relation to Latin America.

distribution models (Graham et al. 2008). However, machine learning techniques, such as maximum entropy and boosted regression trees, are robust to the presence of a moderate level of locational error and still provide useful predictions of species' distributions (Graham et al. 2008). Maximum entropy (MaxEnt) also provides the additional advantage of balancing goodness-of-fit with model complexity, by 'tuning' model settings in a relatively user-friendly way (Muscarella et al. 2014). Model specification and the choice of modeling parameters affect the performance of species' distribution models (Araújo and Guisan 2006, Merow et al. 2013). Model overfitting, for example, is alleviated by species-specific smoothing of settings and also by calibrating and evaluating models with independent datasets (Muscarella et al. 2014).

We used MaxEnt, which is a presence–background method in which the species' distribution is an unknown probability along the full background points (non-negative values that add up to one) (Elith et al. 2011). The values of predictor variables at localities with presumed presences restrict the unknown distributions so that the average and variance values of environmental predictor should be therefore close to empirical values (Graham et al. 2008, Merow et al. 2013). The maximum likelihood approach approximates the unknown distribution using the background point distribution that maximizes the entropy subjected to such constraints (Phillips and Dudík 2008). Therefore, MaxEnt compares the relationship between environmental conditions from species' known distribution to the conditions along the full background. However, the complexity of the fit to the observed values can be adjusted by transformations on the original predictor values ('feature classes' or FCs) (Peterson 2011, Muscarella et al. 2014).

We built species' distribution models that potentially maximized model performance. First, we used a species-specific background. Limiting the study area to the regions that are accessible for a species is crucial for the outcome of species' distribution models (Barve et al. 2011). Therefore, the study area should only include the climate conditions the species probably experience and/or are restricted to, due to biogeographical limitations. To do so, our background was defined as the bounding box of each species' environmental points, plus additional 10 degrees to each bound, a value that is twice the average dispersal capacity for Amazonian primates (Schloss et al. 2012), in a loose dispersal scenario. Environmental layers were then cropped to match the study extent and 10 000 background points were sampled from background extent rasters (only one per cell, without replacement) (Barbet-Massin et al. 2012).

Because we were interested not only in the species' potential distribution but also on the likely effects of climate change, we used the 'block' method to partition the environmental dataset. We did so because the block method is ideal for studies that require transferability across space or time and also to account for spatial autocorrelation in species' occurrence dataset (Muscarella et al. 2014). In this method, data is partitioned by the latitude and longitude lines that divide occurrence localities as equally as possible. Occurrences and background are attributed to a bin depending on their location. Then, we iteratively ran k models, with $k-1$ bins for training and the rest for testing. Metrics of model evaluation are summarized across the k iterations (Muscarella et al. 2014).

To enhance model performance, we 'tuned' MaxEnt models, by selecting among models with different combinations of feature classes – L, LQ, H, LHQ, LQHP, LQHPT (L = linear, Q = quadratic, H = hinge, P = product, T = threshold) (Muscarella et al. 2014). The model most supported by each species' occurrence dataset was chosen by the Akaike information criteria (Akaike 1974), corrected for small sample sizes (AICc), a presence-dependent continuous metric recommended to assess the performance of our models (Lawson et al. 2014). 'Tuned' models selected by AICc are less overfitted and exhibit lower omission rates than MaxEnt default models (Muscarella et al. 2014).

To calculate potential range shifts, we converted continuous predictions of climate suitability into binary maps of 'presence' and 'absence'. We used the 10% omission rate threshold for converting continuous into binary predictions. This threshold allows the models to miss 10% of the presumed presences, restricting environmental characterization to the 90% of the most common conditions across species' ranges. Although this is a simple and relatively less used threshold in species' distribution modeling literature, it can potentially uncover informative distributional areas for species with small numbers of occurrence records (Pearson et al. 2007, Muscarella et al. 2014). Much of Amazonian biodiversity has extensive distributional knowledge gaps (Bush and Lovejoy 2007) due to access constraint, which in turn creates strong sampling biases towards the neighborhood of cities and the main rivers (Schulman et al. 2007). Other traditionally used thresholds, such as maximizing the sum of sensitivity and specificity (Peterson et al. 2011), in addition to the small number of occurrence records for some of the species analyzed here, could generate overly stringent predictions, leaving out much of species' potential distributions.

Dispersal constraints

Neotropical primate species are arboreal and rely on canopy trees to feed, reproduce and to move within their home ranges (Pyritz et al. 2010, Arroyo-Rodríguez and Fahrig 2014). Because deforestation disrupts potential migratory routes for climate-driven primate migration, the effect of climate change on future primate distribution, therefore, is expected to interact with deforestation (Gouveia et al. 2016). Deforestation and the removal of large tree canopy will affect the colonization potential of suitable climates in the future, so that deforested areas will act as barriers to primate dispersal in response to climate change. In addition, other natural elements present in a landscape might affect primate species distribution. The Amazon rivers, for example, are known to delimit the distribution of sister species of primates and are considered an effective biogeographical barrier and a vicariant agent (Boubli et al. 2015).

Here, we explicitly accounted for the dispersal mechanisms that might facilitate or prevent colonization. To do so, we assumed primate dispersal to be constrained by potential barriers, thus restricting primate colonization of suitable climates in the future. We used a cellular automaton model that implements species-specific restrictions into projections of species distribution models under environmental change, within the MigClim R package (Engler et al. 2012). The basic unit of this model is a cell that is occupied or not, at a given time step $t_{initial}$ that defines the initial distribution of the species. Across decadal time steps ($t_{initial}$, $t+1$, $t+2$, …, t_{final}), occupied cells can remain occupied, if environment conditions remain suitable, or can be decolonized, if environment becomes unsuitable. Cells that are unsuitable at one step of the simulation can become colonized at the next step if: 1) environmental conditions become suitable, and 2) the target cell is within reach of a potential source cell (as defined by the dispersal kernel). Therefore, the model is based on a function of distance decay on colonization probabilities, from the source cell to the target cell, across time steps, conditional to the environmental suitability of the target cell.

