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Strategies for mammal conservation under climate change in the Amazon

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Abstract Climate change is not only a major threat to biodiversity, it is also a big challenge to the development of conservation strategies. Scientists and practitioners need to select or avoid areas at greatest risk for species protection, i.e., acting in a proactive or a reactive manner. This proactive/reactive dichotomy takes a particular formulation under the likely changes in climate. Selecting for low-risk areas (usually referred to as climate refugia) is supposed to protect more species with a greater guarantee of their long-term persistence. As a consequence, populations at greatest risk are left unprotected and probably committed to extinction. On the other hand, managing species in high-risk areas is more expensive than setting aside areas of climate refugia and encompasses a set of uncertainties, which makes highly-threatened species more costly and difficult to save. Here, we combine ecological niche models and metrics of climate change to develop spatial conservation schemes for mammals in the Brazilian Amazon. These schemes efficiently identify networks of high-risk and refugia priority areas within species current and future distributions, while complementing the protection already achieved by the Amazon's network of protected areas (PAs). We found that, on average, 25% of mammal distribution is already represented in the established network of PAs. Also, 26% of high-risk and 17% of refugia priority areas overlap with indigenous lands. In addition, species distributions were found

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mostly in high-risk, compared to in refugia priority areas. We highlight that the strategy to be employed does not necessarily should be binary and a mix of both strategies would guarantee the protection of a larger number of species.

Keywords Climate change adaptation · Climate vulnerability · Global changes · Spatial conservation planning · Refugia · Threatened species

Introduction

Human-induced climate change is a major threat to biodiversity for the coming century (Pereira et al. 2010; IPCC 2014a). Predicted impacts of climate change on species range from changes on population abundance (Parmesan 2006; Cruz-McDonnell and Wolf 2016), distribution shifts mainly towards higher latitudes and elevated regions (Parmesan et al. 2003), changes on species' interactions and community composition (Diniz-Filho et al. 2009; Walther 2010), as well as species extinctions when those species are unable to keep pace with their suitable climate or locally adapt to new climatic conditions (Sinervo et al. 2010).

Climate change is not only a major threat to biodiversity but is also a big challenge to the usual approaches employed by scientists and practitioners when planning for biodiversity conservation. Under the climate change perspective, conservation studies have focused on identifying climatically stable areas over time; these are low-risk areas that would potentially serve as climate refugia to species and habitats; i.e., a refugia strategy (Killeen and Solórzano 2008; Carroll et al. 2010; Ashcroft et al. 2012; Loyola et al. 2012, 2013; Terribile et al. 2012; Watson et al. 2013; Schmitz et al. 2015). Such an approach is based on the assumption that species are more likely to persist in less climatically impacted areas, thereby increasing the likelihood of success of limited investments in conservation and maximizing conservation returns (Bottrill et al. 2008). However, this approach usually implies choosing areas where species would be less impacted at the expense of areas where species will suffer more with climate change. As a consequence, populations and species inhabiting impacted regions are left unprotected and might be pushed to extinction.

Guiding conservation efforts only towards areas of climate refugia may be an unreliable choice in some cases. Tropical species, for example, are expected to face the fastest rates of climate change, which may outpace species' abilities to disperse to new favorable climatic areas to cope with changes in climate (Loarie et al. 2009). Beyond the high rates of climate change expected in the tropics, tropical species also experience current climate conditions close to their physiological tolerance limits (Deutsch et al. 2008; Sunday et al. 2014). Exceeding those climatic thresholds may lead to fitness reduction or even extinction (Deutsch et al. 2008; Huey et al. 2012; Kingsolver et al. 2013; Khaliq et al. 2014; Sinervo et al. 2010). Ultimately, their ability to locally adapt to new climate conditions may be diminished by other pressures, such as habitat loss and degradation (Malhi et al. 2008). Therefore, not targeting conservation actions for species at a greater risk means accepting the inevitability of their extinction (Jachowski and Kesler 2009).

With the fastest rates of climate change expected in the tropics (IPCC 2013), along with species' high sensitivity and reduced adaptive capacity (Foden et al. 2013) in this region, decision makers face the challenge of selecting or avoiding the areas at the greatest risk for species as conservation priority (Boon and Beger 2016). Trade-offs cannot be avoided when it comes to biodiversity conservation. Given the limited conservation resources,

deriving more resources to some species implies that other species may receive inadequate investment (Bottrill et al. 2008). Thus, probably the best way forward is to develop conservation metrics that quantitatively assess the trade-offs between strategies, supporting decision makers with reliable information about which adaptation actions are most needed to overcome the threats posed by climate change and where they are most appropriate (Ladle and Whittaker 2011).

In this study, we developed a comprehensive spatial conservation scheme for the Brazilian Amazon to identify the areas on the extremes of a continuum spatial gradient of species' vulnerability to climate change (Watson et al. 2013). At one extreme, we targeted conservation investment to high-risk areas harboring highly vulnerable species that have the most pressing needs for adaptation (something like a reactive approach in conservation prioritization; see Brooks et al. 2006). At the other extreme, we identified priority areas for conservation investment in climatic refugia, which are supposed to safeguard species' long-term persistence (resembling a proactive approach). Hence, our work identifies networks of high-risk and refugia priority areas within species' current and future distributions, while complementing the species protection level already achieved by the Amazon's network of protected areas (PAs). We then evaluated the trade-off of choosing one of those two strategies by comparing species' representation in high-risk and refugia priority areas. Furthermore, we sought to identify more robust spatial schemes by including in our prioritization both important areas to increase the connection between current and future species' distribution and uncertainties associated with alternative climate model projections.

Methods

Scope of study

The Brazilian Amazon holds one of the largest systems of PAs worldwide covering about 1,174,258 km^2 or 23.5% of its surface (Veríssimo et al. 2011). Nevertheless, increasing temperature and rainfall reductions, along with other non-climate threats, such as fires and deforestation, make the Amazon one of the earth's regions most impacted by climate change (Garcia et al. 2014). We might witness a set of expected future impacts on the Amazon, from extreme climatic events (i.e., droughts and floods; Brando et al. 2014; Gloor et al. 2015) to upward species dispersal, mainly towards the mountains (e.g., the Andes), which could act as a climate refugia for species in the future (Parmesan et al. 2003; Morelli et al. 2016). The Amazon harbors the highest number of mammal species among all Brazilian regions, comprising 399 species (Paglia et al. 2012). We chose mammals as our study case because they are a well-studied taxa, their taxonomy is robust, and data on geographic distribution is widely available.

