

ECOGRAPHY

Research

30% land conservation and climate action reduces tropical extinction risk by more than 50%

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Limiting climate change to less than 2°C is the focus of international policy under the climate convention (UNFCCC), and is essential to preventing extinctions, a focus of the Convention on Biological Diversity (CBD). The post-2020 biodiversity framework drafted by the CBD proposes conserving 30% of both land and oceans by 2030. However, the combined impact on extinction risk of species from limiting climate change and increasing the extent of protected and conserved areas has not been assessed. Here we create conservation spatial plans to minimize extinction risk in the tropics using data on 289 219 species and modeling two future greenhouse gas concentration pathways (RCP2.6 and 8.5) while varying the extent of terrestrial protected land and conserved areas from <17% to 50%. We find that limiting climate change to 2°C and conserving 30% of terrestrial area could more than halve aggregate extinction risk compared with uncontrolled climate change and no increase in conserved area.

Keywords: area-based conservation, biodiversity, climate change, conservation planning, extinction risk



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Introduction

Preventing human-driven extinctions of the species sharing the planet with us is among the greatest environmental challenges of our time (Ehrlich and Mooney 1983, Rockström et al. 2009). The Convention on Biological Diversity (CBD) has been agreed by 195 nations to require ‘...maintenance and recovery of viable populations of species’ for the conservation of biodiversity (Convention on Biological Diversity 1992). In the first draft of the post-2020 biodiversity framework developed by the CBD, extinction risk reduction is a goal for 2030 to achieve the longer-term 2050 vision of a world of ‘living in harmony with nature’ (CBD Secretariat 2020). Global extinction rate is a benchmark for planetary boundaries, defining both the sixth mass extinction event and a possible boundary for the Anthropocene geological epoch (Rockström et al. 2009, Dirzo et al. 2014, Ceballos et al. 2015).

Conservation of natural areas and sustainable use of nature are recognized as important instruments with which extinctions and other loss of biodiversity may be avoided (Convention on Biological Diversity 1992). A key target of the draft post-2020 biodiversity framework is to conserve sites of importance for biodiversity through protected and conserved areas covering at least 30% of land and ocean (CBD Secretariat 2020). On land, both conservation and sustainable use are currently challenged by increasing large-scale monoculture and industrial developments, (Austin et al. 2017) making some form of conservation or land-use management essential to realizing these aims in most regions. Without such conservation, loss of species’ habitats will result in increased extinction risk.

In addition to the local-to-global benefit of reducing extinctions and maintaining biodiversity, maintaining natural systems provides a wealth of benefits at all scales. A well-managed system of conserved areas can provide vital ecosystem services, such as water purification and retention, erosion control, the reduction of flooding, maintaining river base flows and opportunities for ecotourism as well as minimizing extinctions (Dudley and Stolton 2003, Mulongoy and Gidda 2008). For example, protected areas containing forests provide an important supply of drinking water to more than a third of the world’s 100 largest cities (Dudley and Stolton 2003). The conservation and effective management of natural areas is currently recognized as an important nature-based solution for climate change mitigation (Griscom et al. 2017, Dudley et al. 2018, Marquet et al. 2019); these areas account for approximately 20% of the CO₂ sequestered by all terrestrial ecosystems (Melillo et al. 2016).

Climate change is now altering ecological conditions across the planet, both on land and in the oceans, and species are shifting their distributions in response to these new conditions (Bellard et al. 2012, Urban 2015, IPBES 2019). Species’ distributions are determined by a combination of climatic and other niche tolerances (including edaphic), geographical barriers and competition, so shifting climatic

conditions result in changes in the areas occupied by species, altering representation in conserved areas and changing or reducing ecosystem benefits (Foden et al. 2007, Lenoir et al. 2008, Pecl et al. 2017). Climate change is causing some species to shift their distributions out of existing conserved areas (Araújo et al. 2004, Heller and Zavaleta 2009, Johnston et al. 2013, Urban 2015), while also enabling some species to colonize new areas (Chen et al. 2011, Angelo and Daehler 2013). Species’ climate niches are unique, meaning that species move individually in response to climate change. Species will be moving at different rates and in different directions, resulting in altered combinations of species in any one location over time.

The interaction between climate change and complex landscapes makes knowing where to conserve species more complicated. Conservation plans that minimize area requirements based on species’ current locations and habitat requirements will no longer be effective as those locations and habitats change. Establishing protected and conserved areas in the right places to facilitate species’ distributional shifts through time can help avoid extinctions due to climate change (Williams et al. 2005, Hannah et al. 2007, Phillips et al. 2008, Alagador et al. 2016, Bagchi et al. 2018). Until now it is unknown how much extinction risk reduction is possible under different extents of conserved area considering the effects of both land use change and climate change (though see Baillie and Zhang 2018).

