Rewiring food webs through trophic rewilding

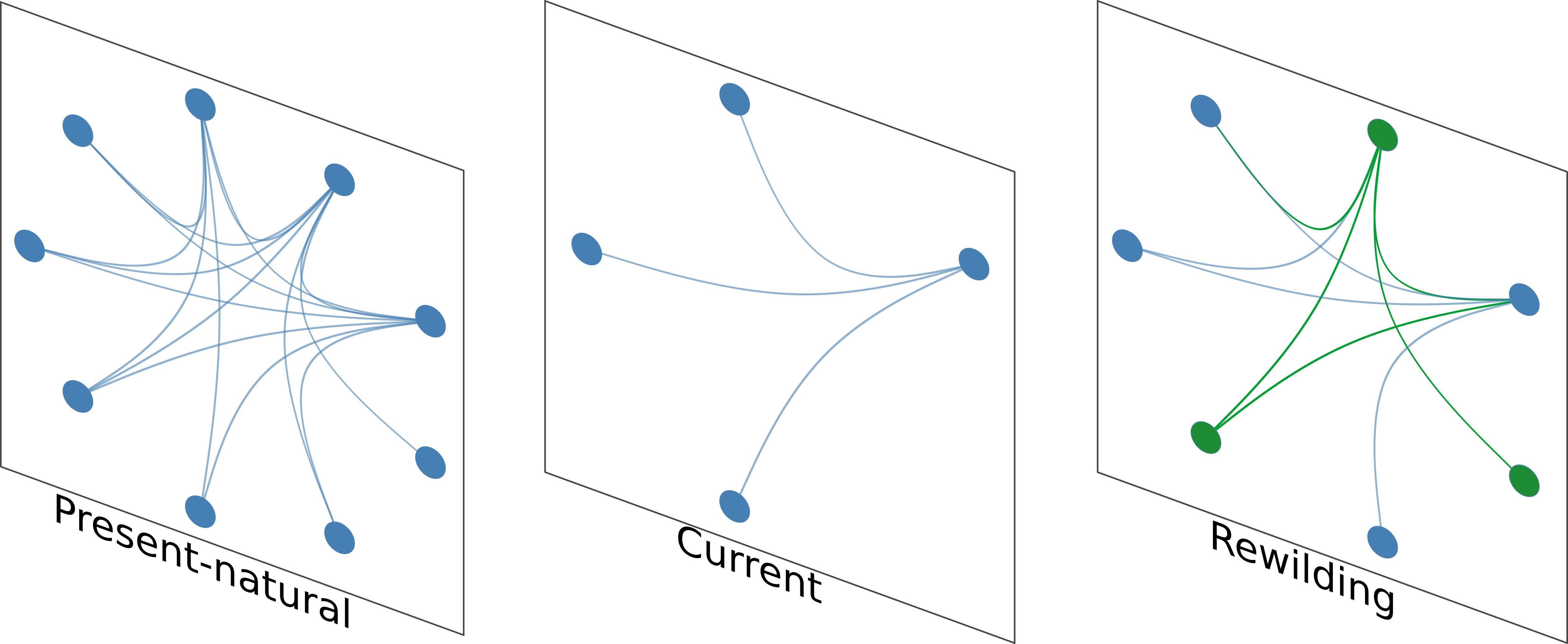
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# Introduction

Humans have defaunated ecosystems worldwide (Dirzo et al. 2014; C. Sandom et al. 2014), removing from the environment species, their ecological interactions (Valiente-Banuet et al. 2015), and the ecological processes associated with them. For example, extinctions of large megaherbivores (> 1,000 kg) has reduced seeds and nutrient dispersal (Guimarães Jr, Galetti, and Jordano 2008; Doughty, Wolf, and Malhi 2013), and extirpations of apex predators have reduced control of prey densities and generated trophic cascades altering ecosystems structure (Estes et al. 2011; A. T. Ford et al. 2014; Ripple et al. 2014; Atkins et al. 2019). As late Pleistocene mammal extinctions have particularly affected large body-sized species (C. Sandom et al. 2014; F. A. Smith et al. 2018), human-driven extinctions have particularly pruned ecological networks of interactions maintained by pre-historic biodiverse megafauna assemblages, modifying ecosystem processes and functions (Gill 2014; Faurby and Svenning 2015; Malhi et al. 2016).

