

Appendix for *Rewiring food webs via trophic rewilding*

Emilio Berti^{1,2,*}, Scott Jarvie^{1,2}, and Jens-Christian Svenning^{1,2}

¹ Section for Ecoinformatics and Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark. \ ² Center for Biodiversity Dynamics in a Changing World (BIOCHANGE), Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark. \ * corresponding author: emilio.berti@bios.au.dk

Keywords: defaunation, human-driven extinctions, food webs, rewilding, mammals, trophic interactions.

Supporting information

Overview

We investigated the potential of trophic rewilding to rewire food webs, ecological networks of “who eats whom” to their pre-historic conditions by inferring the food webs of large protected areas, which are optimal sites for rewilding, under three scenarios: present-natural, a counter-factual scenario where mammals extinctions have not happened and species occupy today their natural geographic distribution [1]; current conditions; and a simulated rewilding scenario where globally extinct mammals are replaced by suitable ecological replacements and extant mammals could re-expand to occupy present-natural ranges. To obtain the mammal assemblages of the protected areas under the present-natural and current scenarios, we used respectively the present-natural and current range maps of the PHYLACINE database [1]. Rewilding assemblages were obtained by choosing for each extinct species the best ecological replacement based on phylogeny, species traits, regional evolutionary history, and suitability to climatic conditions obtained through a species distribution modeling algorithm (SDM), and by adding these replacements to present-natural assemblages excluding extinct species. From the assemblages, we inferred food webs for present-natural, current, and rewilding scenarios by combining a phylogenetic and a trait-based inference approach [2,3]. Statistics were evaluated from these food webs and compared to assess if trophic rewilding can rewire food webs to pre-historic conditions. Particularly, we determined if rewilding can replenish, by replacing extinct species with suitable analogue species, impoverished trophic levels, replace lost predator-prey interactions with analogue links, and substitute evolutionary unique interactions.

Changes to PHYLACINE database

We used the PHYLACINE database [1] to assess species climatic suitability and to compute the evolutionary distinctness of interactions (EDi). Climatic suitability was obtained performing species distribution modeling via Maxent algorithm [4]. To avoid that species distribution models (SDMs) were biased by human pressure that limit geographical distribution of species [5], we train SDMs combining the current species’ geographic range maps with the present-natural ranges, counter-factual scenarios that assume complete absence of anthropogenic pressure through time.

The PHYLACINE database was used also to estimate the best ecological replacement for globally extinct species. To be eligible as candidate replacement, a species must have belonged to the same family of the extinct species and had body mass with the 50% - 150% body mass range of the extinct species. Because *Proboscidean* megaherbivores ($\geq 1,000$ kg; [6]) likely had similar ecological role [7], *Loxodonta africana* and *Elephas maximus* were considered as possible candidates for extinct *Proboscidean* megaherbivores. Also, as megacarnivores (≥ 100 kg, [8]) had similar ecological roles as top-down controllers, if no replacement candidates were found within the 50% - 150% body mass range of an extinct species of families *Felidae* and *Ursidae*, we considered as possible replacements living mammals ≥ 100 kg within the respective families to allow replacement of extinct megacarnivores.

We were aware of few inaccuracies in the PHYLACINE database, which we corrected before geographic distribution maps and body mass were used to model climatic suitability and estimate candidate replacements. In particular, body mass of the extinct species *Sinomegaceros ordosianus*

and *Dusicyon australis* was set equal to the mass of *Sinomegaceros yabei* and *Dusicyon avus*, respectively, and *Bos primigenius*, *Oryx dammah*, *Camelus dromedarius*, and *Elaphurus davidianus* were considered alive and not extinct – SDMs were trained on their present-natural ranges and the species were included in the species pool when searching for candidate replacements.

Species distribution models

Distribution of terrestrial mammals are largely limited by temperature and precipitation patterns. To capture the climatic niche of species, we therefore used 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) from the Worldclim version 2.0 database at 2.5 arc-minute resolution [9]. To minimize potential issues with multi-collinearity, we ensured that the variance inflation factor (VIF) among climatic variables was below 4 [10]; VIF values for Bio 5 = 2.69, for Bio 6 = 3.44, for Bio 16 = 1.83, and for Bio 17 = 1.41. Climate layers were reprojected using bilinear interpolation to a $5km^2$ resolution with a Behrmann equal-area projection, which was used in all downstream analyses.

Climatic suitability of terrestrial mammals was modelled using maximum entropy (Maxent) models using the *maxnet* R-package based on inhomogeneous Poisson processes [11]. Maxent is a presence-background approach, in which environments occupied by a species are contrasted with the available environmental space [12,13]. We used the default settings of Maxent, besides disabling threshold features to avoid locally overfitted response curves [13,14] and the use of 100,000 randomly sampled background records – cf. 10,000 that is commonly used – to ensure greater representation of environmental variables available within background areas [15]. Background buffers were obtained for each species separately around the combined current and present natural ranges, in order to reflect the different dispersal abilities of species. As buffer size, we used the maximum distance from the range centroid to the range edge was used [16,17]. If a species had more than one range, i.e. disjunct ranges, the buffer size was calculated as the highest centroid-edge distance among all ranges ([17]; see figure S# for an example). We only modelled species that had at least 10 presence locations, thus excluding 74 rare island endemics and 2 shrew species with small distribution ranges (*Crocidura allea* and *Crocidura xantippe*). In total, we modeled 4,130 of the 4,206 living terrestrial mammals.

We assessed the predictive performance of Maxent models through five-fold cross validation, by calculating the average continuous Boyce index (CBI; [18]), which indicates how much models discriminate against random expectation, and the average Area Under the Receiver Operating Curve (AUC; [19]), which indicates how well models differentiate between presences and pseudo-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 [20]; 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 used as threshold the suitability value that maximised sensitivity and specificity (MSS) as suggested by

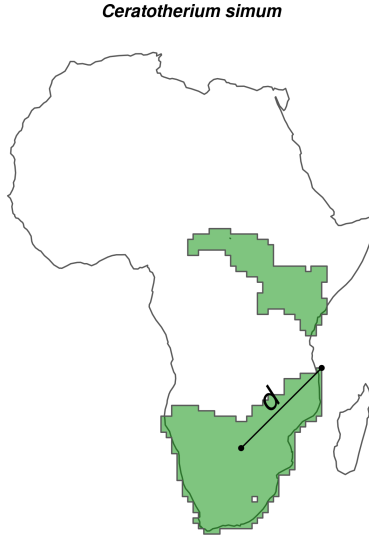


Figure 1: Estimation of species-specific dispersal distance d used to generate presence-background buffers for the Maxent species distribution models. In this example with *Ceratotherium simum*, we evaluated the maximum distance (black line) between centroid and edge (black points) of the largest polygon range of the species (green). We estimated d following the same procedure for each species, resulting in species-specific buffer sizes that reflected the different dispersal capabilities of species.