To address these questions, we created conservation spatial plans for 289 219 tropical plant and vertebrate species that minimized both present and modeled future extinction risk under two greenhouse gas concentration pathways – RCP2.6 and 8.5 – across varying area of terrestrial conservation, from current levels up to 50% conserved, including 30% conserved as suggested in the draft post-2020 framework (CBD 2020). We used widely available vertebrate distribution and occurrence data as well as the most up-to-date compilation of terrestrial plant data (Enquist et al. 2019). Extinction risk results are expressed as the mean, maximum and minimum of our 10-climate model ensemble. Extinction risk can be assessed in multiple ways. The IUCN Red List classifies species into different categories of relative extinction risk, while multiple modeling approaches exist for estimating probability of extinction including the species area relationship (SAR). The Zonation conservation planning software (Moilanen et al. 2014) incorporates SAR theory to produce estimates of extinction risk for every species. We sum these values across species to calculate an aggregate extinction risk (AER), ranging from 0 if no species are at risk to 1 if all species have gone extinct). We then summarize this for three major tropical biogeographic regions – the Neotropics, Afrotropics, and Southeast Asian tropics for both climate scenarios and conservation from present to 50% of terrestrial area. This allows us to assess, for the first time, which natural areas are required to minimize extinction risk of tropical species in the face of climate change and how much extinction risk we may avoid by conserving additional area.

Material and methods

Overview

We modelled present and future geographic ranges of 94 337 plant species and 9722 vertebrate species across the Neotropics, Afrotropics and Southeast Asian tropics. Our methods are described in detail below, under the following: 1) climate models and RCPs – we used 10 GCM selected to be consistent across the three regions and two RCP (2.6 and 8.5) to provide low and high brackets of future climate; 2) spatial planning algorithm – we used Zonation conservation planning software with settings customized to accommodate range shifts under climate change; 3) extinction risk calculation – we used an AER index equal to the sum of individual species' extinction risks, based on SAR; 4) species distribution models – we used Maxent (Phillips et al. 2006) to fit species distribution models at 30 arc-second (~1 km) resolution then project distributions into baseline climate all future climate scenarios at 2.5 arc-minutes (~5 km) for analysis; 5) environmental predictor variables – were taken from standard WorldClim variables plus a custom aridity index; 6) soils data – global soilgrids variables; 7) land use and land cover data – from global consensus landcover dataset; 8) plant data – we used botanical occurrence data assembled and standardized within the BIEN database; 9) vertebrate data – we used publicly available occurrence records verified with IUCN expert range polygons. Details are given below for each of these methods.

Climate models and RCPs

We used 10 GCMs and two climate scenarios for the 2060–2080 timeframe. The GCMs used to drive our biological models include Access 1.0, BCC-CSM1.1, CNRM-cm5, GFDL-cm3, MOHC-HADGEM2-es, NCAR-CCSM4, LASG-FGOALS-g2, NCC-NORESM-m, MIROC-ESM and MPI-ESM-lr. We used a low forcing scenario, RCP2.6, to approximate climate change consistent with meeting the Paris Agreement target of 2.0°C global mean temperature change, and RCP8.5 to approximate business-as-usual, no action on climate change.

Spatial planning algorithm

We used the Zonation Conservation Planning Software ('Zonation'), a tool that allows for simultaneous prioritization of many thousands of conservation features (Moilanen et al. 2005, Moilanen 2007). We applied Zonation at a horizontal spatial resolution of 2.5 arc-minutes (~5 km). Zonation can be used for conservation prioritization under climate change. This configuration of Zonation allows for simultaneous prioritization of a species current range, its modelled future range, and the connectivity between the two limited by a species' capacity to disperse. The protocol for running Zonation

under climate change projections is described in Kujala et al. (2013). Species current ranges were linked to projected future ranges through an interaction layer (Kujala et al. 2013). This layer is transformed by a dispersal kernel with a parameter to limit the interaction to the species total capacity to disperse over the period of analysis. Total dispersal capacity was assumed to be 100 km for vertebrates (roughly 1 km year⁻¹) and 10 km for vascular plants (roughly 0.1 km year⁻¹) following previously published studies (Warren et al. 2013). Species with too few occurrence records to produce a model were included as point locations (Zonation term = 'species of special interest' or SSI) where the range was defined as each grid cell containing ≥1 occurrence record. Equal weighting was used for all conservation features.