Trophic rewilding, defined as the reintroduction of extirpated animals or the introduction of functional ecological replacements for globally extinct species to restore lost ecological processes and promote self-sustaining biodiverse ecosystems (Svenning et al. 2016), has been proposed as an alternative to classical restoration projects to re-establish lost ecological interactions (Perino et al. 2019). For example, rewilding of guanaco (*Lama guanicoe*) in Chile could re-connect isolated ecosystems at a regional scale, increasing seed dispersal and small-scale habitat heteogeneity (Root-Bernstein and Svenning 2017), reintroduction of howler monkeys (*Alouatta guariba*) in Tijuca National Park have rewired ecological interactions and restored seed dispersal (Genes et al. 2019), and reintroduction of wolf in Yellowstone National Park have re-established trophic cascades and vegetation recovery (Beschta and Ripple 2016).

Data on rewilding are scarce, limited in time, and geographically biased (Tanentzap and Smith 2018), and community responses to rewilding can be contradictory and inconclusive, arising the issue of when and how to rewild (Alston et al. 2019). Paleoecological data and comparative methods can highlight similarities between extinct species and suitable replacements and their restoration potential in rewilding projects (Wood, Perry, and Wilmshurst 2017). Particularly, inference of biotic interactions and reconstruction of prehistoric ecological networks have been used to assess the consequences of human-driven extinctions and extirpations of large mammals (Yeakel et al. 2014; Pires et al. 2015; Marjakangas et al. 2018). Similarly, reconstruction of potential rewilded ecological networks can be used to forecast the possible responses of ecosystems to re-introductions and inform rewilding projects of their possible outcomes (M. M. Pires 2017).



Conceptual representation of rewiring food webs through rewilding. Human-driven extinctions and extirpations have modified natural food webs (left) and removed species and trophic interactions (middle). Rewilding aims to restore lost interactions by replacing extinct species with suitable ecological analogues that would rewire food webs and re-establish functionally analogue links (right).

In this study, we investigate how rewilding of terrestrial mammals can potentially restore trophic interactions in protected areas worldwide. We modeled all 4,201 extant terrestrial mammals climatic suitability distribution and we chose suitable ecological replacements for # species that went extinct during the Late Pleistocene. Under this rewilded scenario, we derived the mammal community for the protected areas and inferred their food webs, ecological networks of 'who eats whom'. We compared the rewilded food webs with the food webs we have today under current conditions and with the food webs we would have today in the complete absence of anthropogenic pressure during the Late Pleistocene, inferred using the range maps from the PHYLACINE database (Faurby et al. 2018). To understand the potential of rewilding to restore lost trophic interactions with ecologically analogue links, we compared these three scenarios and tested the following contrasting hypotheses:

1. trophic rewilding can replace lost trophic interactions with ecologically analogue links, restoring food webs to prehistoric conditions
2. trophic interactions lost because of the Late Pleistocene mammals' extinctions cannot be fully restored by trophic rewilding

Particularly, we determined the current interaction debt, how many interactions have been lost because of terrestrial mammal extinctions and extirpations, and the rewilding interaction credit, how many of these can be restored with rewilding (Genes et al. 2017). If hypothesis 1 is correct, current interaction debt is equal to rewilding interaction credit. Moreover, we evaluated the "interactions evolutionary distinctness" (EDi), a measure of how much an interaction is evolutionary unique (Emer et al. 2019), under present-natural, current, and rewilding scenarios to understand if rewilding can restore lost, functionally unique interactions.

# Materials and methods

## Species distribution modeling

To overcome biases introduced by anthropogenic pressures on where terrestrial mammals live, we used current and present natural range maps from the PHYLACINE database (Faurby et al. 2018). Present natural ranges are estimates of where species could be today in the complete absence of influence of modern humans (*Homo sapiens*) through time (Faurby and Svenning 2015). Presence locations were generated within combined current and present natural range maps with a 20 km separation, excluding locations reported above the highest elevation for each species in the International Union for Conservation of Nature (IUCN) Red List or, if not stated, 4,000 m, which is roughly the 95 percentile for upper elevations of mammals reported in the IUCN Red List (IUCN 2016). In total, we identified 4,201 extant terrestrial mammal species with range maps excluding genus *Homo*, pinnipeds, cetaceans, and bats.