[21]. We further assessed the performance of Maxent models by comparing projections of climatic suitability with 136 introduced range maps from [22] ($n = 22$ species) and IUCN ([23]; $n = 114$ species). Introduced range maps were selected from [22] over the IUCN [23] for three species found in both datasets (*Cervus elaphus*, *Ovibos moschatus*, and *Rangifer tarandus*).

Evaluation statistics indicated in general very high to excellent quality of Maxent models. CBI index and AUC were on average very high (Table S#) and ORMTP was in low, indicating that models were in general not overfitted. Importantly, species chosen as rewilding replacement in downstream analyses had in general very high to excellent predictive performance: high CBI and AUC, and low ORMTP (Table S#). Also, much of the species' known introduction ranges were captured by Maxent models (Fig. S#): the median of the predicted introduction range was 0.84, with a median absolute deviation equal to 0.23.

Table 1: summary statistics for the Maxent species distribution models. The continuous Boyce index (CBI) and the area under the receiver operating curve (AUC) measures models performance; the omission rate based on the minimum training presence value (ORMTP) measures models tendency to overfit the data.

	Median	Median absolute deviation	Mean	Standard deviation
CBI	0.93	0.08	0.87	0.15
AUC	0.86	0.01	0.85	0.04
ORMTP	0.02	0.03	0.07	0.15

Table 2: summary statistics for the Maxent species distribution models of the selected candidate replacements ($n = 94$) in the rewilding scenario.

	Median	Median absolute deviation	Mean	Standard deviation
CBI	0.98	0.02	0.96	0.067
AUC	0.83	0.06	0.80	0.069
ORMTP	0.01	0.01	0.02	0.036

Rewilding selection criteria

Reconstructing food webs

Dataset

Statistical analyses

To investigate if trophic rewilding has the potential to restore food web interactions in the 209 protected areas examined to pre-human conditions, we used generalized linear mixed models

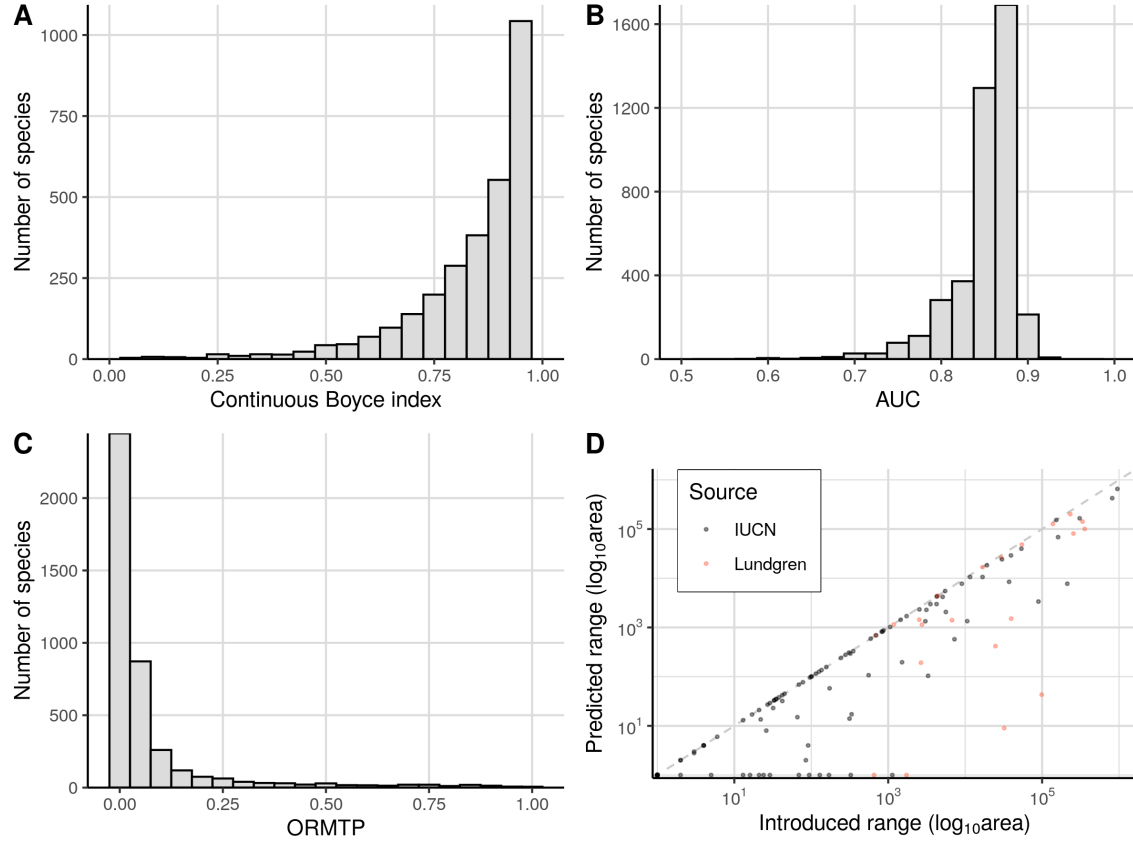


Figure 2: Evaluation statistics of species distribution models (SDMs). Continuous Boyce index (A) and the area under the receiving operating curve (AUC, C) were in general very good to excellent, and SDMs had high performance on discriminating climatic suitable habitats from unsuitable ones. Omission rate of minimum training points (ORMTP, B) was in general low, indicating a that models were not overfit. SDMs could predict most of the area where mammals were introduced by humans during the Late Pleistocene (D). Introduction area was obtained from the IUCN current introduction ranges [23] and the ranges described in [22], both of which were not included in the PHYLACINE present-natural and current ranges [1].