Ecological niche models (ENMs)

We obtained occurrence records for 399 mammal species inhabiting the Amazon (Paglia et al. 2012) from the Global Biodiversity Information Facility (GBIF; www.gbif.org), SpeciesLink project (www.splink.cria.org.br), VertNet (www.vertnet.org), and the Instituto Chico Mendes para Conservação da Biodiversidade (*Chico Mendes Institute for Biodiversity Conservation*——ICMBio; www.icmbio.gov.br/portal) databases. We only modeled the ecological niche of 256 species for which more than 10 independent records were

available. We superimposed species' records onto a grid of 0.083° × 0.083° of latitude/longitude (~ 9 km at the equator), covering the full extent of the Neotropics, given that some species occur beyond the Amazon's extent.

We obtained current bioclimatic variables (1950–2000) derived from monthly temperature and rainfall values from the WorldClim database (www.worldclim.org; version 1.4). We then selected 5 (mean diurnal range, isothermality, max temperature of warmest month, precipitation of wettest month, and precipitation of driest month) out of 19 variables for modeling species' ecological niches. These variables are directly related to species' biology and are often used to explain the pattern of mammal richness and distribution (e.g., Li et al. 2015). We also conducted a factor analysis with Varimax rotation based on the correlation matrix among variables to avoid any collinearity issues (see Supplementary Material, Table S1; Terribile et al. 2012).

We obtained these same climatic variables, with the same resolution as our grid, from future climate models (year 2050) from the WorldClim database (www.worldclim.org/cmip5_5m; version 1.4) derived from three coupled atmosphere–ocean general circulation models (AOGCMs; GISS-E2-R, HadGEM2-ES, MIROC5) under a high-emission greenhouse gases scenario (Representative Concentration Pathway 8.5). These future climate models were generated by applying the delta downscaling method on the original data used by the IPCC's Fifth Assessment Report (AR5; 2014a). We chose the RCP8.5 because actual emission rates since 2000 have been closest to this scenario and because only slight differences are observed among all RCPs by 2050 (Peters et al. 2011; Diffenbaugh and Field 2013; IPCC 2013).

We used the maximum entropy (Maxent; Phillips et al. 2006) modeling method to build species' ENMs. Maxent requires presence-only species' records to generate models and has shown a robust predictive performance compared to other high-performing methods, even with small samples (e.g., 10 records; Elith et al. 2006, 2010; Wisz et al. 2008). Prior to the analysis, we removed duplicates and checked for errors in species' records. These procedures reduce sample biases and improve model predictions (Elith et al. 2010). All models were created using the default settings in Maxent. For each species' model, we randomly split the presence and background data into two subsets for calibration (75%) and validation (25% remaining) and repeated this procedure five times (i.e., cross-validation), generating five niche models for each species for the current period. We projected a continuous model in the future using the three AOGCMs mentioned above and obtained 15 projections per species (5 models × 3 AOGCMs; Fig. 1). To convert the continuous predictions into binary ones, we used a threshold that maximizes sensitivity plus specificity values in a relative operating characteristic curve (Liu et al. 2005). Finally, we used true skill statistic to measure each model's performance (TSS, range from − 1 to + 1, where prediction values less than or equal to zero indicate a performance not better than random; Allouche et al. 2006).

We applied the ensemble-forecasting approach to produce more robust predictions by accounting for uncertainties arising from climate models (Araújo and New 2007; Diniz-Filho et al. 2009). The consensus maps for the current period and for each future climate model was performed by weighting each model according to its performance measured by TSS values (Allouche et al. 2006). Thus, models with the highest TSS values have a higher importance in the consensus model. All analyses were done in R version 3.2.2 (R Core Team 2015) using the packages biomod2 (Thuiller et al. 2009) and LetsR (Vilela and Villalobos 2015) and their dependencies.
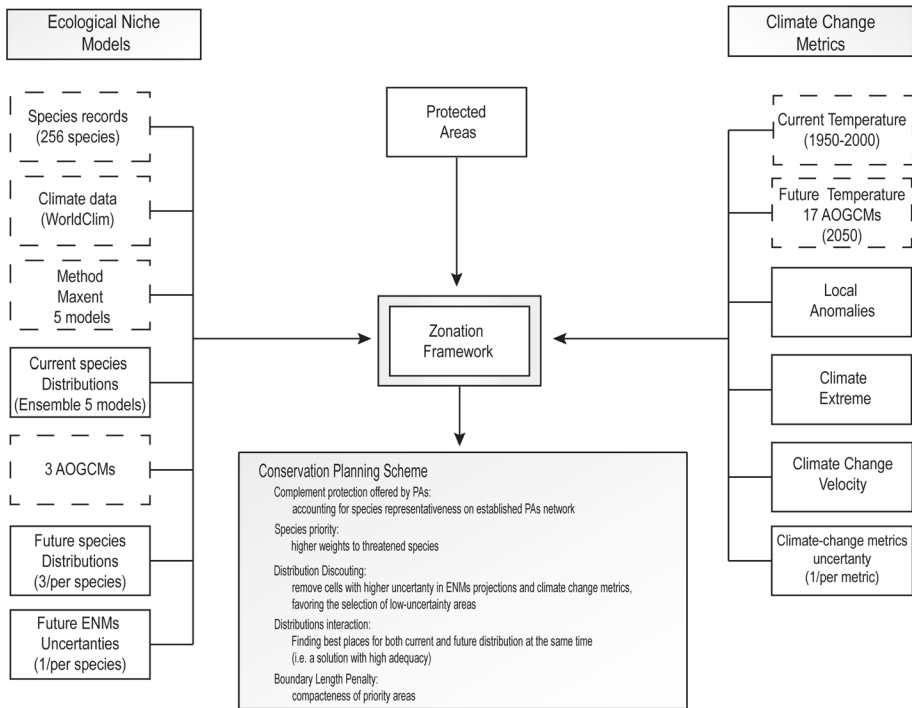
Fig. 1 A schematic representation of the methods used in our spatial conservation planning to identify sets of high-risk and refugia priority areas within mammal distributions in the Brazilian Amazon. Boxes with dashed line were used as primary data for the study, whereas boxes with continuous line were used as input in the Zonation software

Climate change metrics

We used the metrics of climate change to identify high-risk and refugia areas. No single metric can represent the multiple dimensions of climate change. Hence, we calculated the following climate change metrics, each one containing complementary information and different implications for conservation (see Garcia et al. 2014): (i) standardized local anomalies (Williams et al. 2007), (ii) climate extremes (Beaumont et al. 2011), and (iii) velocity of climate change (Hamann et al. 2015; Fig. 1). Standardized local anomalies and climate extremes metrics are mainly related to changes in average and extreme climates, with implications for local species' persistence (Ameca y Juárez et al. 2013; Garcia et al. 2014), whereas climate change velocity is a measure of the rate of climate displacement across the landscape and provides the speed at which species should move across the landscape to keep track of their suitable climates (Loarie et al. 2009).