Extinction risk calculation

Zonation/climate seeks to maximize biodiversity representation – both present and future – and thereby minimize extinction risk, at each area increment, based on a power-law species area relationship (SAR) parameter that can be set for each conservation feature. Here we used the default SAR parameter ($z=0.25$) for all areas in order to transform of the proportion of species ranges conserved at each step of the solution to the per species extinction risk where:

$$\text{Extinction risk} = 1 - (\text{Proportion conserved} ^{0.25})$$

To summarize over all species at different time steps, we calculated aggregate extinction risk (AER) at each step as the sum of individual species' remaining extinction risk across all species normalized by the total number of species.

Species distribution models

Species distribution models were produced with Maxent (Phillips et al. 2006) for species with >10 unique occurrence records (i.e. unique 1 km grid cells in the modelling domain) (van Proosdij et al. 2016). Maxent settings followed the recommendations of Merow et al. (2013, 2014) to produce relatively less complex models (e.g. limiting features to linear, quadratic, and product functions) to minimize overfitting. Modelling domains were limited to a spatial buffer of within 500 km of any valid occurrence record. This likewise limited the projected ranges to within 500 km of any verified observation. Background sampling was a random sample of 10 000 points within the buffered modelling domain. Five model replicates were used in fitting the model and an average of the five replicates was used for the final species model. Parameters from the final model were used to project species suitability for both baseline and future climate scenarios. Default values for regularization coefficients were used and 30% of occurrence records were randomly reserved to assess model performance.

Environmental predictor variables

We chose the following bioclimatic variables from downscaled 20-year normals (Hijmans et al. 2005) baseline (1960–1990) and future (2060–2080) climates based on pan-tropical correlation analysis: mean annual temperature (BIO1), mean diurnal temperature range (BIO2), seasonality of temperature (BIO4), minimum temperature of the coldest month (BIO6), mean annual precipitation (BIO12), seasonality of precipitation (BIO15). We also used an accumulated aridity index that is the sum of the monthly aridity (annual precipitation – PET) for the maximum run of consecutive months where (PET > precipitation). Accumulated aridity index is derived from global monthly extra-terrestrial solar radiation data from Trabucco and Zomer (2019) and monthly maximum temperature, minimum temperature and precipitation from Worldclim ver. 1.4 (Hijmans et al. 2005).

Soils data

Soils variables used in species distribution models were depth to bedrock, pH, clay proportion, silt proportion and bulk density. All soil-related variables were obtained from Soilgrids ver. 1.0 (accessed February 2018) (Hengl et al. 2017). Variables with multiple strata available are the mean of the top 1 m (strata 1–4). Soils variables were included as it has been shown that climate change analyses that do not incorporate soils variability can misrepresent edaphic specialists (Corlett and Tomlinson 2020).

Land cover and land use data

Areas of existing built up land or intensive agriculture were removed from the analysis and therefore those cells are not part of the prioritization solution. Built up and agricultural areas were defined as >50% of pixel coverage for 'urban' and 'agriculture' classes from the 1 km resolution global consensus land cover dataset produced by Tuanmu and Jetz (2014) that were aggregated to match the 2.5 arc-minute resolution of analysis. Existing protected areas (IUCN and WCMC 2018) were solved first using a hierarchical mask so that the conservation priorities take the effects existing protection into account. The analysis domain was limited to the Afrotropics, Neotropics and Indo-Malayan biogeographic realms with the Indonesian plus Papua New Guinea portion of the Australasian realm also included in the Asia domain (Dinerstein et al. 2017).

Plant data

Vascular plant data was extracted from the BIEN ver. 4.1 database using the RBIEN package (Maitner et al. 2018). Occurrence records with geographic information were obtained for 275 372 species of which we modelled 94 337. The BIEN data mainly comprise herbarium collections, ecological plots and surveys (DeWalt et al. 1999, Wisser et al. 2001, Enquist & Boyle 2012, Enquist et al. 2016,

Fegraus 2012, Peet et al. 2012, Forest Inventory and Analysis National Program 2013, Anderson-Teixeira et al. 2015). For details of specimen data sources see Maitner et al. (2018). A full listing of the herbaria data used are given in the Acknowledgements section. The observations in the BIEN database are the product of contributions by 1076 different data contributors, including numerous individual herbaria, and data indexers of herbarium or plot data. Of the herbaria, 550+ are listed in Index Herbariorum. Additionally, BIEN 4.1 includes data from RAINBIO, TEAM, The Royal Botanical Garden of Sydney, Australia, and NeoTropTree. Plot data within BIEN are from the CVS, NVS, SALVIAS, VEGBANK, CTFS, FIA, MADIDI, and TEAM data networks and datasets (<<http://bien.nceas.ucsb.edu/bien/data-contributors/all/>>).