To accommodate species-specific dispersal information, we obtained the maximum distance a species would be able to move from Schloss et al. (2012). Dispersal velocity (km yr^{-1}) was modeled as a function of body mass, diet type and generation length (Schloss et al. 2012). Given the interval of our timesteps (every 10 yr), dispersal velocity was multiplied by 10 to find the maximum dispersal distance expected for each species. That distance was used to parameterize species-specific spatially-explicit dispersal kernels, thus restricting movement to a maximum number of cells as defined by species dispersal abilities. The probability of colonization of a target cell in time $t+1$ by a source cell in time t was, therefore, a function of the distance between them, from 1 (neighboring cells) to zero (distance greater than maximum dispersal distance) (Fig. 2) (Schloss et al. 2012). Given the interval of our timesteps (every 10 yr), dispersal velocity was multiplied by 10 to find the maximum dispersal distance expected for each species.

The initial distribution of the primate species was considered the outcome of the species distribution models (a presence–absence map), after removing areas of known absence (outside 10 km buffer around the IUCN range maps). By doing so, we incorporated border uncertainty but still preserve geographical allometry of species ranges. The maps of potential future distribution, or the projections of the species distribution models onto scenarios of future climate change, therefore, indicated the environmental suitability of all cells within reach of species dispersal ability (Barve et al. 2011), delimited as the species-specific background.

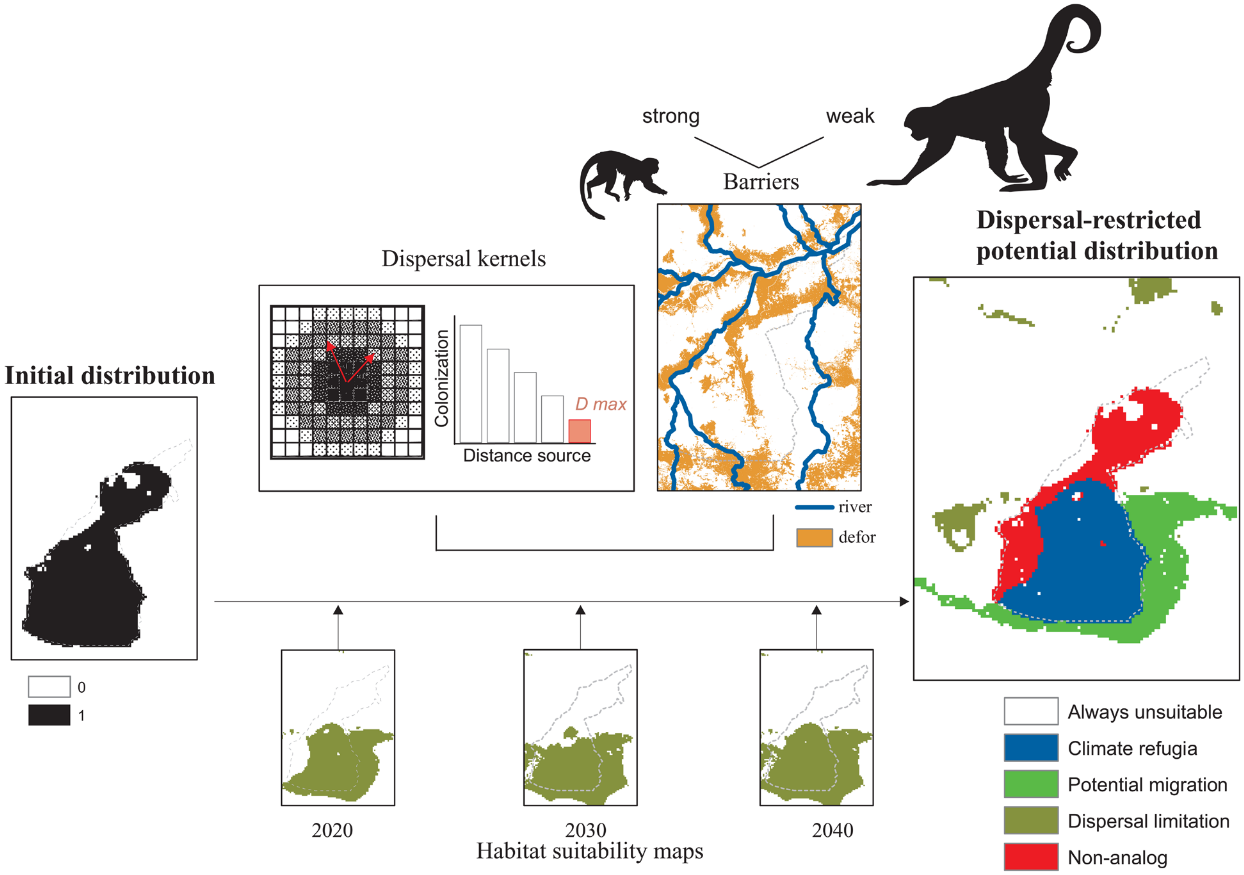

Figure 2. Methods flow used to incorporate dispersal constraints into estimates of potential distribution for Amazon primates. Spatially-explicit dispersal kernels were calibrated with the maximum dispersal distance expected (D_{max}) for each species (obtained from Schloss et al. 2012). Then, the probability of a source cell (initial distribution) to colonize a target cell (habitat suitability maps) was estimated as a function of the distance between such cells up to D_{max}. Rivers and deforested cells were considered barriers (cells that are permanently unsuitable and that prevent dispersal). The strength of rivers in preventing dispersal (weak or strong) was adjusted according to species' likelihood to cross rivers. The final map of dispersal-restricted potential distribution is partitioned into climate refugia (suitable cells in present and future), potential migration (newly suitable cells accessible via dispersal), dispersal limitation (newly suitable cells inaccessible via dispersal) and non-analogs (cells that are suitable in the present but will become unsuitable in the future, thus exposing populations to non-analog climates).