We used climatic variables from the Worldclim v 2.0 database at 2.5 arc-minute resolution (Fick and Hijmans 2017)and reprojected to 5 km using bilinear interpolation and a Behrmann equal-area projection. The four spatially refined variables we chose are maximum temperature of the warmest month (Bio 5), minimum temperature of the coldest month (Bio 6), precipitation of wettest quarter (Bio 16) and precipitation of driest quarter (Bio 17). We selected these variables as they capture extreme conditions and, thus, likely represent surrogates for factors limiting the distributions of species. To minimise potential issues with multi-collinearity, we ensured variance inflation factor (VIF) among climatic variables was below 4 (O’Brien 2007); VIF values for Bio 5 = 2.69, for Bio 6 = 3.44, for Bio 16 = 1.83, and Bio 17 = 1.41.

To model the climatic suitability of terrestrial mammals, we fitted maximum entropy (Maxent) models as implemented in the maxnet R-package based on inhomogenous Poisson processes (S. J. Phillips et al. 2017). Maxent is a presence-background approach, in which environments occupied by a species are contrasted with the available environmental space. To ensure greater representation of environmental variables available for each species, we increased the number of randomly sampled background records up to 100,000 within a buffer of 4,000 km of the present natural range (*here we cite the paper that used 3000km buffer size*). To assess reliability of projections we ran a sensitivity analysis with a buffer size of 500 km. We used the default settings, besides disabling threshold features to avoid locally overfitted response curves (Merow, Smith, and Silander Jr 2013; Merow et al. 2014). To ensure robust predictions, we modelled species that had at least 30 presence locations, thus excluding 396 rare island endemics.

We assessed the performance of Maxent models by calculating the average continuous Boyce index (CBI; Hirzel et al. (2006)) and the average Area Under the Receiver Operating Curve (AUC; Swets (1988)) through five-fold cross validation. The difference between CBI and AUC is that the later simply indicates how well models differentiate between presences and absences regardless of the degree of difference between them. Model fit was inspected by the average omission rate based on the minimum training presence value (ORMTP). CBI values range between -1 and 1, where values > 0 indicate the model's output is positively correlated with the true probability of presence and values < 0 indicate it is negatively correlated with the true probability of presence; AUC values range from < 0.5 for models with discrimination no better than random to 1 for models with perfect discrimination between occupied and unoccupied places (Fielding and Bell 1997); and ORMTP values range from 0 for models that are not overfit to 1 for models that are overfit. To convert continuous suitability predictions to binary layers indicating suitable/unsuitable habitat, we chose as threshold the suitability value that maximized sensitivity and specificity (MSS, Liu, Newell, and White 2016). We further assessed the performance of Maxent models by comparing projections of climatic suitability with introduced ranges from Lundgren et al. (2018) (n = 22 species) and IUCN v.2016-3 (IUCN (2016); n = 114 species; see Supporting Information S# for more details). Introduced ranges were selected from Lundgren et al. (2018) over the IUCN v. 2016-3 (IUCN 2016) for 3 species found in both datasets (*Cervus elaphus*, *Ovibos moschatus*, and *Rangifer tarandus*). We excluded # species with known introduced ranges from comparisons with Maxent models because either they did not have enough points to make robust models (< 30 presence locations; # and #) or the species introduction was within the present natural range (#).

## Suitable ecological replacements

To reduce the chance that species introductions could negatively affect current mammal communities, for example by competition with already present species (Linnell and Strand 2000), we chose for each globally extinct species one and only one ecological replacement according to a conservative selection criterion (Fig. 2). Because phylogenetically related species with comparable body sizes in general have relatively similar ecological roles, we considered as introduction candidates only living mammals within the same family of the extinct species and within a range of body masses from 0.50 to 1.50 the body mass of the extinct species. If reintroductions of living species within the present-natural range of the extinct species were possible, we preferred reintroductions to introductions of non-native taxa, which were excluded from further analyses. We calculated for the remaining candidates the climatic suitable area within the present-natural of the extinct species for each ecoregion, and chose as best replacement the candidate with the largest reintroduction plus introduction range area for each ecoregion separately.