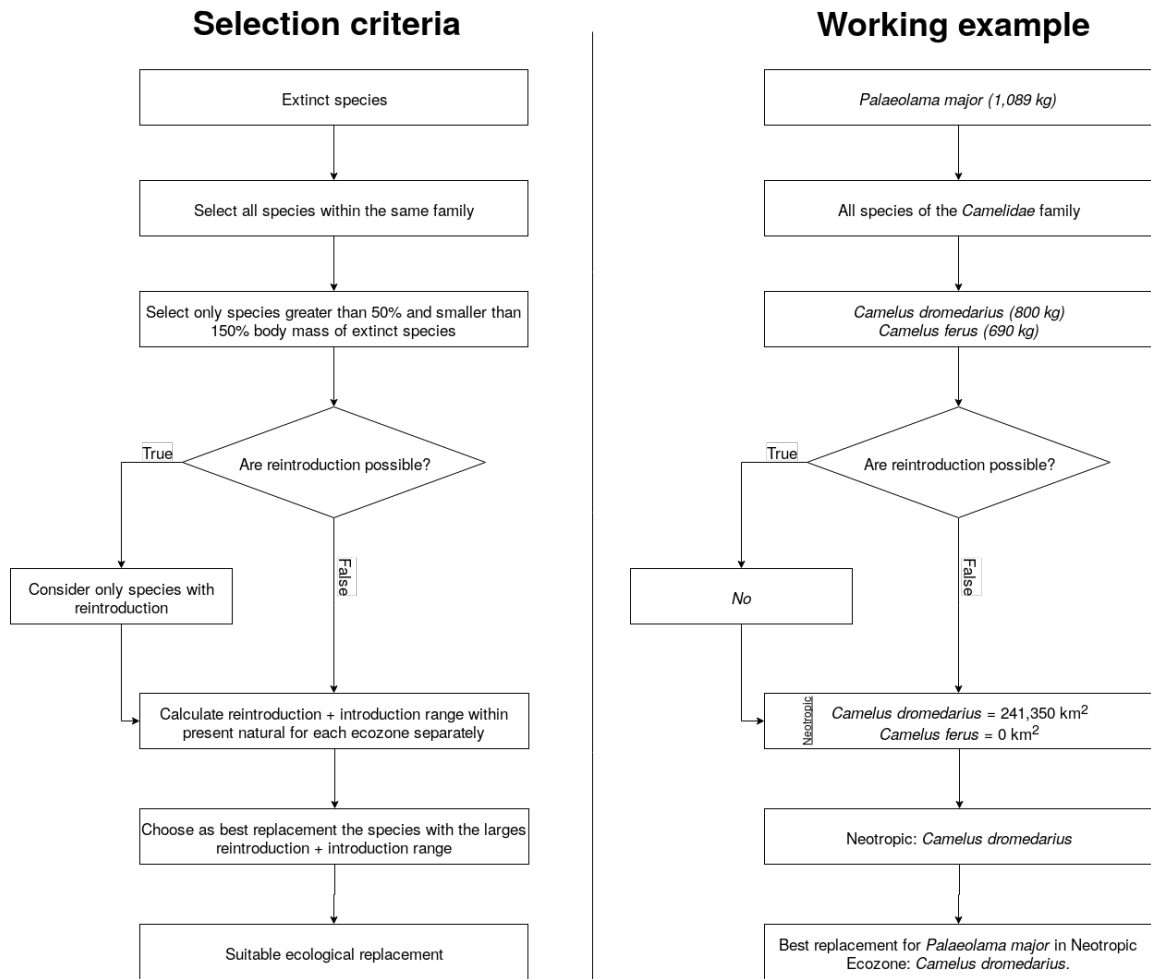


Figure 3: Diagram of selection criteria.

(GLMMs). We selected the error distribution for the GLMMs based on the response data type and to remedy overdispersion [24]. We used a Poisson distribution to model the number of species at each trophic level with the fixed effects scenario, trophic level, and their interaction. A negative binomial distribution was used to model the predator-prey interactions across trophic levels with the fixed effects scenario, the trophic levels involved in the trophic link, and their interaction. For both GLMMs, we used the random effects ‘protected area’ and ‘Ecozone’ to account for non-comparable pseudo-replicates and different ecological histories of mammal assemblages in Ecozones [25]. We assessed the significance among scenarios by performing multiple pair-wise contrasts with Bonferroni correction and estimated the magnitude of the differences using Cohen’s d effect size [26,27]: $d = \frac{\bar{x}_i - \bar{x}_j}{s_{ij}}$, where \bar{x}_i is the sample mean of scenario i , \bar{x}_j the sample mean of scenario j , and s_{ij} the pooled standard deviation of samples i and j .

Finally, we repeated all analyses for 206 areas evenly distributed across Ecozones. By studying the restoration potential of trophic rewilding in protected areas, we could investigate how much trophic rewilding can restore top-down control in areas that are likely suitable for rewilding already. However, by focusing on protected areas, which are unevenly distributed on continents, we might have underestimated the potential of trophic rewilding in areas that did not have large protected areas with strict IUCN management category but that could be suitable for rewilding in the near future, e.g. rural areas in Europe where wildlife is coming back after land abandonment [28,29]. We generated 36 random areas $\simeq 5,000 \text{ km}^2$ randomly in each Ecozone, derived their mammal assemblages for each scenario, inferred their predator-prey food webs under present-natural, current, and rewilding scenario, and performed the same statistical analyses used for the protected areas.

All data processing and analyses were performed in the R programming language version 3.6.1 [30] using packages tidyverse [31], maxnet [4], dismo [32], sf [33], raster [34], doParallel [35], foreach [36], performance [37], emmeans [38], and estimate [39]. All spatial analyses were conducted using the Behrmann cylindrical equal-area projection. Ecozones were derived using the World Wildlife Foundation shapefile (WWF, [40]). Figures were made using packages ggplot2 [41] with maps displayed in the Mollweide projection.