The main tributaries of the Amazon river, namely the rivers Javari, Jutaí, Juruá, Madeira, Purus, Coari, Napo, Putumayo, Negro, Jari, Paru and several medium-sized affluents, were considered natural barriers to primate dispersal.

In the cellular automata model used here, regular unsuitable cells cannot be colonized but do not affect species dispersal (Engler et al. 2012). Barrier cells are regarded as permanently unsuitable for species occupancy, thus cannot be colonized, but they also prevent dispersal across them (Engler et al. 2012). Although rivers are a vicariant agent delimiting the distribution of several Amazon primates, especially the smaller-bodied ones (Boubli et al. 2015), larger primates are able to cross rivers (Nunes 2014, Link et al. 2015). To accommodate that, we reran our analyses modulating the strength of rivers as barriers according to species swimming abilities. As some species of the genus *Ateles* and *Lagothrix* are able to swim long distances (Nunes 2014, Link et al. 2015), rivers were considered a weak barrier to their dispersal. Weak barriers allow dispersal to proceed across two diagonally adjacent barrier pixels, while strong barriers will not (Engler et al. 2012). Rivers were, however, considered a strong barrier to all other species. In addition, the projections of deforestation (Soares-Filho et al. 2006) were considered strong barriers to dispersal of all species (see below). By doing so, rivers or deforested areas prevented Amazon primates to reach newly suitable climates in the future (Fig. 2).

To compare the effect of dispersal on the potential response of species distribution in face of climate change, we created different dispersal scenarios. The first scenario, unlimited dispersal, ignores rivers and deforestation barriers and allows species to colonize all new suitable environment. The second scenario, limited dispersal, includes rivers as barriers to dispersal, but does not account for deforestation projections, on a Pre-Anthropocene case (Smith and Zeder 2013). The third scenario, Anthropocene Limitation, includes both rivers and projections of deforestation as barriers to climate-driven migration, although allows dispersal into some non-barrier cells that became suitable. The fourth scenario, no dispersal, assumes that species will not move in response to climate change, so that newly suitable environment outside its current distribution will not be colonized. All scenarios combine either 'optimistic' or 'pessimistic' projections of climate change and deforestation (e.g. the model of greenhouse gas emission rcp26 and the Mitigation deforestation model were combined into one single 'optimistic' scenario, as well as the rcp85 and the Business-as-usual deforestation model into a 'pessimistic' projection).

Deforestation models

In this work, we considered that deforestation imposes restrictions to habitat suitability and dispersal. Deforested cells cannot be colonized by primates, regardless habitat suitability, i.e. removed from species potential distribution (as a posteriori mask). In addition, deforested cells prevent dispersal from source and target suitable cells. We used an empirically based, policy-sensitive model of deforestation in the Amazon, based on two extreme scenarios of urban development and road paving (Soares-Filho et al. 2006). The first deforestation scenario, Business-as-usual, considers historical trends of deforestation in the last decades and that the highway paving schedule will be met (Supplementary material Appendix 1 Fig. A2). The Business-as-usual scenario also assumes that up to 40% of protected areas will be subject to deforestation, so that compliance to environmental policies will be low, and that no new protected areas will be created (Soares-Filho et al. 2006). The second deforestation scenario, Mitigation, establishes an upper threshold for deforested area and assumes an agro-ecological zoning of land use and the expansion of the network of protected areas in the Amazon. Range shift was calculated as the percent variation in the number of suitable cells for a given species, comparing the current and future potential distribution $(\mathrm{Future}_{size} - \mathrm{Current}_{size}) \times 100/\mathrm{Current}_{size}$.

Data accessibility

The climate data used in this work can be downloaded at <www.ipcc-data.org>. Primate range maps were downloaded at <www.iucnredlist.org>. Deforestation models can be found as supplementary material of Soares-Filho et al. (2006). High-resolution rasters and the species-specific maps may be obtained upon email request (lilianpsales@gmail.com). An example of the R codes used in this paper is available as Supplementary material Appendix 1.

Results

Range shift

Projections of range shift in response to climate change varied considerably for different scenarios of dispersal limitation (Fig. 3, Supplementary material Appendix 1 Table A1). On the Unlimited dispersal scenario, in which dispersal was not limited neither by rivers or deforestation, our projections indicated expansion of climatically suitable areas on both policy scenarios (Mitigation and B.A.U.) for most of the primate species (Fig. 3a–b, Supplementary material Appendix 1 Fig. A3). In a Mitigation policy scenario, if dispersal was allowed towards all suitable environments within an accessible region, 59 species could expand their ranges (range $\mathrm{expansion}_{mean} = 270 \pm 30\%$), while 21 species would be expected to lose range area (range $\mathrm{shrink}_{mean} = -54 \pm 3\%$). Considering a B.A.U. policy scenario, 55 species could expand their ranges (range $\mathrm{expansion}_{mean} = 160 \pm 15\%$), while 25 species would still lose some climatically suitable area (range $\mathrm{shrink}_{mean} = -55 \pm 12\%$).