All climate change metrics were calculated based on current monthly average temperatures (years 1950–2000) and 17 AOGCMs for the year 2050 (see Appendix 1) under a high greenhouse gas-emission scenario (RCP8.5) used by the IPCC's Fifth Assessment Report. Both current and future temperatures were gathered from the WorldClim database (www.worldclim.org; version 1.4) at the resolution of 0.083° × 0.083° of latitude/longitude.

We focused our calculations of climate change metrics on temperature mainly due to the wide uncertainty arising from future rainfall projections in the Amazon region (IPCC 2013). To reduce the uncertainty arising from contrasting AOGCMs, we generated ensemble and uncertainty maps for each climate change metric by calculating the mean and standard deviation (SD) from the 17 AOGCMs, respectively.

Local climate change anomalies were calculated using the difference between current and future temperature conditions weighted by SD of the current inter-annual variability, named standardized temperature difference (SED; Williams et al. 2007). Standardizing the inter-annual variability allows weighting climate trends that are larger compared to inter-annual variability. High SED scores indicate larger local temperature anomalies.

We assessed the extent to which areas in the Amazon will experience extreme mean annual temperatures compared to current climate conditions. We followed Beaumont et al. (2011) and assumed that a future temperature value projected for a certain locality (a single raster cell) may be considered "extreme" when it exceeded two SDs of current variability (see also Ribeiro et al. 2016).

We are aware of more sophisticated methods to identify climate extremes (i.e., extreme value theory; Katz et al. 2005; IPCC et al. 2012). Indeed, these methods are more useful when daily temperature data are available. However, temperatures exceeding 2SD of current values ($M > 2$) represent a good approximation for identifying extreme climate events (Luterbacher 2004; Beaumont et al. 2011) and fit the purpose of this work, as we are dealing with larger timescales.

Climate change velocity represents the rate (km/year) at which a climate condition is expected to shift along the landscape. Consequently, the velocity index also indicates the speed at which an organism must move to keep pace with changes in climate (Loarie et al. 2009; IPCC 2014b). We computed a "forward" climate change velocity by using a distance-based method that represents the shortest distance between a cell in the current climate conditions and a cell where analogous climate conditions will be found in the future (Hamann et al. 2015). See Appendix 1 for a more detailed explanation of the methods used to compute the metric of climate change velocity.

Spatial prioritization analysis

We used Zonation (Moilanen et al. 2005) to develop spatial prioritization schemes to guide conservation efforts toward high-risk or refugia areas facing climate change. Zonation delivers a complementarity-based and nested hierarchical rank of priority sites along the entire studied region (Moilanen et al. 2005). The Zonation method can be divided into two parts. First, it produces a priority ranking, which is generated by iteratively removing grid cells with the least marginal loss; in other words, those cells with the smallest contribution relative to the total conservation value of the region. Second is the cell removal procedure that defines the marginal loss. Here, we used the core-area Zonation removal rule, which emphasizes the selection of areas of high-quality habitats for the rarest and/or most highly weighted features (in our case, species and climate change metrics layers). Therefore, even generally poor-featured cells receive high conservation value if those features have small distribution or high weight (Moilanen et al. 2014).

We used the following primary data as input in the spatial prioritization analysis: (i) ensemble-based continuous suitability maps of the current and future species' distributions (512 layers total, for each current and future species' projected distribution), (ii) climate change metrics representing local anomalies, climate extremes and the velocity of climate

change (3 layers), (iii) species-specific future distribution uncertainty layers (SD) arising from niche models generated with 3 alternative AOGCMs (256 layers; 1 for each species) and, (iv) uncertainty layers related to each climate change metric arising from calculation based on 17 AOGCMs (3 layers; Fig. 1).

To define the priorities for conservation, we established different weights for species and climate change metrics. We assigned weights for species according to their conservation status defined by the Brazilian list of threatened species (see www.icmbio.gov.br/portal/especies-ameacadas-destaque, *in Portuguese*), which in turn is based on IUCN threat categories: non-threatened = 1, vulnerable = 1.25, endangered = 1.5, and critically endangered = 2. Following these weights, vulnerable species were considered 25% more important than non-threatened species in the prioritization process, endangered species were 50% more, and critically endangered species were twice as important as non-threatened species (this is because weights are multiplicative).

Since we aimed to identify areas at a higher risk of being impacted by climate change or areas regarded as climate refugia, we assigned a high weight to climate change metrics compared to species. For each metric of climate change, we assigned a weight resulting from the sum of all species' weights divided by three (resulting in a weight of 267.5 for each metric). To select areas with a higher risk, each climate metric received a positive weight (267.5), thus favoring the prioritization of areas at the greatest risk. By contrast, to avoid high-risk areas (i.e., to identify areas of climate refugia), climate metrics received a negative weight (− 267.5), thus avoiding the prioritization of areas at the greatest risk of climate change. Refugia priority areas were thus selected mainly according to both the level of species threatened and species' rarity, given that these traits received higher weights in the spatial analysis. The specific weight of each feature is an arbitrary choice, although the transformation of IUCN threat categories to an ordinal scale has already been used in other spatial planning analyses (Loyola et al. 2008; Lemes and Loyola 2013), including Brazilian government official plans (e.g., Loyola et al. 2014). We performed a sensitivity analysis to test how the different weight values given to climate change metrics affect the results of a spatial prioritization analysis. We found only slight differences in the prioritization plan results due to using different weights (see Supplementary Material, Table S5).

We also included the federal and state PAs already established in the Amazon as a mask in the spatial conservation analysis, which means that PAs are considered high-priority areas. Polygons of PAs' limits were gathered from databases available at the *Instituto Chico Mendes para Conservação da Biodiversidade* (the Chico Mendes Institute for Biodiversity Conservation; www.icmbio.gov.br/portal) and the Brazilian Ministry of Environment (www.mma.gov.br). According to these data, 23.5% of the Brazilian Amazon's extent is currently covered by PAs (Veríssimo et al. 2011). Considering PAs in our analysis means that our spatial conservation scheme indicates priority areas in which conservation actions should take place to complement the species' protection level already achieved in the region.

Finally, although they are not considered PAs by Brazilian law, Amazon indigenous lands are protected by Brazilian legislation and cover about 22% of the Amazon territory (Veríssimo et al. 2011). Therefore, to evaluate the overlapping pattern of priority areas resulting from our analysis, we superimposed our priority maps over Amazon indigenous lands. In doing so, we could evaluate the additional percentage of species' distribution of our priority maps (areas of risk and refugia) represented in indigenous lands and that complement the representation level already achieved in PAs.