Vertebrate data

Point occurrences for tropical vertebrate species were compiled from GBIF (GBIF download 2019; accessed through R package 'rgbif') and restricted range bird species records (Birdlife International 2018) were combined for a total of 13 847 tropical species, 9722 of which had sufficient occurrence records (>10) for modelling (van Proosdij et al. 2016). Occurrences were filtered to include only those with specific georeferencing coordinates, observations more recent than 1950, and human observations only (no fossil records or museum specimens). Additionally, spatial outliers (more than 500 km from IUCN range polygon or >98th percentile of latitude + longitude) were removed prior to modelling. IUCN and Birdlife International range map polygons for all available terrestrial mammals, birds, reptiles were used to generate the species list and as a means of occurrence record validation (Birdlife International 2018, IUCN and UNEP WCMC 2018).

Results

Our results show that a large reduction in extinction risk can be achieved by moving to a world in which 30% or 50% of terrestrial area is conserved, corresponding to the proposed action targets of the first draft post-2020 CBD framework (CBD 2020). Figure 1 illustrates the modeled reduction in aggregate extinction risk with increasing area conserved, for the Neotropics, Afrotropics and SE Asian tropics respectively. The reduction in extinction risk of up to 82% (ensemble mean) results from both reduced loss of habitat due to land use change and better representation of changing habitats for species moving in response to climate change. Outside of fully natural landscapes, achieving these minimum extinction results requires matching land uses to the habitat needs of species at risk of extinction in a particular area. For instance, shade coffee may provide habitat for many bird species, but not for understory tree species. Actual extinction risk may be somewhat higher because multiple-use or sustainable use landscapes may not provide suitable habitats for all species.

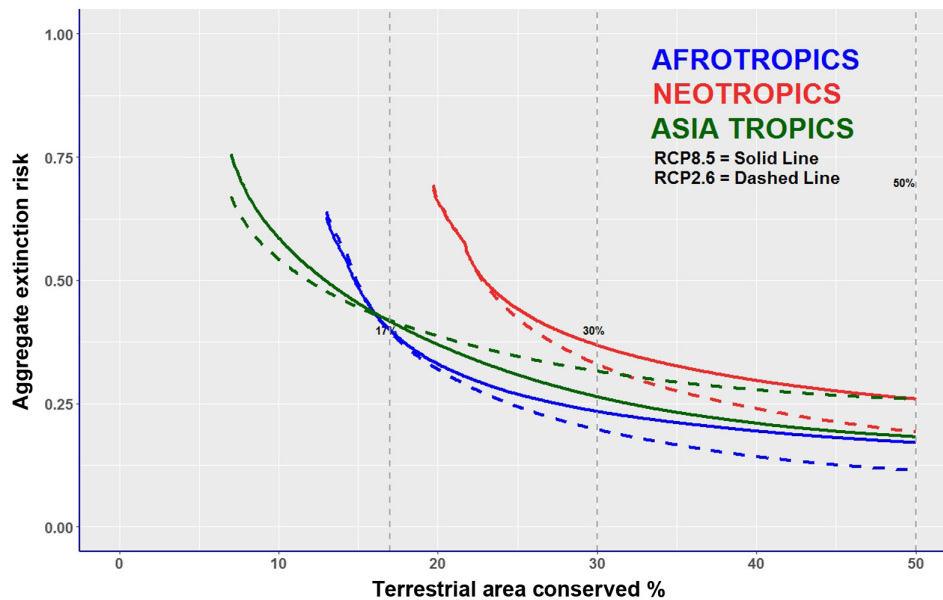


Figure 1. Modeled extinction risk reduction with increasing land conservation. Ensemble mean Aggregate extinction risk (AER) versus % terrestrial area conserved under RCP 2.6 (dashed lines) and RCP 8.5 (solid lines) for the Afrotropics (blue), Neotropics (red) and Asia Tropics (green). Vertical lines show the aggregate extinction risk curve intersection with 17%, 30% and 50% terrestrial area conserved. AER is the mean of individual species extinction risk at each increment of conserved natural land and is scaled from 0 to 1 (zero probability of extinction to likely extinct).