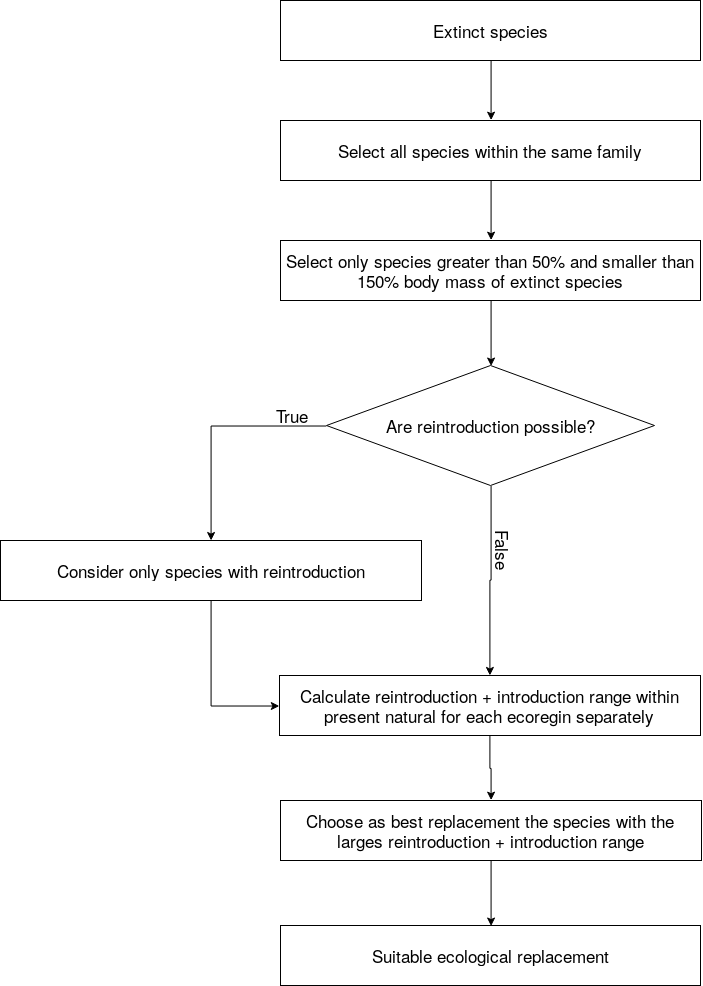


Diagram of selection criteria.

Three exceptions were made to relax these criteria: 1) all *Proboscidea* were considered all together and not separated in the families *Elephantidae*, *Gomphotheriidae*, *Mammutidae*, and *Stegodontidae*; 2) for *Proboscidea*, if no candidates were found within the 0.5 - 1.5 body mass range of an extinct megaherbivore species ( 1,000,000 kg), we considered as candidates all living megaherbivore in the *Proboscidea* order; 3) for *Felidae* and *Ursidae*, if no candidates were found within the 0.5 - 1.5 body mass range of an extinct megacarnivore species ( 100,000 kg), we considered as candidates all living megacarnivore in the *Felidae* and *Ursidae* family, respectively.

## Reconstructing food webs

We evaluate mammal assemblages for # terrestrial protected areas selected from the World Protected Area Database (UNEP-WCMC and IUCN (2019), downloaded on June 2019). We excluded all protected areas with IUCN category status III, IV, V, and VI, cleaned the dataset removing inaccuracies (Jones et al. 2018; Hanson 2019), and simplified geometries joining connected protected areas. Because populations of large mammals require large protected areas (Woodroffe and Ginsberg 1998; Chundawat et al. 2016), we excluded protected areas smaller than and areas where terrestrial mammals were not present during the late Pleistocene. We conducted analyses on the remaining 224 protected areas (Fig. S#).

