Rewiring food webs via trophic rewilding

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* Trophic interactions.

# Abstract

During the late-Quaternary, humans caused mass extinctions of vertebrates, with a selective size-bias towards large mammals, causing losses of top-down trophic processes in ecosystems. Trophic rewilding, the (re)introduction of species to promote self-sustaining biodiverse ecosystems, has been proposed as a restoration strategy to reinstate ecosystems’ trophic complexity. Yet, the extent of restoration possible via trophic rewilding is poorly understood. Here, we combined current ranges of terrestrial mammals, present natural distributions (counter-factual range estimates where human influence through time is considered negligible), and rewilding ranges together with food web inference to examine the effects of late-Quaternary extinctions on ecosystems’ trophic structure and potential recoveries through rewilding. Our results show that trophic complexity and top-down control in terrestrial ecosystems have been severely degraded by human activities and that trophic rewilding can partly rewire food webs and restore a large proportion of lost predator-prey interactions, reinstating ecosystems’ trophic structure. Under the rewilding scenario examined, however, ecosystems remained depleted of higher trophic levels and of top-down trophic interactions with small to large differences compared to natural conditions. Overall, our findings highlight the potential of trophic rewilding to promote self-sustaining, biodiverse ecosystems and stress the need to approach rewilding with a more open-minded perspective.

# Introduction

Humans have degraded ecosystems worldwide, removing from the environment species, their interactions, and the ecological processes associated with them (Ceballos et al., 2015; Dirzo et al., 2014; C. Sandom, Faurby, Sandel, & Svenning, 2014; Valiente-Banuet et al., 2015). Human-driven extirpations of mammals date back to at least the Late Pleistocene, with a large bodied size-selectivity likely causing extinctions of over half of megafauna genera (122 out of 234 genera ≥ 44 kg have gone extinct (Barnosky, 2008; Martin, 1984; C. Sandom et al., 2014; F. A. Smith, Smith, Lyons, & Payne, 2018)). As Late Pleistocene mammal extinctions acutely affected large body-sized species, interactions previously maintained by pre-human biodiverse megafauna assemblages have been removed from ecological networks, modifying ecosystem processes and functions (Faurby & Svenning, 2015; Gill, 2014; Malhi et al., 2016). For example, extirpations of apex predators have reduced control of prey densities and generated trophic cascades altering ecosystems structure and dynamics (Atkins et al., 2019; Estes et al., 2011; A. T. Ford et al., 2014; Ripple et al., 2014).

Trophic rewilding, the (re)introduction of species to restore lost ecological processes and promote self-sustaining biodiverse ecosystems (Svenning et al., 2016), has been proposed to re-establish lost ecological interactions (Perino et al., 2019). For example, reintroduction of wolves in the Yellowstone National Park have restored the landscape of fear and the top-down control effects promoted by large carnivores, re-establishing trophic cascades (Beschta & Ripple, 2016). Rewilding is not universally accepted, however, with criticism on both its conceptual and ecological validity (Hayward et al., 2019; Nogués-Bravo, Simberloff, Rahbek, & Sanders, 2016). In fact, data on rewilding are scarce, limited in time, and geographically biased (Tanentzap & 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). Despite evidence for the restoration potential from rewilding increasing (Perino et al., 2019), there is limited knowledge of the extent with which rewilding can rewire ecological networks with functionally similar interactions to pre-human conditions at global scale.

Macroecological and biogeographical approaches provide an appropriate framework to assess the potential of rewilding to rewire ecological networks at large scales and deep-time perspectives. These approaches can highlight similarities between extinct and extant species and suggest suitable ecological replacements for rewilding (Svenning & Faurby 2017). Moreover, inference of biotic interactions and reconstruction of prehistoric ecological networks can be used to­ examine the consequences of human-driven extinctions and extirpations of large mammals (Marjakangas et al., 2018; Pires et al., 2015; Yeakel et al., 2014). By combining a rewilding scenario supported by paleoecological data with macroecologically-grounded reconstructions of interaction networks it is possible to infer rewilding communities and interactions as well as examine the potential of rewilding to rewire ecological networks to pre-human conditions (M. M. Pires, 2017).