We used a set of configurations in Zonation to produce a more robust spatial conservation scheme to identify high-risk and refugia priority areas (see Appendices 1 and 2 for

further details about the methods). To include uncertainties from alternative AOGCMs in our spatial analysis, we used the info-gap models in Zonation. Info-gap models penalize areas where predictions of species' distributions and changes in the climate are more contrasting due to the higher uncertainties arising from three AOGCMs. In doing so, we favored the selection of low-uncertainty areas, thus providing a more confident solution. We also used the Zonation distribution interactions component to produce more resilient solutions to climate change that account for species-specific connectivity requirements. This component sought to identify areas important to maintaining the connectivity between the current and future species' distributions (Rayfield et al. 2009; Carroll et al. 2010).

Results

Overall, the ENMs had high TSS values (0.65 ± 0.16), indicating good model fit, and for most species (60%), these values were higher than 0.7. Combined model projections indicated high species richness in the north of the Amazon and low species richness in the southern portions of the biome, both for the current time and for the year 2050 (Fig. 2a, b). Projections for 2050 forecasted a reduction in species richness within almost all regions of the Amazon, although some highly elevated regions, mainly those in the south Amazon, would gain species (Fig. 2b). In total, 50% of species are predicted to lose an average
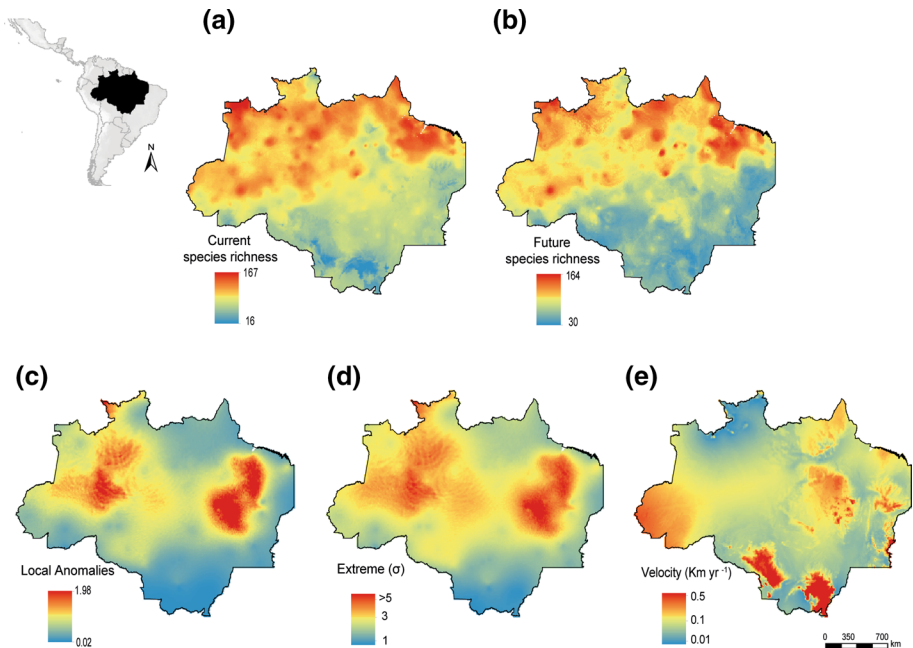
Fig. 2 Pattern of species richness for mammals in Brazilian Amazon and projected climate change according to three climate change metrics used in this study. **a**, **b** Patterns of mammal species richness projected for current (**a**) and future (year 2050, **b**) forecasted by ecological niche models. **c**–**e** Maps of projected changes in mean annual temperature between the current and future (year 2050) ensemble of climate models according to three climate-change metrics: standard local anomalies (**c**), climate extreme (**d**) and climate change velocity (**e**)

of 26% (± 9%) of their climatically suitable areas, whereas other species are expected to gain around 80% (± 21%) of climate suitable areas (Supplementary Material, Table S2). The variation among predicted future species' distributions has risen from alternative AOGCMs, which was low, and has mainly been concentrated on the Amazon River Basin (Supplementary Material, Fig. S2).

Climate change metrics depicted complementary information about climate-related exposure and local anomalies, and climate extremes showed a similar pattern compared to velocity (Fig. 2c–e). The northwest and the northeast are the portions of the Amazon expected to experience the highest local anomalies and climate extremes, which may exceed more than 5 σ of the current temperature variability (Fig. 2c, d). As expected, since climate velocity accounts for the heterogeneity of the landscape, high-elevation regions in the Amazon could experience high rates of temperature shift (Fig. 2e). This means that species inhabiting these areas should disperse at a rate of up to 0.5 km/year (around 5 km/decade) until 2050 to keep pace with their suitable temperatures. When comparing different conservation strategies (areas where species will be at higher risk and areas of climate refugia), some of the top-priority areas are located in the Amazon's "Arc of Deforestation"—a highly fragmented region of the Amazon and a frontier for agribusiness (Fig. 3; Pacheco 2009).

On average, more current and future species' distribution was found in high-risk areas than in refugia priority areas (Fig. 4). The representativeness of species in these two conservation strategies was uneven according to mammal orders and according to species' threat category (Fig. 5). Two primate species, *Ateles chamek* (the chamek spider monkey) and *Lagothrix lagotricha* (the common woolly monkey), represent a major concern for conservation because (i) they are already classified as threatened species, (ii) they had more than 40% of their distribution in high-risk areas, (iii) these species are likely to lose suitable climatic conditions in 2050, and (iv) they were poorly represented in both PAs and areas of climate refugia (see Supplementary Material, Fig. S2).

On average, 25% (± 4%) and 24% (± 4%) of the modeled current and future mammal distribution are already represented by the established network of PAs, respectively. These representation levels were well fitted among species according to their IUCN threat categories (Fig. 5a) and among mammal orders (Fig. 5b), although one species (*Tapirus terrestris*, the tapir) had approximately 10% of its distribution in PAs (Fig. 5b, Supplementary Material, Table S2).

Furthermore, we found that 26% of high-risk priority areas and 17% of refugia priority areas are covered by Amazon's indigenous lands. Those figures represent an extra of 6% (± 2%) and 4% (± 4%) of mammal representation in high-risk and refugia priority areas, respectively (Supplementary Material, Tables S3, S4). Therefore, a total of 30% (± 4%) of current and 28% (± 4%) of future species' distributions are represented by PAs and indigenous lands.