Statistical model

Trophic levels

The number of species per trophic level in each scenario was modeled as count data using a Poisson distribution for errors. Because the analyses were conducted on food webs that are not replicates, but pseudo-replications, we performed generalized linear mixed model regressions using scenario and trophic level as fixed effects and food webs as random factor. Moreover, Ecozones are defined based on diverging ecological and evolutionary histories and hence they were included as an additional random factor in the model to account for differences in Ecozones that are not directly comparable – i.e. Ecozones were considered pseudo-replication rather than replicates. The complete statistical model took the mathematical form:

$$N_{i,j} = \nu + \Sigma + (\nu \Sigma) + E_i + W_j + \epsilon_{i,j} \quad (1)$$

where $N_{i,j}$ is the number of species, ν the effect of each trophic level, Σ the effect of each scenario,

($\nu \Sigma$) the interaction term between trophic level and scenario, E_i the effect of the Ecozone, W_j the effect of the food web, and $\epsilon_{i,j}$ the residual deviations. Specifying Ecozones and food webs as random effects means that E_i and W_j are drawn from normally distributed samples: $E_i \sim \mathcal{N}(\mu_e, \sigma_e)$ and $W_j \sim \mathcal{N}(\mu_w, \sigma_w)$.

Number of predator-prey interactions among trophic levels was also modeled as a discrete count distribution using a negative binomial distribution for the errors, as data was significantly overdispersed. We performed generalized linear mixed model regressions with scenario and the trophic link – categorical variable indicating the trophic levels of prey and predators – as fixed effect. Similarly to the number of species per trophic level, we included also food webs and Ecozones as random effect. The complete statistical model took the mathematical form:

$$L_{i,j} = \lambda + \Sigma + (\lambda \Sigma) + E_i + W_j + \epsilon_{i,j} \quad (2)$$

where $L_{i,j}$ is the number links between two trophic levels, λ the effect of each trophic link, Σ the effect of each scenario, $(\lambda \Sigma)$ the interaction term between trophic levels link and scenario, E_i the effect of the Ecozone, W_j the effect of the food web, and $\epsilon_{i,j}$ the residual deviations. Specifying Ecozones and food webs as random effects means that E_i and W_j are drawn from normally distributed samples: $E_i \sim \mathcal{N}(\mu_e, \sigma_e)$ and $W_j \sim \mathcal{N}(\mu_w, \sigma_w)$.

Statistical analyses of trophic levels were performed using *R* package *lme4* [42]. The working code for the number of species per trophic level was:

```
model <- glmer(
  Proportion ~ -1 + Scenario * Trophic_level + (1 | Ecozone) + (1 | Web),
  data = dat,
  family = 'poisson',
)
```

For the number of links among trophic levels the working code was:

```
model <- glmer.nb(
  Proportion ~ -1 + Scenario * Edge + (1 | Ecozone) + (1 | Web),
  data = dat,
  control = glmerControl(optimizer = "bobyqa", optCtrl=list(maxfun=10e6))
)
```

We used *R* package *emmeans* [38] and *estimate* [39] to perform pairwise contrasts adjusting with the Bonferroni correction and we directly obtained the difference across scenarios of the number of species in trophic level or trophic interaction among trophic levels, the p-value of the contrast, and the effect size of the change as Cohen's d [26].

Species distribution models: climatic suitability maps

We performed maximum entropy species distribution models (SDMs) using Maxent algorithm [4] with species-specific buffer sizes reflecting the different dispersal abilities of species to train the model on background points. Dispersal ability of species was estimated as the maximum distance

(d) between geographic range centroid and edge; if there were more than one range polygon, we calculated d for the polygon with the larger area [16,17].

We evaluated SDMs performance by calculating the continuous Boyce index (CBI) and the area under the receiver operating curve (AUC) [18] and quantified the tendency of models to overfit data by using the omission rate based on the minimum training presence value (ORMTP). Moreover, we assessed model performance by comparing climatic suitability ranges with known species introduction ranges obtained from the IUCN [23] and from the introduced megafauna ranges dataset in [22]. Species introduction ranges were obtained from the IUCN shapefile by retaining only geometries with known introduction ranges (*origin* = 3; [23]). When species were present in both datasets, we prioritized [22].