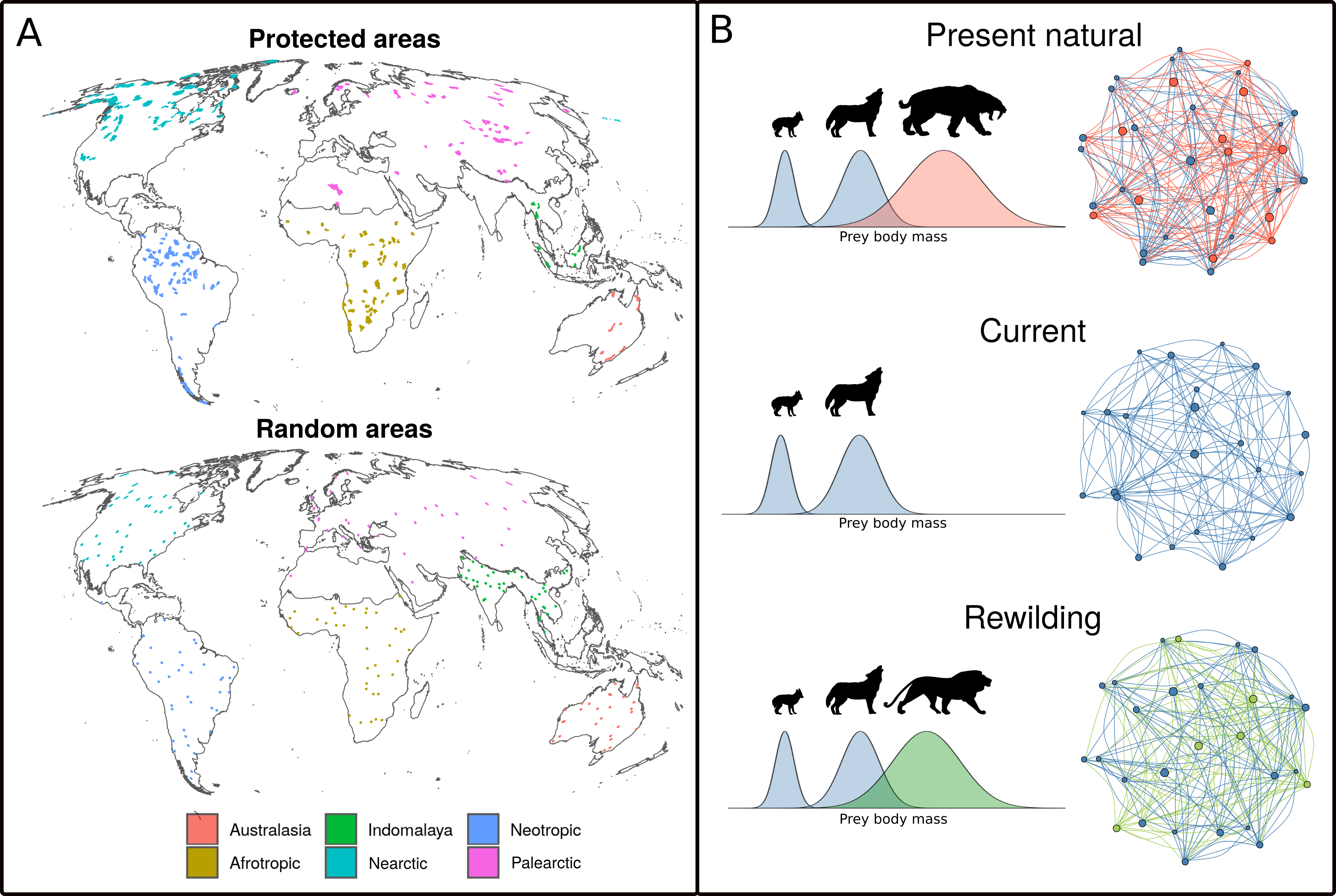


Fig #. A) Map showing protected areas >= 5,000 km^2 (top) and random areas >= 5,000 km^2 (bottom) included in the study. Colours show the six Ecozones included in the study. B) Conceptual representation of the framework used. Dietary niches of species were derived using phylogenetic and trait-based approaches and food webs were inferred using species' diet and geographic distributions under the three scenarios examined. In the network representation of the food webs, species are nodes and predator-prey interactions are edges. Late Pleistocene human-driven extinctions have removed species and trophic interactions (red nodes and edges). Trophic rewilding aims to restore lost interactions by replacing extinct species with suitable ecological analogues (green nodes) that can rewire food webs establishing functionally analogue links (green edges).