If dispersal was restricted solely by rivers but not by deforestation, in the limited dispersal scenario, several species would still be able to expand their ranges, but range losses would become more common (Fig. 3c–d, Supplementary material Appendix 1 Fig. A3). In such case, in a Mitigation scenario, 42 species could expand their ranges (range $\mathrm{expansion}_{mean} = 265 \pm 43\%$), while 38 species should undergo range contraction (range $\mathrm{shrink}_{mean} = -81 \pm 12\%$). In the B.A.U. policy scenario under limited dispersal, 37 species expanded their ranges (range $\mathrm{expansion}_{mean} = 113 \pm 24\%$), but 43 species should lose area (range $\mathrm{shrink}_{mean} = -80 \pm 7\%$).

In the more realistic Anthropocene limitation scenario, although dispersal was restricted by rivers and deforested areas, a few species should still able to migrate towards some (but not all) suitable environments expanding their ranges, while most species should experience reductions in their ranges (Fig. 3e–f, Supplementary material Appendix 1 Fig. A3). On Mitigation policy scenario, 33 species could expand their ranges (range $\mathrm{shift}_{mean} = 91 \pm 13\%$), while 47 species are predicted to experience range contractions (range $\mathrm{shift}_{mean} = -78 \pm 15\%$). On an Anthropocene B.A.U. scenario, only 15 species would be expected to expand their ranges (range $\mathrm{shift}_{mean} = 58 \pm 11\%$), while 65 species should have their ranges reduced (range $\mathrm{shift}_{mean} = -71 \pm 17\%$).

If no dispersal was allowed so that species' distribution do not move as response to climate change, the no dispersal scenario, all species would be expected to lose a large proportion of their distribution (Fig. 3g–h, Supplementary material Appendix 1 Fig. A3). No species expanded their ranges on any policy scenario (range $\mathrm{expansion}_{mean} = 0.00$), and range reductions often resulted in more than 80% of loss (Mitigation range $\mathrm{shrink}_{mean} = -89 \pm 5\%$; B.A.U. range $\mathrm{shrink}_{mean} = -92 \pm 3\%$).

Biodiversity redistribution

Projections of primate richness varied from 2 to 16 species per cell, with a highest richness on the flanks of the Amazon river and in the Andean portion of the Amazon basin. In both prospects of climate change (Mitigation and B.A.U.), primate richness is expected to be concentrated in the Andean Amazon, with apparent movement towards the Andes mountains. Deforestation also reduced the number of