Supplementary figure and tables

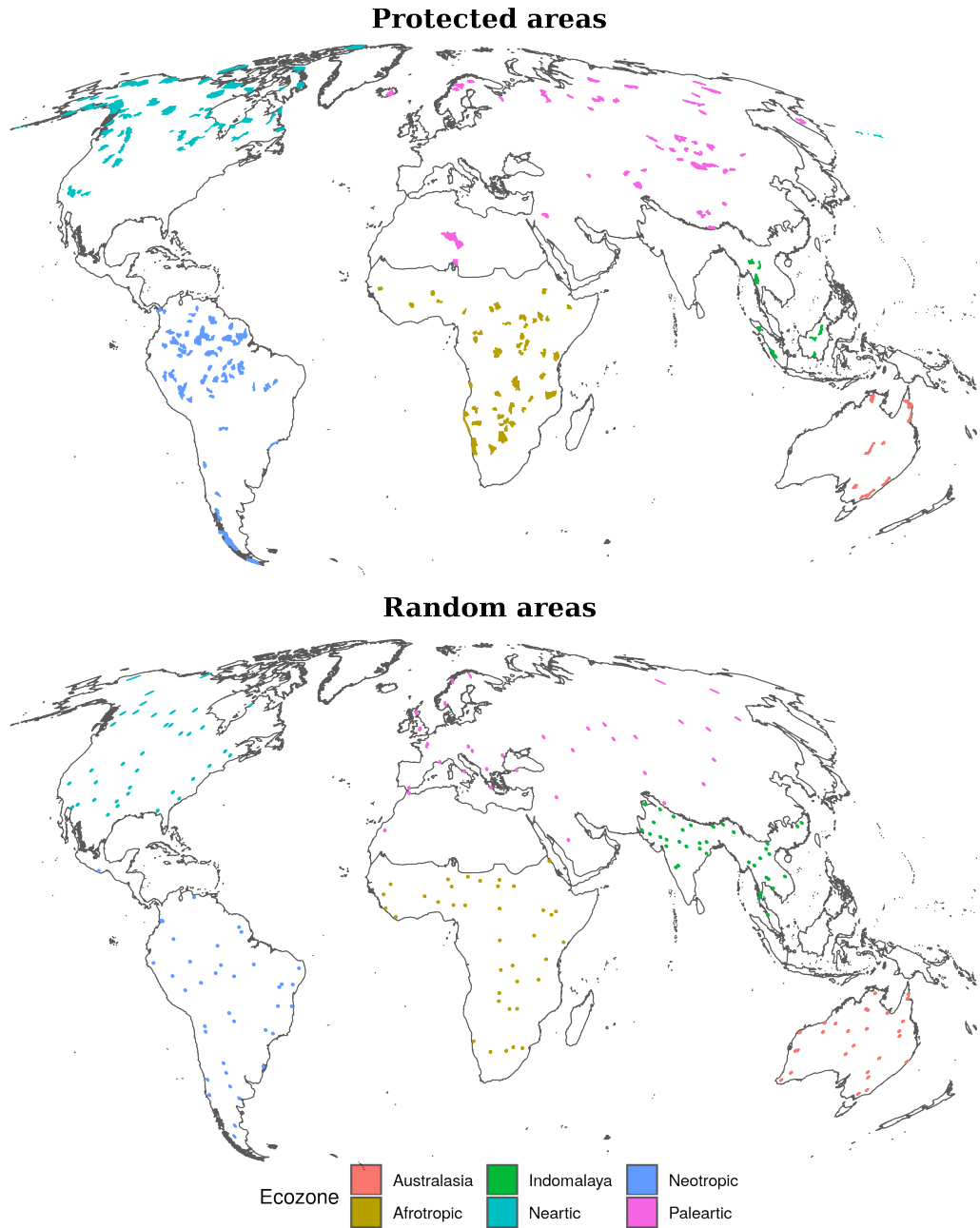


Figure 4: Large ($\geq 5,000 \text{ km}^2$) protected (top) and random areas (bottom). For each area mammals community was derived and food web inferred under the three studied scenario: present natural, current, and rewilding. Colors of the areas show to which Ecozone they belong; Ecozones boundaries are shown as continuous borders.

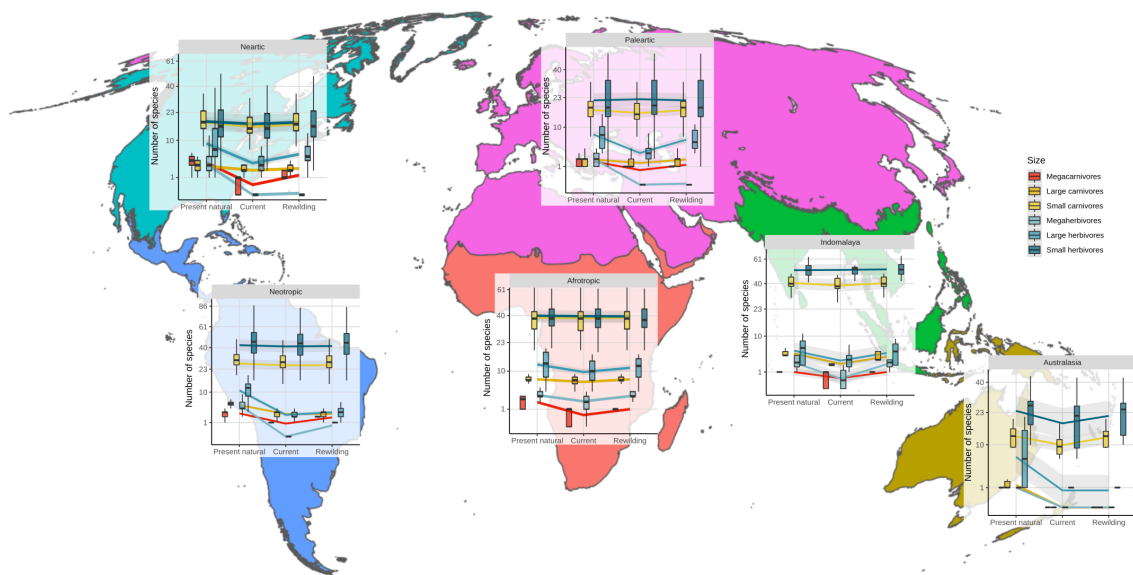


Figure 5: Number of species per trophic levels in protected areas $\geq 5,000 \text{ km}^2$ for each Ecozone.

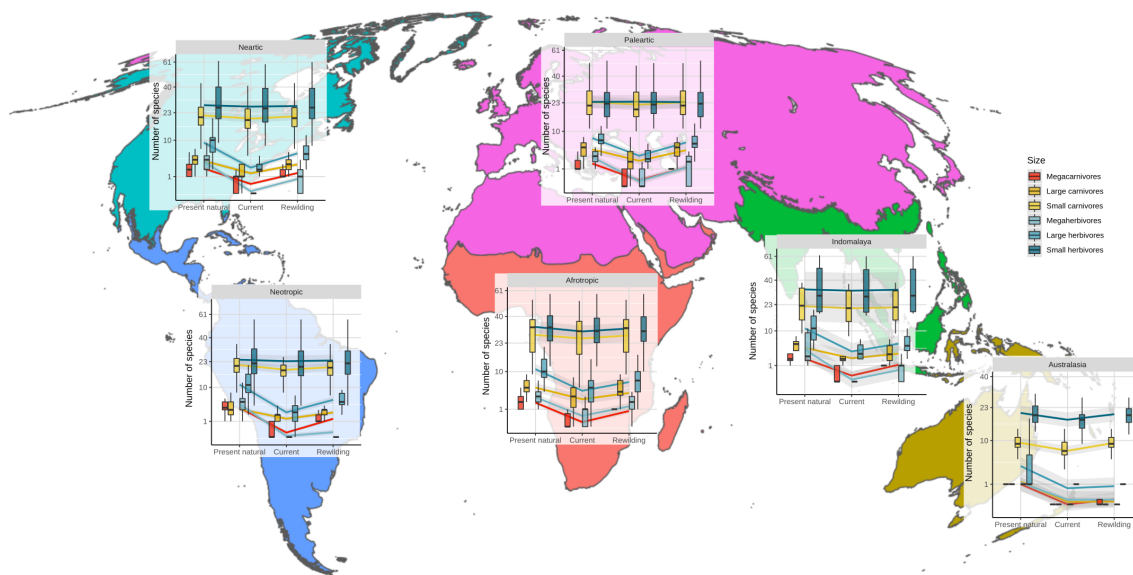


Figure 6: Number of species per trophic level in random areas $\geq 5,000 \text{ km}^2$ for each Ecozone.