In this study, we investigate the potential of rewilding to rewire terrestrial mammal food webs to pre-*Homo sapiens* conditions in large (>=5,000 km^2) areas worldwide. Specifically, we infer food webs for three scenarios: 1) present natural, i.e. a counter-factual scenario where mammals have not been influenced by human activities through time (Faurby & Svenning, 2015; Faurby et al., 2018); 2) current conditions; and 3) a rewilding scenario where extant species can re-expand to present natural ranges and extinct species can be replaced by closely related, similarly sized functional analogues that tolerate similar climates. We then compare the food webs for the three scenarios to investigate how much current food webs are impoverished of predator-prey interactions and whether rewilding can rewire food webs to a pre-human state. Specifically, building on the terminology of Genes, Cid, Fernandez, & Pires (2017), we quantify: a) current debt, i.e. how many species and interactions have been lost because of past extinctions; b) rewilding credit, i.e. how many lost species and interactions can be reintroduced or replaced under the rewilding scenario; and c) rewilding deficit, i.e. how much past losses cannot be restored via rewilding. By comparing debt, credit, and deficit, we assess if rewilding credit can balance current debt.

# Materials and methods

Specifically, building on the terminology of Genes, Cid, Fernandez, & Pires (2017), we quantify: a) current debt, i.e. how many species and interactions have been lost because of past extinctions; b) rewilding credit, i.e. how many lost species and interactions can be reintroduced or replaced under the rewilding scenario; and c) rewilding deficit, i.e. how much past losses cannot be restored via rewilding. By comparing debt, credit, and deficit, we assess if rewilding credit can balance current debt.

We quantified current extinction debt and rewilding credit and deficit in large (>= 5,000 km^2) protected areas (n = 209) with strict International Union for Conservation of Nature (IUCN) management category (Ia, Ib, and II). Rewilding is more feasible in large, strictly managed protected areas and human-wildlife coexistence less problematic. However, these large protected areas are concentrated in areas with low biodiversity (Daru et al., 2019); we therefore repeated the analyses using counter-factual areas >= 5,000 km^2 (n = 206) randomly scattered worldwide to investigate a global rewilding scenario without geographic biases. In summary, i) we ran correlative species distribution models (SDMs) to identify climatically suitable habitat for terrestrial mammals, ii) we then selected for each globally extinct species a closely related, similarly sized functional analogue, following conservative criteria, iii) we inferred food webs under present natural, current, and rewilding scenarios and iv) contrasted them to examine if rewilding can restore current defaunated food webs to pre-human conditions. We ran the analyses for protected and random areas separately; in the following sections we describe in details the methods used for protected areas, implying that the same was done for random areas where applicable.

## Species distribution models

Correlative SDMs are projections in geographic space of species' environmental suitability niches reconstructed through correlation of species' presence with abiotic environmental predictors (Elith & Leathwick, 2009). 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). Following previous descriptions of PHYLACINE (Faurby & Svenning, 2015; Faurby et al., 2018), current ranges were generated from the IUCN range polygon maps for current, natural, and reintroduced ranges only (IUCN, 2016). 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 & Svenning, 2015). The present natural ranges combine knowledge of species' current IUCN range with historic distributions, fossil co-occurrence data, and range modifications caused by humans (Faurby & Svenning, 2015; Faurby et al., 2018). We generated presence locations within combined current and present natural range maps with a 20 km separation distance, excluding locations reported above the highest elevation for each species in the IUCN Red List or, if not stated, 4,000 meters, which is roughly the 95 percentile for upper elevations of mammals (IUCN, 2016). Elevation was determined for presence locations using the EarthEnv-DEM90 digital elevation model (Robinson, Regetz, & Guralnick, 2014). In total, we identified 4,206 extant terrestrial mammal species with range maps.

As environmental predictors for the correlative SDMs, we used four climatic variables from the Worldclim database (Fick & Hijmans, 2017): maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of wettest quarter, and precipitation of driest quarter. We selected these variables as they capture extreme conditions and, thus, likely represent factors limiting the distributions of terrestrial mammals. To model the climatic suitability of terrestrial mammals, we fitted maximum entropy (Maxent) models as implemented in the recently released *maxnet* R-package (S. J. Phillips, Anderson, Dudík, Schapire, & Blair, 2017). Maxent is a presence-background approach, in which environments occupied by a species are contrasted with the available environmental space (Elith et al., 2011; Merow, Smith, & Silander Jr, 2013). For the background areas, we calculated species-specific buffers around the combined current and present natural ranges to reflect the dispersal abilities of each species, where the maximum distance from the range centroid to the range edge was used (Hof et al., 2018; Poo-Muñoz et al., 2014). When a species had a disjunct range, the buffer area was calculated from the largest continuous range following Hof et al. (2018) (see electronic supplementary material, figure S1). We excluded 76 species with restricted ranges from modelling distributions as they had less than 10 presence points. In total, we modelled 4,130 of the 4,206 living terrestrial mammals. Predictive performance and model overfitting were assessed through five-fold cross validation and by comparing predicted suitable ranges with introduced range maps from IUCN (2016) and Lundgren, Ramp, Ripple, & Wallach (2018), which were not used to train Maxent models (Appendix #).