Discussion

The successful adaptation of natural systems to climate change will depend on the conservation managers' ability to identify areas at higher risk and areas of climate refugia, as well as their ability to point out which conservation actions will be better for alleviating the effects of climate change on biodiversity. Recent research has focused on identifying high-risk or refugia areas separately in different studies. As a consequence, decision-makers are not provided with sufficient and adequate information on how to scrutinize and explicitly

(a)

(b)
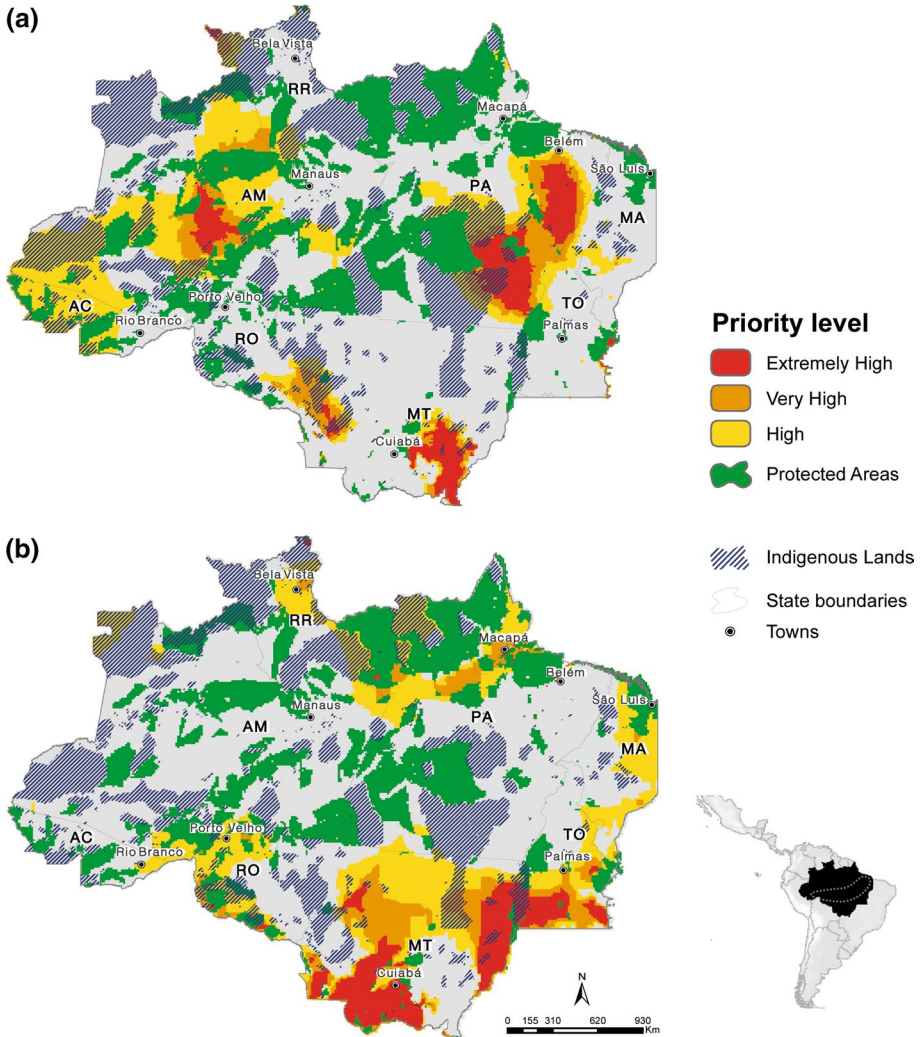
Fig. 3 Spatial distribution of priority areas of contrasting strategies to alleviate the impacts of climate change on mammal species in the Brazilian Amazon. **a** Areas at higher risk and **b** areas of climate refugia. Areas are classified according to the degree of priority to complement species representativeness already achieved in protected areas (PAs). Given that priority areas are nested, protected areas are contained within the 'extremely high' priority areas (PA + 5%) of the whole area, which are nested in the 'very high priority areas' (PA + 10%), which in turn is nested in 'high priority areas' (PA + 25%). The Amazon "arc of defor-estation" is shown in dashed gray lines

evaluate the trade-offs resulting from investing in one strategy over another and thus are more likely to make inefficient choices (Ladle and Whittaker 2011). Here, by combining ENMs for a large number of species and metrics of climate change, we were able to iden-tify a set of high-risk and refugia priority areas towards which conservation efforts should be targeted to reduce the impacts of climate change on mammals found in the Brazilian Amazon. Moreover, our scheme delivers an explicit and quantifiable way to compare the

Fig. 4 Performance curves quantifying the proportion (mean and standard deviation) of the distribution of 256 mammal species in the Amazon within each set of high-risk (dark red) and refugia (blue) priority areas. A hierarchical nested ranking of priority areas are shown so that protected areas are contained within the 'extremely high' priority areas (PA + 5%) of the whole area, which are nested in the 'very high priority areas' (PA + 10%), which in turn is nested in 'high priority areas' (PA + 25%). (Colour figure online)
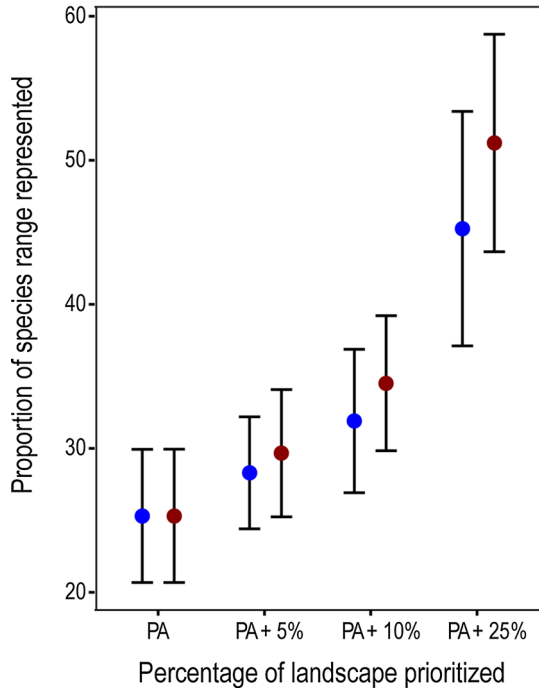

trade-offs between two strategies by assessing species' representation in high-risk and refugia priority areas.

The Amazon network of PAs has been established by reasons other than climate change (e.g., to avoid deforestation, Veríssimo et al. 2011); yet, we found that, on average, a quarter of current and future mammal distributions is already represented in this network. That representativeness implies that the large number of PAs—covering around 23% of the Brazilian Amazon—might compensate for the fact that several low-effective areas for biodiversity conservation are part of the network. While one should not overcome poor quality with greater quantity when it comes to biodiversity protection (Pressey et al. 2015), it seems that this situation establishes the current status quo of the Amazon network of PAs in Brazil (at least for mammals).

In addition to PAs, Amazon indigenous lands, although not legally regarded as PAs by the Brazilian law, shelter six and four percent of high-risk and refugia priority areas, respectively. These protection levels complement the species' protection already achieved by PAs and enhances it. Although climate change is a threat that PAs cannot stop (Araujo et al. 2004; Lemes et al. 2013), these areas play a fundamental role in safeguarding species against the effects of climate change and deforestation (Nepstad et al. 2006). The PAs are supposed to offer more ecological opportunities (e.g., different microclimatic conditions, reducing non-climatic stressors) essential for increasing species' resilience and their capacity to adapt to climate change, even when risks cannot fully be eliminated (IPCC 2014a, b; Lovejoy 2006).