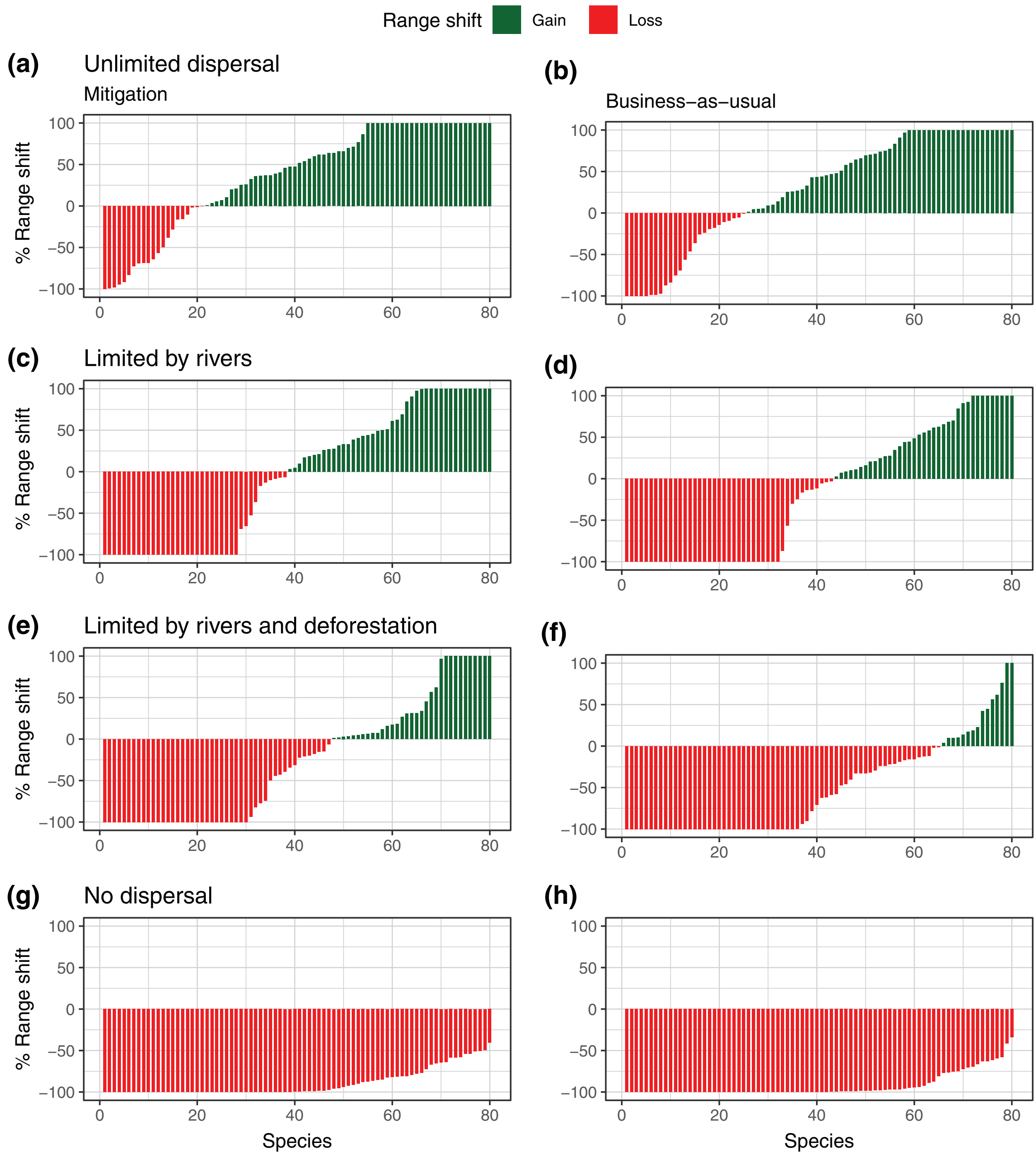

Figure 3. Range shift per species, in face climate change and deforestation under different dispersal scenarios. Panels indicate dispersal scenarios, with varying degrees of constraint of species dispersal (from unlimited to no dispersal). Mitigation and Business-as-usual indicate prospects of human development and the consequent projections of climate change and deforestation. Range expansion values are presented up to the limit of 100% increase, to enhance readability. For exact values, see Supplementary material Appendix 1 Table A1.

primate species able to persist in nearly half of the Amazon territory, especially in Brazil.

The Peruvian Andes and the Western Brazilian Amazon are climate refugia for several primate species (Fig. 4a–b). In these regions, up to eight species would maintain their range within preferred climates without the need to move. Deforestation projections were also relatively low for these places. The Eastern flanks of the Northern mountains would also host the zones of potential migration (Fig. 4c–d) to a large number of species (from 8 to 16 species).

Our simulations suggest dispersal limitation will prevent primate species from occupying climatically suitable areas up

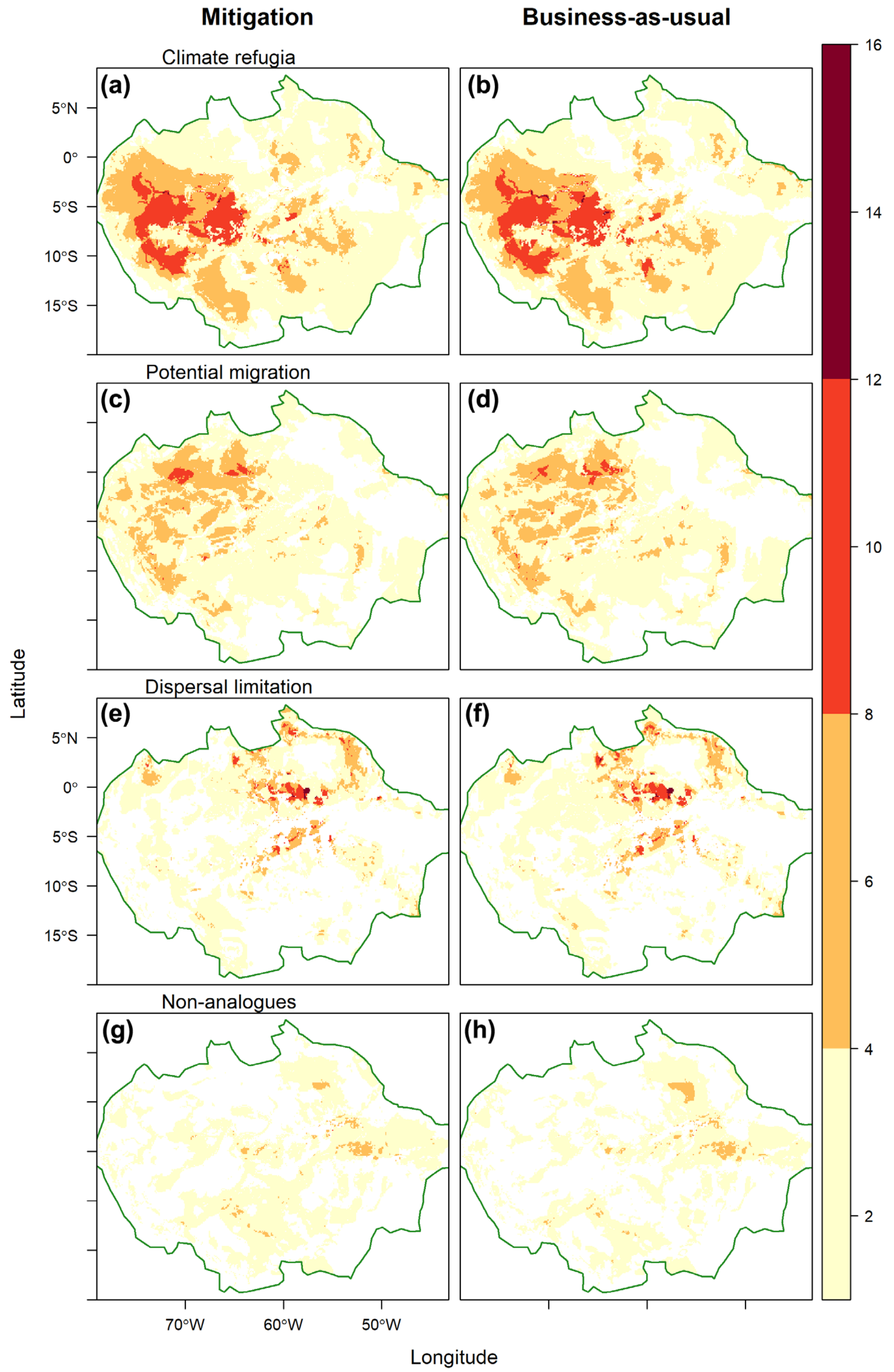

Figure 4. Range dynamics of Amazon primates. Dispersal constraints were applied to projections of potential distribution Amazon primates. Mitigation and B.A.U. are prospects of human development, greenhouse gas emissions and road paving. Colors (from yellow to red) indicate number of species predicted to undergo range dynamics (sum of cell-based projections for each species) across the Amazon.

the Amazon and Negro Rivers and south of the Madeira River (Fig. 4e–f). The Guyanas (Guyana, Suriname and French Guyana) and southern Brazil also appear as suitable though inaccessible regions due to dispersal limitation for Amazonian primates in face of climate change. Our predictions indicate high probability of exposure to non-analog climates, for most of the Amazonian territory (Fig. 4). Exposure to non-analog climates seem, however, to be highest near the largest urban centers such as the cities of Santarém, Manaus and Boa Vista, in Brazil.