## Rewilding selection criteria

Following previous studies (Fig #; Berti et al. in prep; Jarvie et al. in prep), we searched for rewilding candidates that were phylogenetically close and functionally similar to globally extinct species and that could tolerate climatic conditions of their ranges. We always prioritized population restorations, i.e. reintroductions into present natural ranges, over introductions of functional analogues, as moving species’ outside their indigenous range is inherently riskier than reintroductions due to unforeseeable uncertainties and ecological risks (**Fernández et al. 2017**). For each globally extinct species, we selected as rewilding replacements the species from the same family that had similar size (within the 50% range of extinct species' body mass) and that had the largest climatically suitable range within the present natural of the extinct species. Because several proboscidean families went globally extinct, the two living extant elephants of the *Proboscidea* order (*Elephas maximus* and *Loxodonta africana*) were allowed to replaced other megaherbivores (>= 1,000 kg; Malhi et al. (2016)) within the *Proboscidea* order, as *E. maximus* and *L. africana* are frequently considered as ecological similar to extinct members of this group (J. Donlan, 2005; Janzen & Martin, 1982; Josh Donlan et al., 2006). Also, megacarnivores (>= 100 kg) within *Felidae* and *Ursidae* families were allowed to replace any other megacarnivore within the respective families, as they likely play similar ecological roles regulating the abundance and activity of large herbivores that are smaller than megaherbivores (Atkins et al., 2019; A. T. Ford et al., 2014; Laundré, Hernández, & Ripple, 2010; Ripple et al., 2014).

We assessed rewilding replacements separately for each ecozone, biogeographic realms characterized by separated evolutionary histories and patterns of extinctions (Malhi et al., 2016; Olson et al., 2001), as they delimit areas within which ecological and evolutionary processes operate most strongly (Olson & Dinerstein, 2002; Olson et al., 2001). We excluded ecozones for Antarctic and Oceania because they do not have extant terrestrial mammals or large protected areas >= 5,000 km^2, respectively. To avoid possible negative impacts of introducing functional analogues into the present-natural ranges of similarly-sized -- i.e. within 50% of the body mass -- extant species of the same taxonomic group, we excluded introductions of rewilding candidates if their proposed ranges overlapped with the ranges of reintroduced species. This was done to limit the risk of displacing extant native species through competition (Linnell & Strand, 2000). If there were more than one rewilding candidate identified, we selected as the species that had the largest climatically suitable range overlapping with the present-natural range of the extinct species in the focal ecozone. We did not select species for rewilding that violated any of the above criteria. See electronic supplement material, figure S# for a schematic representation of the selection criteria.

## Reconstructing food webs

We reconstructed mammal assemblages within 209 large terrestrial protected areas (≥ 5,000 km2; figure 1), selected from the World Database of Protected Area (UNEP-WCMC & IUCN (2019), downloaded on June 2019). Following previous global studies (Jones et al., 2018; Runge et al., 2015), we excluded protected areas without detailed geographic information, proposed and designated sites not considered protected areas internationally, sites with an unknown status, UNESCO Biosphere Reserves, and marine-only sites as well as the marine portion of coastal sites. As large areas with limited human use facilitate establisingh self-sustaining population of large mammals (Chundawat, Sharma, Gogate, Malik, & Vanak, 2016; Woodroffe & Ginsberg, 1998), we kept only protected areas with strict IUCN management category (Ia, Ib, and II) and total surface ≥ 5,000 km2 after dissolving adjacent areas together. To investigate the effects of human activities outside the current network of protected areas, which does not overlap with biodiversity hotspots (Daru et al., 2019), we reconstructed food webs also for counter-factual areas randomly distributed around the World (figure 1). For each area, we obtained mammal assemblages under present natural and current scenarios using present natural (including extinct species) and current range maps from the PHYLACINE database (Faurby et al., 2018). The rewilding assemblage was estimated from combined reintroduction (present natural including only extant species and current distributions) and rewilding ranges obtained using SDMs and selection of the best candidate functional analogues for extinct species.