The spatial distribution of natural areas needed to achieve these reductions in extinction risk is illustrated for each of the three major tropical regions in our study in Fig. 2A–C. Many areas highlighted are recognized as global biodiversity hotspots (Myers et al. 2000), indicating the continued importance of conserving these regions of high endemism. Many also correspond to areas recently identified as plant rarity hotspots (Enquist et al. 2019). Mountain ranges and other areas of high topographic diversity feature prominently, likely due to existing high biodiversity, high endemism, and comparatively high climate and microclimate diversity (Rahbek et al. 2019a, b) coupled with the comparatively low velocity of climate change in these areas (Loarie et al. 2009). However, as the core area algorithm used (Moilanen 2007) prioritizes representation of all species, and will try to link niche-tracking to areas already conserved to the greatest degree possible, spatial priorities capture many distinct ecosystems and climate types including lowland habitats.

The areas our prioritization highlighted as important for species on the move include many areas that are also high conservation priority under current climate. This is because conserving a species from present to future begins with conservation of the species' current range, since this serves as the starting point for any future dispersal. Restricted-range species are concentrated in mountainous areas (Rahbek et al. 2019a, b), where species' movements in response to climate change will generally be upslope with warming temperatures (Peters and Darling 1985, Halpin 1997) or into nearby areas with suitable microclimates in complex terrain (Hannah et al. 2014, Rahbek et al. 2019b). Low velocity of climate change

in mountains (Loarie et al. 2009) and decreasing area with elevation mean that species' upslope movements will occur over shorter distances in mountains (Serra-Diaz et al. 2014), further concentrating restricted-range species near current montane centers of endemism (Enquist et al. 2019).

We observe a steep drop-off in modeled AER with increasing conservation of (primarily montane) natural area (Table 1). If conservation is limited to existing protected areas, AER is projected to be high under both climate change scenarios – ranging from 60 to 77% under both RCP 8.5 and 2.6. Moving to 30% land conservation combined with lowering climate change (RCP2.6) results in reduction of modeled AER by 52–68% (ensemble mean) across all regions when compared with existing levels of conservation and higher (RCP8.5) climate change. Unsurprisingly, the greatest extinction risk reduction could be achieved by conserving 50% of terrestrial area with a low climate change scenario; this combined action reduces modeled extinction risk by 72–82% in the ensemble mean (Table 1). Conserving 30% or 50% of land but with high climate change (RCP8.5), reduces modeled extinction risk between 46–66% and 62–76% respectively across the three regions under business-as-usual climate change (RCP 8.5) in the ensemble mean. Reducing climate change from business as usual (RCP 8.5) to the RCP 2.6 scenario which is more consistent with limiting mean global temperature change to 2.0° could reduce extinction risk 5–6% more under 30% land conservation. In contrast, with no increase in existing conservation area (<17% area), the same climate policy is projected to result in roughly –2 to 12% additional decrease in ensemble mean extinction risk.