Conflict zones between primate dispersal and deforested cells are mainly concentrated in the Central Amazonia (Fig. 5), especially in Brazil, along the major tributaries of the Amazon River and close to the largest urban centers (blue triangles in the map). Most protected areas in the Amazon will not alleviate the conflict between biodiversity and anthropogenic pressures in the future. Future conflict zones for most primate species are not within protected areas (Fig. 5). Only a few protected areas encompass regions that might enable primate migration towards suitable climates but these areas are subjected to high probability of deforestation. Thus, the areas of potential migration that might be disrupted by deforestation are outside protected areas.

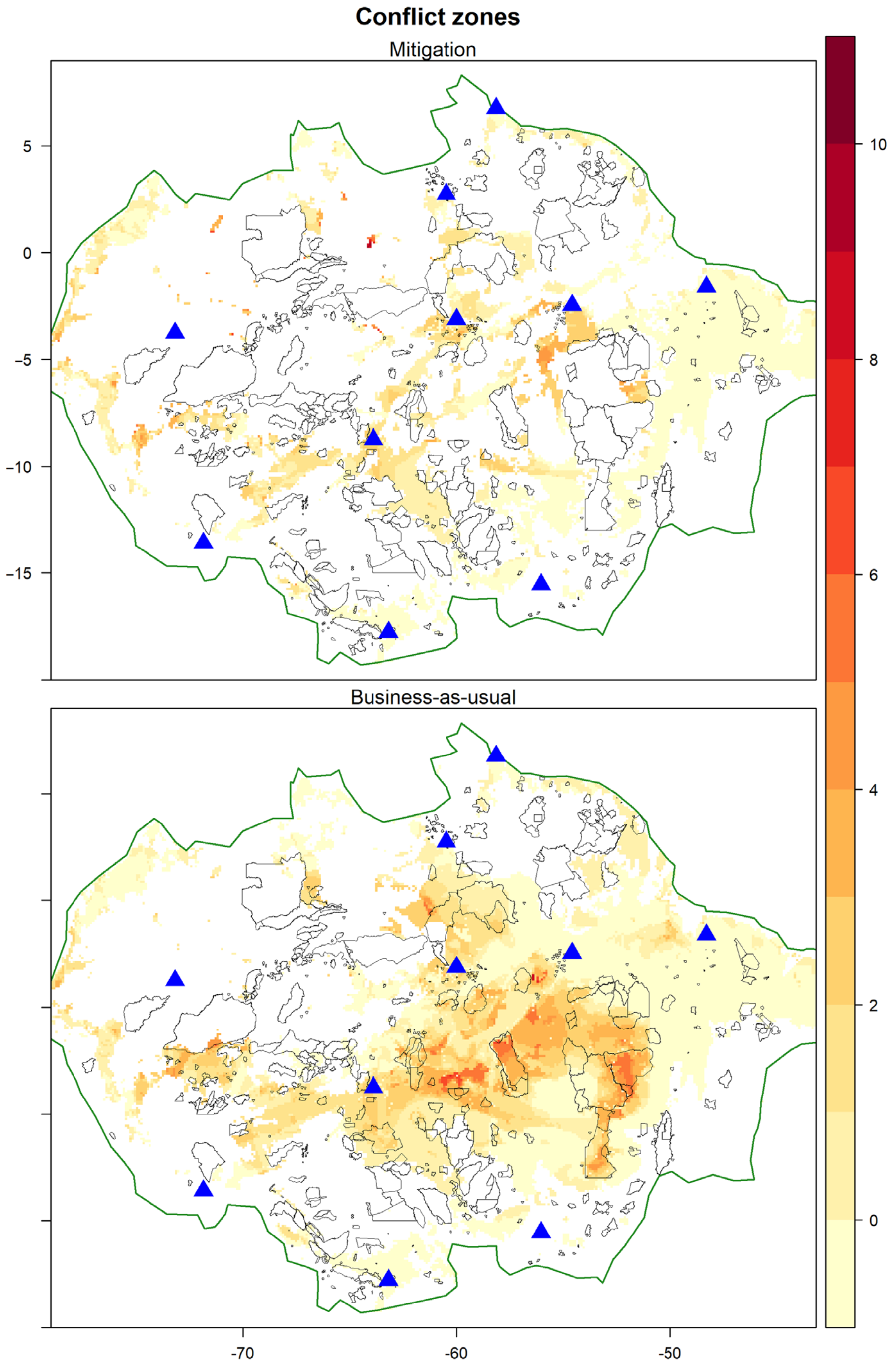

Figure 5. Conflict zones between Amazon primate redistribution and human settlements. Colors indicate migratory potential disrupted by deforestation, in terms of richness of species for which cells might work as dispersal routes. Reddish colors indicate that a cell might work as migratory routes for several species, while yellow to white colors indicate that cells might work as migratory routes for a few or no species. Empty grey polygons indicate protected areas in the Amazon. Blue triangles point out the largest cities of the Amazon basin.