Varied metrics of climate change hold complementary information about the challenges and opportunities for species (Garcia et al. 2014). Species exposed to local temperature anomalies exceeding current inter-annual variability are more likely to experience
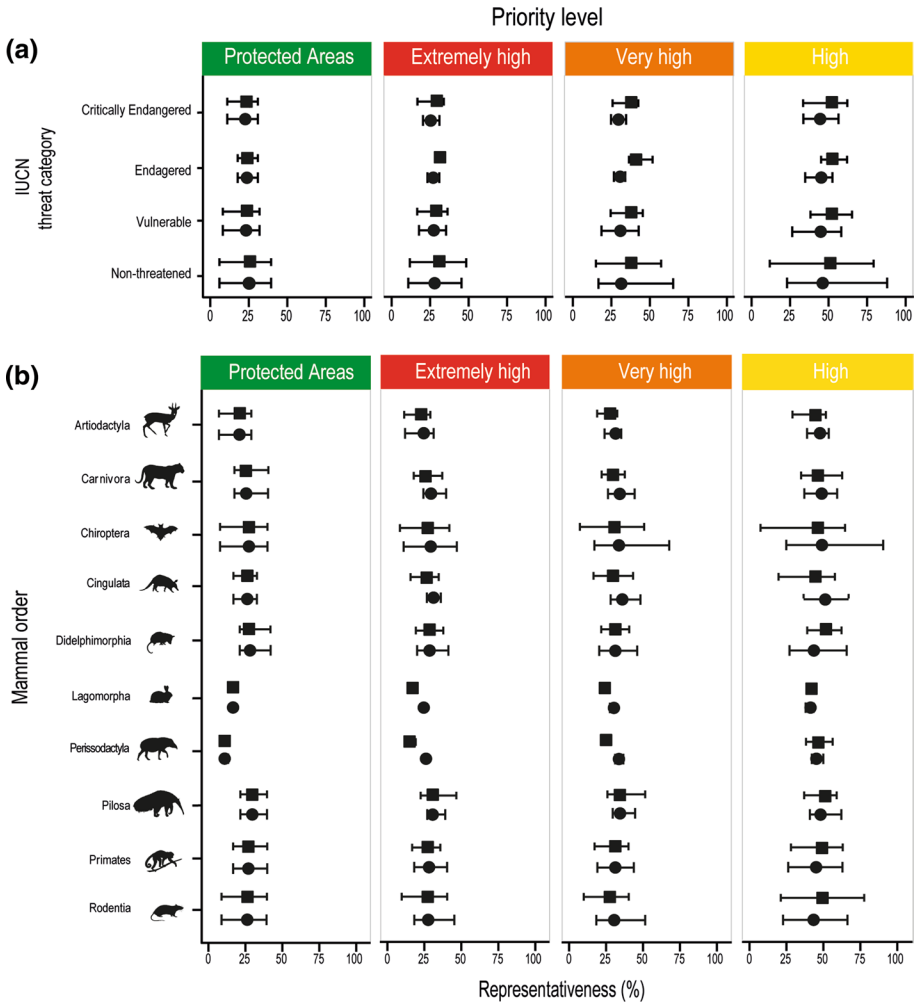
Fig. 5 Percentage (minimum, mean, and maximum values) of current and future (year 2050) species distributions represented in high-risk (square) and refugia (circle) priority areas for alleviating the impact of climate change on mammals in the Brazilian Amazon. Representation level is showed according to species' IUCN threat category (**a**) and taxonomic order (**b**) in each set of priority areas shown in Fig. 3. Given that priority areas are nested, protected areas are contained within the 'extremely high' priority areas (PA + 5%) of the whole area, which are nested in the 'very high priority areas' (PA + 10%), which in turn is nested in 'high priority areas' (PA + 25%). The Amazon "arc of deforestation" is shown in dashed gray lines

population declines (IPCC 2014b). Conversely, climate extremes are pervasive and, depending on their intensity and frequency, can drastically reduce population size (i.e., "population die-offs"; Ameca y Juárez et al. 2012). Furthermore, species occupying extensive flat areas or confined to isolated habitats (e.g., mountaintops) might be unable to move fast enough and cover longer distances to match changes in climate and thus more likely to experience range contractions (Garcia et al. 2014). Given that these three metrics represent the different dimensions of climate change, considering them in combination may be a

reasonable choice to decide where and which adaptation actions will be more appropriated and, consequently, more effective.

All particularities of tropical regions might make conventional conservation actions (such as establishing PAs or setting aside "climate refugia" in low-impacted areas) non-effective in the face of the large amount and high rate of climate change expected in these regions (IPCC 2013). We found that two mammal species represent major conservation concern in the face of climate change. Those species are already classified as threatened by the IUCN and might experience range contraction due to the loss of suitable climatic conditions. They are also poorly represented in PAs and in areas of climate refugia, and, more importantly, more than 40% of their distribution is present in high-risk areas. Aside from being threatened by climate change, these species are categorized as vulnerable and have experienced population reductions. While *Lagothrix lagotricha* has been systematically hunted for food (Peres 1991), *Ateles chamek*, although widely distributed in the Neotropics, is threatened mainly due to habitat deforestation.

One should ask, "What would have happened if there had been no conservation actions for the species most threatened by climate change?". Basically, there are two answers to that question: (i) We assume some loss and decide not to manage species perceived at the most risk, or (ii) we decide to enhance conservation actions through expanding the PA network, increasing landscape resilience and connectivity, mitigating other threats, implementing some kind of ex situ conservation, or implementing even more contentious strategies, such as the assisted translocation of species (see a review in Heller and Zavaleta 2009). The second answer to the question is arguably the only option that can make a difference for the conservation of species at the highest risk. The success of conservation actions depends on their ability to pre-empt future climate change to reduce impacts and to increase species' capacity to adapt to climate change.

Certainly, we do not advocate that all conservation strategies for protecting biodiversity under climate change should be directed to species in the areas at the greatest risk. Identifying and protecting areas of climate refugia is also paramount to increasing species' persistence under climate change and to improve the scope of natural adaptation (Game et al. 2011). However, given that financial resources addressed to conservation are scarce, a trade-off between investing finite conservation funds in low- versus high-risk areas exists and should be considered in conservation planning. Our spatial conservation scheme offers a way to identify a network of high-risk and refugia priority areas and explicitly quantifies the trade-offs related to species' representation in these areas. In addition, our approach is robust because it takes into account both uncertainties arising from alternative climate models and areas important to connecting species' current and future distributions.