We constructed food webs for each area by combining phylogenetic inference with a trait-based approach (Pomeranz et al. 2019) . Phylogeny has been shown to be a good predictor of trophic interactions (Eklöf, Helmus, Moore, & Allesina, 2011), as studies show that species share more similar resources the more closely they are related (Gray et al., 2015). We performed phylogenetic inference at the family level, a reasonable 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 respective families. We then used a trait-based approach to remove interactions inferred using phylogeny that were not supported by macroecological evidence (Pomeranz, Thompson, Poisot, & Harding, 2019). This trait-based approach uses the relationship between the body mass of prey and predators, which structures trophic interactions in current and Pleistocene food webs (Owen-Smith & Mills, 2008; Segura, Farina, & Arim, 2016; Williams & Martinez, 2000). Following previous studies (Gravel, Poisot, Albouy, Velez, & Mouillot, 2013; Pomeranz et al., 2019), we used the 10% and 90% regression quantiles to obtain dietary niches of carnivores, i.e. the body mass range of their prey. We performed the quantile regression on data from the ECOWeB database (J. E. Cohen, 2010), the Global Biotic Interactions (GLOBI) database (Poelen, Simons, & Mungall, 2014), and two published savannah food webs (Baskerville et al., 2011; Visser, Freymann, & Olff, 2011).

After food webs were inferred, we assigned species to trophic levels by diet and body mass, reflecting the trophic and ecological role of species in food webs (Malhi et al. 2016). For carnivores, we divided them into three groups: i) megacarnivores ≥ 100 kg, which are generally apex predators and dominate food webs; ii) large carnivores 21.5 - 99 kg, which can predate on large prey and are subjected to top-down control from megacarnivores; and iii) small carnivores < 21.5 kg, which can predate only on smaller prey (Carbone, Mace, Roberts, & Macdonald, 1999). For herbivores, we also divided them into three functional groups: i) megaherbivores ≥ 1,000 kg, which are mostly free from predation; ii) large herbivores 45 - 999 kg, which are predated only by large carnivores and megacarnivores; and iii) small herbivores < 45 kg, which are predated and therefore controlled by all carnivores trophic levels.

## Statistical analyses

For each food web under current, present natural, and rewilding scenarios, we calculated: 1) the number of species present at each trophic level, and 2) the number of predator-prey interactions connecting different trophic levels. In particular, we compared the number of species in each trophic level between present natural and current conditions to estimate current trophic richness debt, and between current and rewilding scenarios to assess rewilding trophic richness credit. Similarly, we compared the number of trophic interactions across trophic levels between present natural and current and between current and rewilding scenarios to obtain the current interaction debt and the rewilding interaction credit. Moreover, we investigated the difference in the number of species per trophic level and the number of interactions between trophic level under present natural and rewilding scenarios to quantify the amount of current debts that cannot be balanced by rewilding credit. We called this difference "rewilding deficit".

To estimate significance and magnitude of differences among the above scenarios, we used generalized linear mixed models (GLMMs). We selected the error distribution for the GLMMs based on the response data type and to remedy overdispersion (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). 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 (Olson et al., 2001). 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 (J. Cohen, 1988; Sawilowsky, 2009).

All data processing and analyses were performed in the R programming language version 3.6.1 (R Core Team, 2018) using packages tidyverse (Wickham, 2017), maxnet (S. Phillips, 2017), dismo (R. J. Hijmans, Phillips, Leathwick, & Elith, 2017), sf (Pebesma, 2018), raster (R. J. Hijmans, 2019), doParallel (Corporation & Weston, 2018), foreach (Microsoft & Weston, 2017), quantreg (Koenker, 2019), performance (Lüdecke, Makowski, & Waggoner, 2019), emmeans (Lenth, 2019), and estimate (Makowski & Lüdecke, 2019). All spatial analyses were conducted using the Behrmann cylindrical equal-area projection. Ecozones were derived using the World Wildlife Foundation shapefile ([WWF](https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world), Olson & Dinerstein (2002)). Figures were made using packages ggplot2 (Wickham, 2016) with maps displayed in the Molleweide projection.