Table 3: list of extinct species and their best functional analogue replacements for each Ecozone. We found a suitable replacement for 127 of the 334 extinct species during the late Quaternary. In total, 94 extant mammals were selected as best ecological replacements.

Extinct	Replacement	Ecozone
Vombatus hacketti	Lasiorhinus latifrons	Australasia
Arctodus simus	Ursus arctos	Neartic
Arctodus simus	Ursus arctos	Neotropic
Arctotherium wingei	Ursus americanus	Neotropic
Tremarctos floridanus	Ursus americanus	Neartic
Tremarctos floridanus	Ursus americanus	Neotropic
Ursus spelaeus	Ursus arctos	Paleartic
Catagonus stenocephalus	Pecari tajacu	Neotropic
Muknalia minima	Pecari tajacu	Neartic
Muknalia minima	Pecari tajacu	Neotropic
Tapirus augustus	Tapirus indicus	Indomalaya
Tapirus augustus	Tapirus indicus	Paleartic
Tapirus merriami	Tapirus bairdii	Neartic
Tapirus rondoniensis	Tapirus terrestris	Neotropic
Tapirus veroensis	Tapirus bairdii	Neartic
Tapirus veroensis	Tapirus bairdii	Neotropic
Kolpochoerus majus	Hylochoerus meinertzhageni	Afrotropic
Metridiochoerus compactus	Phacochoerus africanus	Afrotropic
Sus bucculentus	Sus scrofa	Indomalaya
Stegodon orientalis	Elephas maximus	Indomalaya
Stegodon orientalis	Elephas maximus	Paleartic
Stegodon trigonocephalus	Elephas maximus	Indomalaya
Elasmotherium sibiricum	Ceratotherium simum	Paleartic
Stephanorhinus kirchbergensis	Ceratotherium simum	Indomalaya
Stephanorhinus kirchbergensis	Ceratotherium simum	Paleartic
Petauroides ayamaruensis	Pseudochirulus canescens	Australasia
Petauroides ayamaruensis	Pseudochirulus schlegeli	Australasia
Bettongia anhydra	Bettongia lesueur	Australasia
Bettongia pusilla	Bettongia lesueur	Australasia
Bettongia pusilla	Bettongia penicillata	Australasia
Potorous platyops	Potorous gilbertii	Australasia
Perameles eremiana	Perameles bougainville	Australasia
Ochotona whartoni	Ochotona alpina	Neartic
Neovison macrodon	Neovison vison	Neartic
Conilurus albipes	Conilurus penicillatus	Australasia
Conilurus capricornensis	Conilurus penicillatus	Australasia
Notomys amplus	Notomys mitchellii	Australasia
Notomys longicaudatus	Notomys mitchellii	Australasia
Notomys macrotis	Notomys mitchellii	Australasia
Notomys mordax	Notomys alexis	Australasia

Extinct	Replacement	Ecozone
Notomys mordax	Notomys aquilo	Australasia
Notomys mordax	Notomys fuscus	Australasia
Notomys robustus	Notomys fuscus	Australasia
Pseudomys glaucus	Pseudomys novaehollandiae	Australasia
Pseudomys gouldii	Pseudomys desertor	Australasia
Brachyprotoma obtusata	Conepatus leuconotus	Neartic
Manis paleojavanica	Smutsia gigantea	Indomalaya
Mammut americanum	Loxodonta africana	Neartic
Mammut americanum	Loxodonta africana	Neotropic
Lagorchestes asomatus	Lagorchestes hirsutus	Australasia
Macropus greyi	Thylogale billardieri	Australasia
Metasthenurus newtonae	Macropus rufus	Australasia
Onychogalea lunata	Petrogale lateralis	Australasia
Procoptodon browneorum	Macropus giganteus	Australasia
Procoptodon gilli	Macropus rufus	Australasia
Protemnodon hopei	Macropus antilopinus	Australasia
Protemnodon hopei	Macropus giganteus	Australasia
Protemnodon hopei	Macropus rufus	Australasia
Protemnodon nombe	Macropus giganteus	Australasia
Protemnodon tumbuna	Macropus giganteus	Australasia
Simosthenurus maddocki	Macropus giganteus	Australasia
Sthenurus andersoni	Macropus rufus	Australasia
Thylogale christenseni	Dorcopsulus vanheurni	Australasia
Troposodon minor	Macropus giganteus	Australasia
Wallabia kitcheneri	Macropus fuliginosus	Australasia
Aztlanolagus agilis	Lepus californicus	Neartic
Aztlanolagus agilis	Lepus californicus	Neotropic
Aztlanolagus agilis	Sylvilagus floridanus	Neotropic
Hystrix kiangsenensis	Hystrix brachyura	Indomalaya
Hystrix kiangsenensis	Hystrix brachyura	Paleartic
Hystrix refossa	Hystrix indica	Indomalaya
Hystrix refossa	Hystrix indica	Paleartic
Hexaprotodon sivalensis	Choeropsis liberiensis	Indomalaya
Cuvieronius hyodon	Elephas maximus	Neartic
Cuvieronius hyodon	Loxodonta africana	Neotropic
Notiomastodon platensis	Elephas maximus	Neotropic
Homotherium latidens	Panthera tigris	Paleartic
Homotherium serum	Panthera onca	Neartic
Homotherium serum	Panthera onca	Neotropic
Leopardus amnicola	Catopuma badia	Neartic
Leopardus amnicola	Leopardus wiedii	Neotropic
Miracinonyx trumani	Puma concolor	Neartic
Panthera atrox	Panthera tigris	Neartic
Panthera atrox	Panthera leo	Neotropic