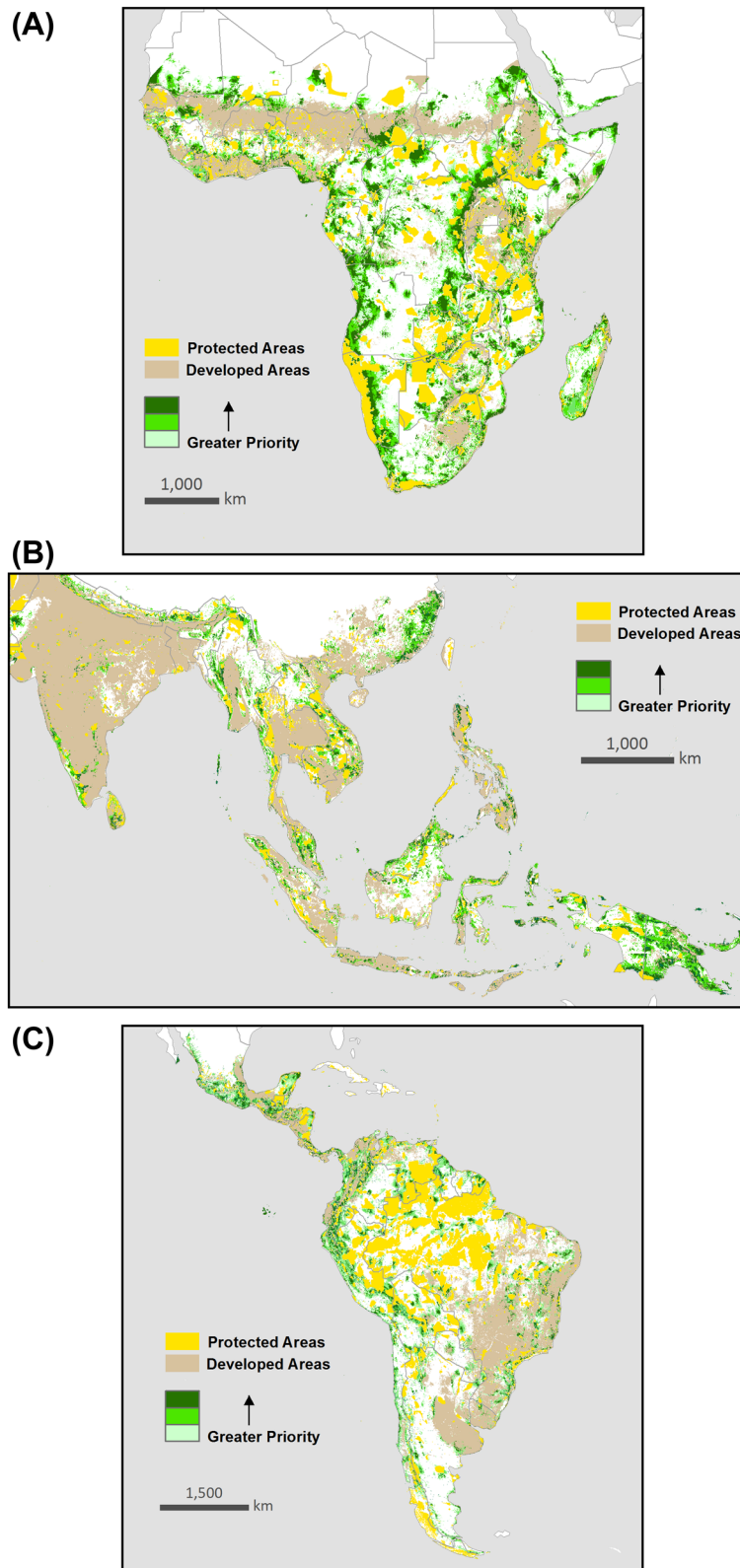


Figure 2. (A–C) Spatial prioritizations for land conservation to minimize extinction risk. Zonation spatial solutions to minimize extinction risk in the Afrotropics (A), SE Asia tropics (B) and Neotropics (C). AER values in Fig. 1 are derived from these spatial solutions. Areas of darkest green are highest priority areas to minimize extinction risk at 17% land conservation. Successively lighter shades of green represent areas that minimize extinction risk at 30% and 50% land conservation. Existing conserved areas registered in the World Database of Protected Areas are shown in yellow. Priorities are selected to maximize representation of all species in both baseline (1960–1990) and future ranges (RCP8.5 2060–2080).

Table 1. Aggregate extinction risk (AER) under varying land conservation areas and climate change. Ensemble mean, maximum and minimum AER for high (RCP 8.5) and low (RCP 2.6) climate scenarios and three levels of land conservation (existing protected areas, 30% land conservation and 50% land conservation) for Asia, Africa and the Neotropics. Values are summed extinction risk across all species, scaled 0 (zero extinction risk for all species) to 1 (100% extinction risk for all species). The 'change' columns represent the percent difference in AER relative to the current protected areas under RCP 8.5. The extinction risk values in Table 1 are presented in continuous form in Fig. 1.

	Ensemble mean	Mean ensemble change	Ensemble max	Max ensemble change	Ensemble min	Min ensemble change
Neotropics						
RCP8.5						
Existing protected area*	0.686	–	0.765	–	0.631	–
30% land conservation [#]	0.370	–46.1	0.468	–38.8	0.332	–47.4
50% land conservation	0.259	–62.2	0.368	–51.9	0.219	–65.3
RCP2.6						
Existing protected area	0.693	–2.6	0.735	–3.4	0.675	–0.8
30% land conservation	0.332	–51.6	0.400	–58.2	0.301	–62.3
50% land conservation	0.192	–72.0	0.269	–74.9	0.159	–74.8
Afrotropics						
RCP8.5						
Existing protected area	0.628	–	0.657	–	0.601	–
30% land conservation	0.234	–62.7	0.267	–60.2	0.195	–67.6
50% land conservation	0.171	–72.8	0.217	–71.8	0.140	–76.7
RCP2.6						
Existing protected area	0.639	1.8	0.653	–0.6	0.629	4.7
30% land conservation	0.197	–68.6	0.220	–66.5	0.178	–70.4
50% land conservation	0.114	–81.8	0.140	–78.7	0.097	–83.9
Asia Tropics						
RCP8.5						
Existing protected area	0.756	–	0.771	–	0.745	–
30% land conservation	0.261	–65.5	0.300	–61.1	0.227	–69.5
50% land conservation	0.182	–75.9	0.223	–71.1	0.152	–79.6
RCP2.6						
Existing protected area	0.671	–11.2	0.762	–1.2	0.614	–17.6
30% land conservation	0.314	–58.5	0.360	–69.2	0.231	–69.0
50% land conservation	0.259	–65.7	0.313	–80.5	0.143	–80.8