Conservation planning is a fundamentally iterative process (Margules and Pressey 2000). A spatial conservation plan is paramount to developing a dynamic conservation strategy under climate change. This strategy, however, constitutes only one important source of information that, in a second planning phase, should be weighted and complemented with other non-climatic threats and socioeconomic concerns to develop a more comprehensive conservation plan (Knight et al. 2006). For instance, we found that some of the top-priority areas for both strategies are situated in the Amazon's "Arc of Deforestation", where most of the Brazilian Amazon deforestation occurs. That overlay probably implies greater conservation challenges and possibly conflicts with socioeconomic activities in these regions.

Selecting low-risk areas (i.e., climate refugia) is supposed to protect a larger number of species with a greater guarantee of their long-term persistence, thus maximizing conservation returns. This strategy, however, also implies that highly threatened species are

left unprotected and are allowed to pass to extinction (Jachowski and Kesler 2009). On the other hand, managing species in high-risk areas is more expensive than setting aside areas of climate refugia and encompasses a set of uncertainties (e.g., arising from species' future distribution, climate models, success of conservation actions), which makes highly threatened species more costly and difficult to save. The strategy to be employed should not necessarily be binary, however, and a mix of both strategies will guarantee the protection of a larger number of species. We have no reason to believe that one strategy is more appropriate than the other given that different adaptation strategies are needed for different species and areas. However, conservation managers and decision-makers will only make the best decision if they can explicitly evaluate and identify where and which adaptation strategy is the most appropriated to avoid species extinctions. Ultimately, successful adaptation will require not only a scheme to identify priority areas for conservation but an organized effort at a larger policy context to strengthen and implement the adaptation needs to climate change.

References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232

Ameca y Juárez EI, Mace GM, Cowlishaw G, Pettorelli N (2012) Natural population die-offs: causes and consequences for terrestrial mammals. Trends Ecol Evol 27:272–277

Ameca y Juárez EI, Mace GM, Cowlishaw G, Cornforth WA, Pettorelli N (2013) Assessing exposure to extreme climatic events for terrestrial mammals. Conserv Lett 6:145–153

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends Ecol Evol 22:42–47

Araujo MB, Cabeza M, Thuiller W, Hannah L, Williams PH (2004) Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob Change Biol 10:1618–1626

Ashcroft MB, Gollan JR, Warton DI, Ramp D (2012) A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. Glob Change Biol 18:1866–1879

Beaumont LJ, Pitman A, Perkins S, Zimmermann NE, Yoccoz NG (2011) Impacts of climate change on the world's most exceptional ecoregions. Proc Natl Acad Sci USA 108:2306–2311

Boon PY, Beger M (2016) The effect of contrasting threat mitigation objectives on spatial conservation priorities. Mar Policy 68:23–29

Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET, Grantham H, Kark S, Linke S, McDonald-Madden E, Pressey RL, Walker S, Wilson KA, Possingham HP (2008) Is conservation triage just smart decision making? Trends Ecol Evol 23:649–654

Brando PM, Balch JK, Nepstad DC, Morton DC, Putz FE, Coe MT, Silverio D, Macedo MN, Davidson EA, Nobrega CC, Alencar A, Soares-Filho BS (2014) Abrupt increases in Amazonian tree mortality due to drought–fire interactions. Proc Natl Acad Sci USA 111:6347–6352

Brooks TM, Mittermeier RA, da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. Science 313:58–61

Carroll C, Dunk JR, Moilanen A (2010) Optimizing resiliency of reserve networks to climate change: multi-species conservation planning in the Pacific Northwest, USA. Glob Change Biol 16:891–904

Cruz-McDonnell KK, Wolf BO (2016) Rapid warming and drought negatively impact population size and reproductive dynamics of an avian predator in the arid southwest. Glob Change Biol 22:237–253

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. Proc Natl Acad Sci USA 105:6668–6672

Diffenbaugh NS, Field CB (2013) Changes in ecologically critical terrestrial climate conditions. Science 341:486–492

Diniz-Filho JAF, Mauricio Bini L, Fernando Rangel T, Loyola RD, Hof C, Nogués-Bravo D, Araújo MB (2009) Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. Ecography 32:897–906

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JMcCM, Townsend Peterson A, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Foden WB, Butchart SHM, Stuart SN, Vié JC, Akçakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L, Donner SD, Katariya V, Bernard R, Holland RA, Hughes AF, O'Hanlon SE, Garnett ST, Şekercioğlu ÇH, Mace GM (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8:e65427

Game ET, Lipsett-Moore G, Saxon E, Peterson N, Sheppard S (2011) Incorporating climate change adaptation into national conservation assessments. Glob Change Biol 17:3150–3160

Garcia RA, Cabeza M, Rahbek C, Araújo MB (2014) Multiple dimensions of climate change and their implications for biodiversity. Science 344:1247579

Gloor M, Barichivich J, Ziv G, Brienen R, Schöngart J, Peylin P, Ladvocat Cintra BB, Feldpausch T, Phillips O, Baker J (2015) Recent Amazon climate as background for possible ongoing and future changes of Amazon humid forests. Glob Biogeochem Cycles 29:1384–1399

Hamann A, Roberts DR, Barber QE, Carroll C, Nielsen SE (2015) Velocity of climate change algorithms for guiding conservation and management. Glob Change Biol 21:997–1004

Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142:14–32

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos Trans R Soc B 367:1665–1679

IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5). Cambridge University Press, New York, 1535

IPCC (2014a) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change

IPCC (2014b) Summary for policy makers. Climate change 2014: impacts, adaptation and vulnerability—contributions of the Working Group II to the Fifth Assessment Report, p 1–32

IPCC, Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner G-K, Allen SK, Tignor M, Midgley PM (2012) Managing the risks of extreme events and disasters to advance climate change adaptation—SREX summary for policymakers

Jachowski DS, Kesler DC (2009) Allowing extinction: should we let species go? Trends Ecol Evol 24:180

Katz RW, Brush GS, Parlange MB (2005) Statistics of extremes: modeling ecological disturbances. Ecology 86:1124–1134

Khaliq I, Hof C, Prinzinger R, Böhning-Gaese K, Pfenninger M (2014) Global variation in thermal tolerances and vulnerability of endotherms to climate change. Proc Biol Sci R Soc 281:20141097

Killeen TJ, Solórzano LA (2008) Conservation strategies to mitigate impacts from climate change in Amazonia. Philos Trans R Soc Lond B 363:1881–1888

Kingsolver JG, Diamond SE, Buckley LB (2013) Heat stress and the fitness consequences of climate change for terrestrial ectotherms. Funct Ecol 27:1415–1423

Knight AT, Cowling RM, Campbell BM (2006) An operational model for implementing conservation action. Conserv Biol 20:408–419

Ladle R, Whittaker R (eds) (2011) Conservation biogeography. Wiley-Blackwell, Oxford