Extinct	Replacement	Ecozone
<i>Panthera spelaea</i>	<i>Panthera tigris</i>	Neartic
<i>Panthera spelaea</i>	<i>Panthera tigris</i>	Paleartic
<i>Smilodon fatalis</i>	<i>Panthera tigris</i>	Neartic
<i>Smilodon fatalis</i>	<i>Panthera leo</i>	Neotropic
<i>Smilodon populator</i>	<i>Panthera leo</i>	Neartic
<i>Smilodon populator</i>	<i>Panthera tigris</i>	Neotropic
<i>Equus francisci</i>	<i>Equus ferus</i>	Neartic
<i>Equus francisci</i>	<i>Equus ferus</i>	Neotropic
<i>Equus hydruntinus</i>	<i>Equus ferus</i>	Paleartic
<i>Equus ovodovi</i>	<i>Equus ferus</i>	Paleartic
<i>Hippidion devillei</i>	<i>Equus ferus</i>	Neotropic
<i>Hippidion principale</i>	<i>Equus quagga</i>	Neotropic
<i>Elephas iolensis</i>	<i>Loxodonta africana</i>	Afrotropic
<i>Elephas iolensis</i>	<i>Loxodonta africana</i>	Paleartic
<i>Elephas namadicus</i>	<i>Elephas maximus</i>	Indomalaya
<i>Elephas namadicus</i>	<i>Elephas maximus</i>	Paleartic
<i>Elephas naumanii</i>	<i>Elephas maximus</i>	Indomalaya
<i>Elephas naumanii</i>	<i>Elephas maximus</i>	Paleartic
<i>Mammuthus columbi</i>	<i>Elephas maximus</i>	Neartic
<i>Mammuthus columbi</i>	<i>Elephas maximus</i>	Neotropic
<i>Mammuthus primigenius</i>	<i>Elephas maximus</i>	Indomalaya
<i>Mammuthus primigenius</i>	<i>Elephas maximus</i>	Neartic
<i>Mammuthus primigenius</i>	<i>Elephas maximus</i>	Paleartic
<i>Cryptonanus ignitus</i>	<i>Thylamys venustus</i>	Neotropic
<i>Dasyapus bellus</i>	<i>Dasyapus kappleri</i>	Neartic
<i>Dasyapus bellus</i>	<i>Dasyapus kappleri</i>	Neotropic
<i>Lagostomus crassus</i>	<i>Lagostomus maximus</i>	Neotropic
<i>Agalmaceros blicki</i>	<i>Odocoileus virginianus</i>	Neotropic
<i>Cervalces scotti</i>	<i>Alces alces</i>	Neartic
<i>Haploidoceros mediterraneus</i>	<i>Cervus elaphus</i>	Paleartic
<i>Megaloceros giganteus</i>	<i>Alces alces</i>	Paleartic
<i>Morenelaphus brachyceros</i>	<i>Ozotoceros bezoarticus</i>	Neotropic
<i>Navahoceros fricki</i>	<i>Odocoileus virginianus</i>	Neartic
<i>Navahoceros fricki</i>	<i>Odocoileus virginianus</i>	Neotropic
<i>Paraceros fragilis</i>	<i>Ozotoceros bezoarticus</i>	Neotropic
<i>Rucervus schomburgki</i>	<i>Rucervus eldii</i>	Indomalaya
<i>Sangamona fugitiva</i>	<i>Cervus canadensis</i>	Neartic
<i>Sinomegaceros ordosianus</i>	<i>Alces alces</i>	Paleartic
<i>Sinomegaceros yabei</i>	<i>Alces alces</i>	Indomalaya
<i>Sinomegaceros yabei</i>	<i>Alces alces</i>	Paleartic
<i>Neochoerus aesopi</i>	<i>Hydrochoerus hydrochaeris</i>	Neartic
<i>Neochoerus aesopi</i>	<i>Hydrochoerus hydrochaeris</i>	Neotropic
<i>Canis dirus</i>	<i>Canis lupus</i>	Neartic
<i>Canis dirus</i>	<i>Canis lupus</i>	Neotropic

Extinct	Replacement	Ecozone
Dusicyon avus	Lycalopex griseus	Neotropic
Protocyon troglodytes	Chrysocyon brachyurus	Neotropic
Theriodictis tarijensis	Chrysocyon brachyurus	Neotropic
Camelops hesternus	Camelus ferus	Neartic
Camelops hesternus	Camelus dromedarius	Neotropic
Hemiauchenia macrocephala	Lama guanicoe	Neartic
Hemiauchenia macrocephala	Lama guanicoe	Neotropic
Hemiauchenia paradoxa	Camelus dromedarius	Neotropic
Palaeolama major	Camelus dromedarius	Neotropic
Palaeolama mirifica	Lama guanicoe	Neartic
Palaeolama mirifica	Lama guanicoe	Neotropic
Palaeolama mirifica	Vicugna vicugna	Neotropic
Palaeolama weddelli	Camelus dromedarius	Neotropic
Antidorcas australis	Pelea capreolus	Afrotropic
Antidorcas bondi	Sylvicapra grimmia	Afrotropic
Bootherium bombifrons	Connochaetes taurinus	Neartic
Bubalus palaeokerabau	Bos javanicus	Indomalaya
CapriniGen spA	Tragelaphus scriptus	Afrotropic
Damaliscus hypsodon	Tragelaphus scriptus	Afrotropic
Damaliscus niro	Alcelaphus buselaphus	Afrotropic
Euceratherium collinum	Bison bison	Neartic
Euceratherium collinum	Bison bison	Neotropic
Gazella atlantica	Ammotragus lervia	Paleartic
Gazella bilkis	Capricornis crispus	Afrotropic
Gazella bilkis	Naemohedus caudatus	Afrotropic
Gazella bilkis	Procapra gutturosa	Afrotropic
Gazella bilkis	Procapra przewalskii	Afrotropic
Gazella bilkis	Eudorcas albonotata	Paleartic
Gazella saudiya	Gazella gazella	Afrotropic
Gazella saudiya	Gazella gazella	Paleartic
Gazella tingitana	Gazella cuvieri	Paleartic
Hemitragus cedrensis	Capra pyrenaica	Paleartic
Hippotragus leucophaeus	Alcelaphus buselaphus	Afrotropic
Hippotragus leucophaeus	Damaliscus pygargus	Afrotropic
Megalotragus priscus	Alcelaphus buselaphus	Afrotropic
Megalovis guangxiensis	Pseudois nayaur	Indomalaya
Megalovis guangxiensis	Pseudois nayaur	Paleartic
Oreamnos harringtoni	Ovis canadensis	Neartic
Oreamnos harringtoni	Ovis canadensis	Neotropic
Peloroavis antiquus	Bos primigenius	Paleartic
Rusingoryx atopocranion	Kobus ellipsiprymnus	Afrotropic
Sivacobus sankaliai	Capricornis thar	Indomalaya
Sivacobus sankaliai	Capricornis thar	Paleartic
Soergelia minor	Capra sibirica	Paleartic