* IUCN categories I–VI.

[#] IUCN categories I–VI+OECM.

Discussion

Our analysis suggests that 30% land conservation combined with climate change action could reduce extinction risk by half or more across multiple conservation/climate combinations in all three tropical regions. Models show that even without lowered climate change (RCP8.5), 30% land conservation could reduce AER by at least half in the ensemble mean, except in the Neotropics. The lower levels of modeled reduction in the Neotropics are likely due to the high number of rare species in the Andes, distributed over a relatively large area that can not be completely captured with 30% land conservation. 30% land conservation could therefore pay major benefits to biodiversity conservation and is a strong target for CBD post-2020 consideration.

The analysis also suggests that 50% land conservation could lead to an even larger decrease in extinction risk, resulting in over 80% reduction in all regions when coupled with lower climate change (RCP2.6). Roughly half of the world's ecoregions have already lost 50% or more of their original natural habitat (Dinerstein et al. 2017) so this longer-term vision of 50% land conservation would require restoration in many areas. Careful targeting of this restoration can have

important long-term benefits for biodiversity. Geographic targeting at coarse scales can be accomplished by selecting priority areas indicated in Fig. 2A–C. Finer-scale priorities can be further elaborated by conducting local systematic spatial planning for climate change using methods similar to this study.

Natural areas can be conserved through a wide range of mechanisms, from government-designated protected areas to multiple-use land management such as community conservancies and other effective area-based conservation measures (OECM) (Dudley et al. 2018, Dinerstein et al. 2019). Which approach is the most appropriate will depend on the local environmental and social context (Brown et al. 2003). What is clear is that large-scale industrial land uses, particularly monoculture and plantations, are becoming increasingly prevalent, so achieving the results reported here will require active policy or land use management intervention to maintain natural areas in high priority locations of highest value to species' present and future ranges.

The modeled reductions in extinction risk we report depend on specific spatial configurations in our conservation solutions that in turn depend on GCM and species model variants. The uncertainty associated with our GCM

variants is relatively low. Across 10 general circulation models (GCM), the average ratio of ensemble mean to maximum is 0.85 and of ensemble mean to minimum is 1.17 for the 30% conserved area target. Species modelling uncertainty is higher than the uncertainty associated with climate models (Araújo and Guisan 2006). Modeling a large number of species over a broad spatial domain at relatively fine resolution requires substantial compute resources, which is then multiplied when several GCMs and climate pathways are considered. It is an acknowledged limitation of this study that we report the results of only one species distribution model method, as it has been found that choice of modeling method is often the largest source of variation in species range projections (Diniz-Filho et al. 2009, Garcia et al. 2012). Exploring solution space with multiple species models is important and is a priority for our research group and we recommend that the results presented here be vetted against alternative species modeling techniques. Use of ensemble species modeling methods and the uncertainties they represent is a key recommendation of recently agreed upon standards for biodiversity assessments (Araújo et al. 2019) and is therefore an opportunity to refine the results presented here. Indeed, the approach described in Kujala et al. (2013) which was followed this study offers a template to incorporate species model uncertainty as well as climate model uncertainty in the prioritization.

Despite this limitation, there are multiple reasons for us to believe that these results, using only one species distribution model method (Maxent) are likely robust at the scale of our analysis. First, our conservation planning algorithm, Zonation, seeks solutions that minimize extinction risk, which means minimizing range loss in rare species. Rare species are concentrated in tropical and Mediterranean mountains (Enquist et al. 2019, Rahbek et al. 2019a, b). These areas will emerge as high priority under current and future climate, regardless of species model. Second, we include species that have too few records to be modeled. These species are included in the conservation prioritizations with their current occurrences set equal to their future occurrences. Since most species are rare (Enquist et al. 2019), nearly one-third of the species driving our priorities are these rare species with too few occurrences to model. These species and the spatial priorities to conserve them are independent of species models. Third, species will be predominantly moving upslope in tropical mountains, so while exact locations of conservation importance for individual species may be dependent on species models, general tropical montane locations, becoming even more concentrated as climate changes, dominate our general global results. Since rare plant species are common and >90% of our modelled species are plants, including non-modelled species reduces the biases associated with exclusive reliance on the more widespread species with enough records to model. Finally, Rare species are concentrated where past climate change could be tracked with limited movement (Sandel et al. 2011), likely reflecting frequent limited dispersal ability in these species (Foden et al. 2013) so at the spatial resolution of our study, their future ranges are likely to be