Dispersal affected the outcome of climate change for the distribution of all Amazon primates, although some species were likely to lose range even under unlimited dispersal (Supplementary material Appendix 1 Fig. A4). The species *Plecturocebus moloch*, *Lagothrix poeppigii*, *Alouatta nigerrima*, *Saguinus imperator*, *Aotus nancymaae*, *Plecturocebus cupreus*, *Chiropotes albinasus*, *Plecturocebus aureipalatii*, *Alouatta discolor*, *Cheracebus torquatus*, *Plecturocebus hoffmannsi*, *Cebus kaapori*, *Mico humeralifer*, *Plecturocebus caligatus*, *Saimiri vanzolinii*, *Mico leucippe*, *Mico saterei*, *Plecturocebus baptista*, *Mico mauesi*, *Saguinus bicolor*, *Callibella humilis* are expected to experience range contractions even in a Mitigation scenario with no dispersal constraints. Progressive inclusion of dispersal constraints successively increased range contraction, both in frequency and magnitude (Supplementary material Appendix 1 Table A1). However, some primate species were predicted to expand their range sizes more than 10 times in the Anthropocene scenario (e.g. *Cheracebus medemi*, *Plecturocebus caquetensis*). Most species predicted to undergo large range shift (either expansion or contraction) have currently small range sizes (Supplementary material Appendix 1 Fig. A5). Projections for species with wide distribution are less uncertain (smaller variability) than those for small-ranged species. The Pitheciidae family presented the largest variation in predicted range shift, with some species losing large amounts of climate area and others nearly quintupling their ranges. The Callitrichids also exhibited large variation on predicted range shift. Interestingly, the Aotidae family was the most convergent in terms of range variation, with most species expanding their ranges, though in a small proportion (Supplementary material Appendix 1 Fig. A6).

Discussion

Climate change will cause the redistribution of biodiversity, with ecological, social and economic impacts across the globe (Pecl et al. 2017). Climate-driven migrations, however, will only allow occupancy of newly suitable climates if permeable migratory routes allow dispersal across landscapes (Engler and Guisan 2009). We investigated how deforestation and climate change will interact to redistribute the Amazon primate fauna in face of climate and land-use change and found that dispersal into fragmented landscapes will likely define the outcome of climate change on species distributions. If species could migrate into all newly suitable climates in the future, most species would be expected to expand their ranges and respond favorably to climate change. However, as dispersal constraints (natural and anthropogenic) are considered, predictions of range expansion are infrequent and range contraction gets more likely. In an extreme scenario where species are unable to migrate, being forced to stay within the limits of their current geographical ranges, all species would be expected to undergo range contractions.

Range contraction in response to climate change is a generally assumed pattern for primates (Estrada et al. 2017). Contrary to other studies, we found that most species could exhibit range expansions, if dispersal into environments that become suitable under climate change were possible. Range contractions were only prevalent when dispersal limitation confined species to current geographical borders of their distribution. If species are not allowed to colonize the novel suitable environments that may surround their current ranges, populations may become confined to non-analogue climates. Exposure to non-analogue climates is expected for several Amazon mammals (Ribeiro et al. 2016) and might cause physiological stress on populations inhabiting non-optimal climates (Dillon et al. 2010), ultimately leading to local extinctions (Urban 2015). Further, Amazonian primate species will also be exposed to non-analog climate conditions at a rate greater than the global average (Graham et al. 2016, Ribeiro et al. 2016). Here, in the no dispersal scenario, all the studied primate species were predicted to experience range contractions or to cope with non-analog climate conditions.

Some species, however, seem to be able to benefit from climate change, with predicted range expansion in different scenarios of dispersal and deforestation. Range expansion could, in such cases, promote colonization of unoccupied territories. Climate change could, therefore, modify the ratio between species that are considered 'native' and 'non-native' (Mainali et al. 2015), by allowing primate range expansion across current geographic boundaries. Primate species that have higher dispersal abilities (Nunes 2014), generalist diets or those that explore abundant resources with low competition pressure (e.g. exudativory by some Callithrichids – Sussman and Kinzey 1984) might be able to thrive in anthropogenic landscapes (Hockings et al. 2015, Kalbitzer and Chapman 2018). In fact, callithrichids and pitheciids exhibited diverse responses, with nearly half species expanding and half losing range, in a realistic Anthropocene scenario. This suggests that biological characteristics that enhance dispersal (e.g. vagility) or colonization success (e.g. wider physiological tolerance and/or a flexible diet) in face of climate-induced migrations may not be phylogenetically preserved. However, species response to climate change seems to rely on species-specific or species–environment idiosyncrasies that prevent us from observing a general trend on range shift for each group.

Effects of climate change on species distribution are probably related to environmental tolerances (Foden et al. 2013). Here, primate species with wide distributions exhibited smaller variation on their potential future range size. A wide range size indicates that a species is be able to tolerate a broad array of climatic conditions (Sales et al. 2017a), feed on diverse or well-distributed resources and may also be related to superior competitiveness (Adler et al. 2013). Therefore, climate change is less likely to expose these species to non-analog climates and consequent deleterious effects on populations, thus suggesting that large range sizes also provide a buffer against environmental fluctuation. On the other hand, some primate species occupy such a small area, that even small environmental variation may expose all populations to physiological stress (Oswald et al. 2011) or resource shortage. Those narrow-ranged species are also vulnerable to non-climatic stressors, such as Allee effect and population stochasticity, that impact small populations (Sexton et al. 2009). Different mechanisms related to geographical range size may, therefore, influence species' vulnerability to climate change.