Extinct	Replacement	Ecozone
Spirocerus kiakhtensis	Bos primigenius	Palaearctic
Caipora bambuorum	Brachyteles arachnoides	Neotropic
Protopithecus brasiliensis	Brachyteles arachnoides	Neotropic
Stockoceros conklingi	Antilocapra americana	Neartic
Stockoceros conklingi	Antilocapra americana	Neotropic
Tetrameryx shuleri	Antilocapra americana	Neartic
Tetrameryx shuleri	Antilocapra americana	Neotropic

References

- [1] Faurby S, Davis M, Pedersen RØ, Schowaneck SD, Antonelli A, Svenning J-C. PHYLACINE 1.2: The phylogenetic atlas of mammal macroecology. *Ecology* 2018;99:2626–6. doi:10.1002/ecy.2443.
- [2] Gravel D, Poisot T, Albouy C, Velez L, Mouillot D. Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution* 2013;4:1083–90.
- [3] Pomeranz JP, Thompson RM, Poisot T, Harding JS. Inferring predator–prey interactions in food webs. *Methods in Ecology and Evolution* 2019;10:356–67.
- [4] Phillips S. Maxnet: Fitting ‘maxent’ species distribution models with ‘glmnet’. 2017.
- [5] Jarvie S, Svenning J-C. Using species distribution modelling to determine opportunities for trophic rewilding under future scenarios of climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2018;373:20170446.
- [6] Svenning J-C, Pedersen PB, Donlan CJ, Ejrnæs R, Faurby S, Galetti M, et al. Science for a wilder anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences* 2016;113:898–906.
- [7] Janzen DH, Martin PS. Neotropical anachronisms: The fruits the gomphotheres ate. *Science* 1982;215:19–27.
- [8] Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW. Megafauna and ecosystem function from the pleistocene to the anthropocene. *Proceedings of the National Academy of Sciences* 2016;113:838–46.
- [9] Fick SE, Hijmans RJ. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 2017;37:4302–15.
- [10] O’Brien RM. A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity* 2007;41:673–90.
- [11] Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. Opening the black box: An open-source release of maxent. *Ecography* 2017;40:887–93.
- [12] Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of maxent for ecologists. *Diversity and Distributions* 2011;17:43–57.
- [13] Merow C, Smith MJ, Silander Jr JA. A practical guide to maxent for modeling species’ distributions: What it does, and why inputs and settings matter. *Ecography* 2013;36:1058–69.
- [14] Merow C, Smith MJ, Edwards Jr TC, Guisan A, McMahon SM, Normand S, et al. What do we gain from simplicity versus complexity in species distribution models? *Ecography* 2014;37:1267–81.
- [15] Guevara L, Gerstner BE, Kass JM, Anderson RP. Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. *Global Change Biology* 2018;24:1511–22.
- [16] Poo-Muñoz DA, Escobar LE, Peterson AT, Astorga F, Organ JF, Medina-Vogel G. *Galictis cuja* (mammalia): An update of current knowledge and geographic distribution. *Iheringia Série Zoologia*

2014;104:341–6.

- [17] Hof C, Voskamp A, Biber MF, Böhning-Gaese K, Engelhardt EK, Niamir A, et al. Bioenergy cropland expansion may offset positive effects of climate change mitigation for global vertebrate diversity. *Proceedings of the National Academy of Sciences* 2018;115:13294–9.
- [18] Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A. Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling* 2006;199:142–52.
- [19] Swets JA. Measuring the accuracy of diagnostic systems. *Science* 1988;240:1285–93.
- [20] Fielding AH, Bell JF. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 1997;24:38–49.
- [21] Liu C, Newell G, White M. On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution* 2016;6:337–48.
- [22] Lundgren EJ, Ramp D, Ripple WJ, Wallach AD. Introduced megafauna are rewilding the anthropocene. *Ecography* 2018;41:857–66.
- [23] IUCN. The iucn red list of threatened species, version 2016-3 2016.
- [24] Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology with r. Springer Science & Business Media; 2009.
- [25] Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, et al. Terrestrial ecoregions of the world: A new map of life on earth a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 2001;51:933–8.
- [26] Cohen J. Statistical power analysis for the behavioural sciences 1988.
- [27] Sawilowsky SS. New effect size rules of thumb. *Journal of Modern Applied Statistical Methods* 2009;8:597–9.
- [28] Chapron G, Kaczensky P, Linnell JD, Arx M von, Huber D, Andrén H, et al. Recovery of large carnivores in europe’s modern human-dominated landscapes. *Science* 2014;346:1517–9.
- [29] Deinet S, Ieronymidou C, McRae L, Burfield IJ, Foppen RP, Collen B, et al. Wildlife comeback in europe: The recovery of selected mammal and bird species 2017.
- [30] R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2018.
- [31] Wickham H. The tidyverse. R Package Ver 11 1 2017.
- [32] Hijmans RJ, Phillips S, Leathwick J, Elith J. Dismo: Species distribution modeling. 2017.
- [33] Pebesma E. Simple Features for R: Standardized Support for Spatial Vector Data. *The R Journal* 2018;10:439–46. doi:10.32614/RJ-2018-009.
- [34] Hijmans RJ. Raster: Geographic data analysis and modeling. 2019.
- [35] Corporation M, Weston S. DoParallel: Foreach parallel adaptor for the ‘parallel’ package. 2018.
- [36] Microsoft, Weston S. Foreach: Provides foreach looping construct for r. 2017.
- [37] Lüdtke D, Makowski D, Waggoner P. Performance: Assessment of regression models perfor-

mance. 2019.

[38] Lenth R. Emmeans: Estimated marginal means, aka least-squares means. 2019.

[39] Makowski D, Lüdecke D. Estimate: Estimate effects, contrasts and means. 2019.

[40] Olson DM, Dinerstein E. The global 200: Priority ecoregions for global conservation. *Annals of the Missouri Botanical Garden* 2002:199–224.

[41] Wickham H. Ggplot2: Elegant graphics for data analysis. Springer-Verlag New York; 2016.

[42] Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 2015;67:1–48. doi:10.18637/jss.v067.i01.