within the same selection unit as their present range, reducing or eliminating the uncertainty that arises from lack of ability to simulate their future range.

The AER and spatial results reported here show that on coarse scales and across broad domains, we know where to conserve to be most effective in meeting international conservation goals, even as climate changes. Conserving the areas highlighted in our results can pay large dividends in carbon sequestration to reduce climate change, as well as providing other ecosystem services while reducing extinction risk and maintaining biodiversity. However, the converse is not necessarily true – maximizing carbon sequestration may not automatically conserve these critical biodiversity and climate priorities (Di Marco et al. 2015). Carbon sequestration, both above-ground and below-ground, may be higher in lowland ecosystems. A strategy to maximize per unit area carbon sequestration by pushing agriculture and other development into more marginal uplands will require clearing more habitat to meet production needs, in the very habitats that are most important to conserve (Di Marco et al. 2015, Rahbek et al. 2019a, b). In some cases, a strategy of conserving more upland area (to sequester the same amount of carbon) could meet the same carbon goal, provide substantial ecosystem services such as watershed protection, while having much greater biodiversity benefit and potentially, as tradeoff, allowing some lowland areas with high agricultural potential to be developed.

Achieving these multiple biodiversity and ecosystem service benefits in the real world requires continuous, iterative planning. No set of priorities can be completely or instantaneously realized in a world of multiple competing development interests that play out over time. Rather, in the real world, conservation and development planning moves incrementally and often imperfectly. So while the spatial priorities presented here can greatly reduce extinction risk, real world planning to reduce extinction risk will need to accept compromises and reorder priorities as choices (many times less than optimal) are made. More important than a perfect set of priorities is an ongoing planning process that considers climate change effects on biodiversity and ecosystem services. Such a process can ensure that at every decision point about which areas are to remain natural or to be developed, the highest priority areas for biodiversity under climate change are identified. While the highest priority area may not always be conserved, systematic bias towards the highest priority remaining sites will progressively drive solutions towards reduction of extinction risk. For this reason, it is important to establish systematic conservation planning for biodiversity and climate change as a key process within government offices in charge of conservation and development planning, as they should continuously update priorities for conservation as solutions are implemented, as well as when knowledge of changes in species distributions and other effects of climate change increases.

Ongoing systematic conservation planning allows for assimilation of new data and improved climate models. For

the conservation of biodiversity, uncertainties need not stand in the way of action. By building systematic planning processes that serve communities and nations for decades, progressive reduction in uncertainty will result in continually improved conservation and development outcomes. The perfect should not be the enemy of the good; our land use plans will never be perfect, but they can be good, they can incorporate consideration of conservation and species movements due to climate change and they can continually improve. Doing so can help ensure that all of the species that share this planet with us will continue to thrive, and provide benefits to people, even as climate changes.

Data availability statement

Data are available from the Figshare Digital Repository: doi: 10.6084/m9.figshare.c.4868019 (Hannah et al. 2019).

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RFA, RIOG, RM, RNG, RYU, S, SALA, SANT, SAPS, SASK, SBT, SEL, SIU, SJRP, SMDB, SMF, SNM, SOM, SP, SRFA, SPF, SPSF, SQF, STL, STU, SVG, TAI, TAIK, TAMU, TAN, TEF, TENN, TEPB, TFC, TI, TKPM, TNS, TO, TU, UAM, UB, UCR, UEC, UFG, UFMU, UFP, UGDA, UJAT, ULM, UME, UNA, UNB, UNR, UNSL, UPGB, UPEI, UPNA, USAS, USJ, USM, USNC, USZ, UT, UTC, UTEP, UWU, V, VAL, VALD, VEN, VMSS, VT, W, WAG, WAT, WII, WELT, WFU, WMNH, WS, WTU, WU, Z, ZSS, ZT, CUVC, LZ, AAS, AFS, BHCB, CHAM, FM, PERTH, SAN.

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