Another issue related to species range size may be particularly relevant in the case of narrow-ranged species. The largest tributaries of the Amazon river are a vicariant agent to speciation and delimit the distribution of several Amazon primate species (Boubli et al. 2015). Vicariant speciation events disrupt and isolate a formerly continuous population, which may evolve as two separate species. This implies that, currently, species may occupy only a fraction of the potential climate niche due to the vicariant role of rivers on preventing occupancy of areas with suitable climate. In other words, there must be areas that are climatically suitable to many species, but with occupancy prevented by dispersal limitation due to the formation of Amazon rivers. As niche modelling uses current distribution to characterize the climate niche of species, results may underestimate the climatically suitable area in the future (Peterson et al. 2018). This also implies that the realised niche is significantly smaller than the potential niche (Soberón and Peterson 2005). If so, those mathematical artifacts should indicate that narrow-ranged species in the present are also less likely to have range expansion in the future, simply as a result of the poor estimation of their climatic niches. Accordingly, species with large ranges may be less limited by barriers to dispersal, and thus there is a closer matching between realised and potential niches. Although these historical contingencies may generate biases in our estimates, if rivers limited dispersal enough to promote speciation, it means that the constraining effect of dispersal limitation is large. Therefore, dispersal limitation likely be the main driver of Amazon primate range shifts, even for species with narrow ranges.

We found that dispersal defines the response of Amazon primate distribution to climate change. Dispersal limitation is known to restrict climate-driven movements of tropical species to the upslope direction, given the large distances between temperature zones (Lawler et al. 2013). In this work, dispersal limitation is predicted to prevent occupancy of regions in the Guyanas and in southern Brazil, which probably reflect different geographical patterns of landscape barriers. In the case of Guyanas, the main tributaries of the Amazon river work as a natural biogeographical barrier to potential climate-driven migrations of primates which occupy the southern flank of the rivers. The constraining effect of Amazon rivers on primate dispersal will prevent faunal migrations in response to climate change and confine population to non-analogue climates. However, deforestation projections in the Amazon are mainly concentrated in the 'Arch of Deforestation' (Soares-Filho et al. 2006), a region of high agricultural pressure from cattle-ranching and soya plantations. As primates are mainly arboreal and poor dispersers in deforested landscape matrix (Schloss et al. 2012, Marsh et al. 2013), the deforestation projected for the 'Arch of Deforestation' creates another constraint to climate-driven faunal migrations towards suitable regions in southern Brazil. Potential movements of Amazon primates towards southern and cooler latitudes are therefore mainly restricted by deforestation.

The redistribution of biodiversity due to climate change will create potential areas of conflict between migratory routes and human settlements. Here, we highlighted the regions that could potentially work as 'stepping stones' for climate-driven faunal migrations but are in cells predicted to be deforested. Those regions indicate potential migratory routes predicted to be disrupted by deforestation. We found that most of the conflict areas neighbor the largest Amazonian cities in Brazil, near the Central Amazonia. In such places, conservation units could act as 'stepping stones' and facilitate climate-driven migrations. As temperature increases, conservation units could, therefore, provide habitat conditions that permit species' temporary persistence, enough to allow effective movements towards more suitable climates. In Brazil, where most of Amazon deforestation occurs (Soares-Filho et al. 2006), the network of protected areas covers more than 23% of its territory (Veríssimo et al. 2011). However, and unfortunately, our predicted conflict zones are not within the territory of protected areas. This indicates that most protected areas in the Amazon will not alleviate the conflict between biodiversity and anthropogenic pressures in the future.

We included the effects of climate change and deforestation separately, in which deforestation created non-suitable areas, impossible to be crossed by Amazon primates. However, the existence of climate-induced feedbacks on deforestation and fire dynamics in the Amazon (Malhi et al. 2008, Coe et al. 2013) creates a more dismal conservation scenario. In low latitudes, deforestation projections lead to temperature rise (Bala et al. 2007, Longobardi et al. 2016). In the Amazon, both forests clearing and selective cut affect regional climate and hydrological regimes. Clearing generates drier and warmer micro-habitats, more susceptible to fire, which releases smoke and affects cloud formation, in a negative feedback of fire susceptibility (Malhi et al. 2008, Nepstad et al. 2008). Besides disrupting landscape dispersal routes for primates, the increase in deforestation rates in the Amazon (Fearnside 2015) will lead to deforestation–climate feedbacks on ecosystem resilience (Zhang et al. 2015). These stressors will act in synergism on the Amazon fauna, which is already intrinsically vulnerable to climate change (Pacifici et al. 2018). Therefore, our projections are probably conservative, as we did not consider these effects in synergism.

In conclusion, we show that the outcome of climate change on species distribution will be highly dependent on the existence of permeable landscapes across the potential migratory routes. If Amazonian primates were able to disperse towards suitable environments, most species would cope with the effects of climate change redistributing. However, deforestation leads to, among other things, disruption of migratory routes to arboreal and canopy-dependent species, such as the Amazon primates, confining them to areas that might become unsuitable. Conflict zones between biodiversity redistribution and human development will lay outside the network of protected areas in the Amazon, so the potential for conservation units to work as 'stepping stones' is limited. If species are not able to migrate in response to climate change, exposure to non-analogue climates will likely have deleterious effects on population fitness. Considering the need for climate-driven dispersal, the planning of conservation corridors could enhance permeability of future landscapes and allow successful migrations towards suitable climates in the future. This could prevent population declines or the extinction of some of the unique primates in the Amazon region.

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Supplementary material (available online as Appendix ecog-04499 at <www.ecography.org/appendix/ecog-04499>). Appendix 1.