Food webs were constructed for each protected area by combining phylogenetic inference with a trait-based approach. Phylogeny has been shown to be a good predictor for trophic interactions (Eklöf et al. 2011), as species tend to share more similar resources the closer they are phylogenetically (Gray et al. 2015). Moreover, by including a trait-based approach, we removed interactions inferred using phylogeny alone that were not supported by macroecological evidence and that were unlikely to occur (Pomeranz et al. 2019). As trait-based inference method, we used for carnivores the relationship between body masses of prey and predators, which structures trophic interactions in current and Pleistocene food webs (Williams and Martinez 2000; Owen-Smith and Mills 2008; Segura, Farina, and Arim 2016). Particularly, we used for carnivores the 10% and 90% regression quantiles to obtain the dietary niches of carnivores (Gravel et al. 2013; Pomeranz et al. 2019).

Phylogenetic inference was carried out at the family level, a trade-off between accuracy of predictions and data availability (Gray et al. 2015). Each observed interaction between a prey and a predator was assigned to all species of the same family of the prey and the predator, respectively. These phylogenetically permitted interactions were then pruned and predator-prey links that laid outside the interval between 10% and 90% regression quantiles were removed (Gravel et al. 2013; Pomeranz et al. 2019). Quantile regression analysis was performed simultaneously on all mammal carnivores using data from ECOWeB database, GLOBI database, and two published savanna food webs (Cohen 2010; Baskerville et al. 2011; Visser, Freymann, and Olff 2011; J. H. Poelen, Simons, and Mungall 2014).

Herbivores were divided in browsers and grazers using the MammalDIET database (Kissling et al. 2014). Moreover, megaherbivores (> 1,000 kg) that were not predated by other mammals were separated in a different trophic group, as these species are free from predation and significantly affect the habitats they use (Le Roux, Kerley, and Cromsigt 2018). Because carnivores trophic position depends on species body size, we avoided possible species' misplacements due to data limitations by classifying carnivores in trophic levels defined by body mass. We divided carnivores into: small carnivores (< 21.5 kg, (Carbone et al. 1999)); intermediate carnivores (< 100 kg); and megacarnivores (>= 100 kg, (Malhi et al. 2016)).

For each food web, we calculated how many species were present at each trophic level under current, present-natural, and rewilding conditions, and the number of interactions connecting different trophic levels. We called the difference between the number of species in present-natural and current food webs the "species richness debt", and the difference between the number of species in current and rewilded food webs the "species richness credit". Similarly, we called "interactions debt" and "interactions credit" the difference between the number of interactions between present-natural and current and between current and rewilded food webs evaluated for each trophic step. To make comparison possible among food webs, we normalized number of species in each trophic level and the number of interactions among trophic levels for the values of the present-natural food web, our reference baseline.

Evolutionary distictness (ED) is defined as the contribution of species to the evolutionary history of its clade (Jetz et al. 2014). Similarly, interactions evolutionary distinctness (EDi) measures how much an interaction between two species is unique in an ecological network because of the phylogenetic isolation of the two interacting species (Emer et al. 2019). To calculate EDi, we estimated ED of all mammals using 100 phylogenetic trees chosen at random from the PHYLACINE database (Faurby et al. 2018) and summed the ED of two interacting species to obtain the EDi of that interaction (Emer et al. 2019). EDi was calculated for all interactions in each food web under the three scenarios: present-natural, current, and rewilded. To assess if there were differences among scenarios, we performed multiple pair-wise chi-square tests on the probability density functions of the EDi correcting for the multiple comparison using the Bonferroni correction.

Food web statistics were summarized at the ecozone level. We attributed protected areas to ecozones using the shapefile obtained from The Nature Conservancy (https://www.nature.org/en-us/, Olson and Dinerstein (2002)). All data processing, analyses, and figures were performed in the R progamming language (R Core Team 2018) using packages tidyverse (Wickham 2017), rglobi (J. Poelen, Gosnell, and Slyusarev 2018), maxnet (S. Phillips 2017), dismo (R. J. Hijmans et al. 2017), sf (Pebesma 2018), raster (R. J. Hijmans 2019), ape (Paradis and Schliep 2018), picante (Kembel et al. 2010), tmap (Tennekes 2018), doParallel (Corporation and Weston 2018), and foreach (Microsoft and Weston 2017). All spatial analyses were conducted using the Behrmann cylindrical equal-area projection.

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