Lemes P, Loyola RD (2013) Accommodating species climate-forced dispersal and uncertainties in spatial conservation planning. PLoS ONE 8:e54323

Lemes P, Melo AS, Loyola RD (2013) Climate change threatens protected areas of the Atlantic Forest. Biodivers Conserv 23:357–368

Li Y, Li X, Sandel B, Blank D, Liu Z, Liu X, Yan S (2015) Climate and topography explain range sizes of terrestrial vertebrates. Nat Clim Change. https://doi.org/10.1038/nclimate2895

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. Nature 462:1052–1055

Lovejoy TE (2006) Protected areas: a prism for a changing world. Trends Ecol Evol 21:329–333

Loyola RD, de Oliveira G, Diniz-Filho JAF, Lewinsohn TM (2008) Conservation of Neotropical carnivores under different prioritization scenarios: mapping species traits to minimize conservation conflicts. Divers Distrib 14:949–960

Loyola RD, Lemes P, Faleiro FV, Trindade-Filho J, Machado RB (2012) Severe loss of suitable climatic conditions for marsupial species in Brazil: challenges and opportunities for conservation. PLoS ONE 7:e46257

Loyola RD, Lemes P, Nabout JC, Trindade-Filho J, Sagnori MD, Dobrovolski R, Diniz-Filho JAF (2013) A straightforward conceptual approach for evaluating spatial conservation priorities under climate change. Biodivers Conserv 22:483–495

Loyola R, Machado N, Vila-Nova DA, Martins E, Martinelli G (2014) Áreas prioritárias para conservação e uso sustentável da flora brasileira ameaçada de extinção. Andrea Jakobsson Estúdio: Instituto de Pesquisas Jardim Botânico, Rio de Janeiro

Luterbacher J (2004) European seasonal and annual temperature variability, trends, and extremes since 1500. Science 303:1499–1503

Malhi Y, Roberts JT, Betts RA, Killeen TJ, Li W, Nobre CA (2008) Climate change, deforestation, and the fate of the Amazon. Science 319:169–172

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253

Moilanen A, Franco AMA, Early RI, Fox R, Wintle B, Thomas CD (2005) Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc R Soc Biol Sci 272:1885–1891

Moilanen A, Veach V, Meller L, Arponen A, Kujala H (2014) Zonation—spatial conservation planning methods and software. Version 4. User manual

Morelli TL, Daly C, Dobrowski SZ, Dulen DM, Ebersole JL, Jackson ST, Lundquist JD, Millar CI, Maher SP, Monahan WB, Nydick KR, Redmond KT, Sawyer SC, Stock S, Beissinger SR (2016) Managing climate change refugia for climate adaptation. PLoS ONE 11:e0159909

Nepstad D, Schwartzman S, Bamberger B, Santilli M, Ray D, Schlesinger P, Lefebvre P, Alencar A, Prinz E, Fiske G, Rolla A (2006) Inhibition of Amazon deforestation and fire by parks and indigenous lands. Conserv Biol J Soc Conserv Biol 20:65–73

Pacheco P (2009) Agrarian reform in the Brazilian Amazon: its implications for land distribution and deforestation. World Dev 37:1337–1347

Paglia AP, da Fonseca GAB, Rylands AB, Herrmann G, Aguiar LMS, Chiarello AG, Leite YLR, Costa LP, Siciliano S, Kierulff MCM, Mendes SL, da Tavares VC, Mittermeier RA, Patton JL (2012) Lista Anotada dos Mamíferos do Brasil 2ª Edição

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pereira HM, Leadley PW, Proença V, Alkemade R, Scharlemann JPW, Fernandez-Manjarrés JF, Araújo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guénette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496–1501

Peres CA (1991) Humboldt's woolly monkeys decimated by hunting in Amazonia. Oryx 25:89–95

Peters GP, Marland G, Le Quéré C, Boden T, Canadell JG, Raupach MR (2011) Rapid growth in CO_2 emissions after the 2008–2009 global financial crisis. Nat Clim Change 2:2–4

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Pressey RL, Visconti P, Ferraro PJ (2015) Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. Philos Trans R Soc Lond B 370:20140268

R Core Team (2015) R: A language and environment for statistical computing. In: R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Rayfield B, Moilanen A, Fortin M-J (2009) Incorporating consumer–resource spatial interactions in reserve design. Ecol Model 220:725–733

Ribeiro BR, Sales LP, De Marco P, Loyola R (2016) Assessing mammal exposure to climate change in the Brazilian Amazon. PLoS ONE 11:e0165073

Schmitz OJ, Lawler JJ, Beier P, Groves C, Knight G, Douglas ABJ, Bullock J, Johnston KM, Klein ML, Muller K, Pierce DJ, Singleton WR, Strittholt JR, Theobald DM, Trombulak SC, Trainor A (2015) Conserving biodiversity: practical guidance about climate change adaptation approaches in support of land-use planning. Nat Areas J 35:190–203

Sinervo B, Mendez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, Villagran-Santa Cruz M, Lara-Resendiz R, Martinez-Mendez N, Calderon-Espinosa ML, Meza-Lazaro RN, Gadsden H, Avila LJ, Morando M, De la Riva IJ, Sepulveda PV, Rocha CFD, Ibarguengoytia N, Puntriano CA, Massot M, Lepetz V, Oksanen TA, Chapple DG, Bauer AM, Branch WR, Clobert J, Sites JW (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328:894–899

Sunday JM, Bates AE, Kearney MR, Colwell RK, Dulvy NK, Longino JT, Huey RB (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc Natl Acad Sci USA 111:5610–5615

Terribile LC, Lima-Ribeiro MS, Araújo MB, Bizão N, Collevatti RG, Dobrovolski R, Franco AA, Guilhaumon F, Lima JDS, Murakami DM, Nabout JC, De Oliveira G, De Oliveira LK, Rabelo SG, Pires M, Telles DC, Diniz-Filho JAF (2012) Areas of climate stability of species ranges in the Brazilian Cerrado: disentangling uncertainties through time. Nat Conserv 10:152–159

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD – a platform for ensemble forecasting of species distributions. Ecography 32:369–373

Veríssimo A, Rolla A, Vedoveto M, Futada SDM (2011) Protected areas in the Brazilian Amazon: challenges and opportunities. http://hdl.handle.net/11465/1216

Vilela B, Villalobos F (2015) letsR: a new R package for data handling and analysis in macroecology. Methods Ecol Evol 6:1229–1234

Walther G-R (2010) Community and ecosystem responses to recent climate change. Philos Trans R Soc Lond B 365:2019–2024

Watson JEM, Iwamura T, Butt N (2013) Mapping vulnerability and conservation adaptation strategies under climate change. Nat Clim Change 3:989–994

Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. Proc Natl Acad Sci USA 104:5738–5742

Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14:763–773