# Results

Predictive performance of SDMs was on average very high to excellent, while model overfitting was generally low (electronic supplementary material, Table S1 and figure S2). The projected climatic suitability ranges captured much of the known introduction ranges of species obtained from Lundgren et al. (2018) and IUCN (2016) (electronic supplementary material, Table S1 and figure S2). These results indicate the SDMs give…. Due to our conservative rewilding selection criteria, we found no replacements for the extinct families *Archaeolemuridae*, *Chaeropodidae*, *Diprotodontidae*, *Macrauchenidae*, *Megaladapidae*, *Megatheriidae*, *Mylodontidae*, *Nesophontidae*, *Nothrotheridae*, *Palaeopropithecidae*, *Prolagidae*, *Proterotheriidae*, *Thylacinidae*, *Thylacoleonidae*, and *Toxodontidae*. In total, we identified 94 living species that could be used as ecological replacements for 127 of the 334 extinct terrestrial mammals (electronic supplementary material, Table S3).

In large protected areas ≥ 5,000 km2, we found a lower number of species in trophic levels under current conditions than in the present natural scenario except for small herbivores and small carnivores (Table 1, figure 1). The biggest decrease in numbers were for megacarnivores, megaherbivores, and large herbivores, with large (Cohen's *d* ≥ 0.80) or very large (*d* ≥ 1.20) differences. Under the rewilding scenario, the number of megacarnivores, megaherbivores, and large herbivores significantly increased from current conditions, with small or medium effect sizes. For large carnivores, however, the number of species did not increase significantly under rewilding. Nevertheless, the total number of species for trophic levels to present natural levels for megacarnivores, megaherbivores, large carnivores, and large herbivores remained much smaller than the present natural.

In large random areas we observed similar, but more pronounced patterns than in large protected areas (figure 2). All trophic levels, except small herbivores and small carnivores, have been heavily depleted (Table 1). Compared to protected areas, the effect sizes for large random areas were equal or greater. For the conservative rewilding scenario, species richness at each trophic level richness increased from current conditions but not to present natural levels. The recovery was larger in magnitude compared to protected areas. Notably, rewilding deficit, i.e. the difference between rewilding and present natural trophic level richness, was comparable between random and protected areas (Table 1), showing a similar relative restoration potential of trophic rewilding. The effect of late-Quaternary extinctions and extirpations was generally higher in random areas than in protected areas, although the restoration potential from rewilding was also higher in the random areas as the number of species per trophic level increased in similar proportions in protected and random areas.

Table 1: Differences between regression coefficients estimates from generalised linear mixed models for the number of species per trophic level among scenarios: present natural, current, and rewilding. The differences were obtained by performing multiple pair-wise contrasts accounting for variation across Ecozones and food webs. Superscripts show the *p*-value of the contrasts adjusted with a Bonferroni correction and subscripts show the magnitude of the effect size of the change using Cohen's *d*.

| Trophic level | Present natural - Current | Current - Rewilding | Present natural - Rewilding |
| --- | --- | --- | --- |
|  | **Protected areas** |  |  |
| Megacarnivores (≥100 kg) | 1.240.00very large | -0.600.00medium | 0.640.00medium |
| Megaherbivores (≥1,000 kg) | 1.790.00very large | -0.610.00medium | 1.180.00large |
| Large carnivores (21.5 - 99 kg) | 0.350.00small | -0.130.06very small | 0.220.00small |
| Large herbivores (45 - 999 kg) | 0.820.00large | -0.330.00small | 0.490.00small |
| Small carnivores (< 21.5 kg) | 0.060.01very small | -0.040.19very small | 0.020.79very small |
| Small herbivores (< 45 kg) | 0.030.40very small | -0.011.00very small | 0.021.00very small |
|  | **Random areas** |  |  |
| Megacarnivores (≥100 kg) | 1.890.00very large | -1.210.00very large | 0.670.00medium |
| Megaherbivores (≥1,000 kg) | 2.490.00huge | -1.310.00very large | 1.190.00large |
| Large carnivores (21.5 - 99 kg) | 0.680.00medium | -0.480.00small | 0.200.00small |
| Large herbivores (45 - 999 kg) | 1.100.00large | -0.590.00medium | 0.500.00medium |
| Small carnivores (< 21.5 kg) | 0.090.00very small | -0.070.01very small | 0.020.92very small |
| Small herbivores (< 45 kg) | 0.040.06very small | -0.020.57very small | 0.020.91very small |

Table 1: Differences between regression coefficients estimates of the number of species per trophic level among scenarios. Differences were obtained performing multiple pair-wise contrasts accounting for variation across Ecozones and food webs. Superscripts show the p-value of the contrasts adjusted with the Bonferroni correction and subscripts show the effect size of the change (Cohen's *d* (J. Cohen, 1988; Sawilowsky, 2009)).

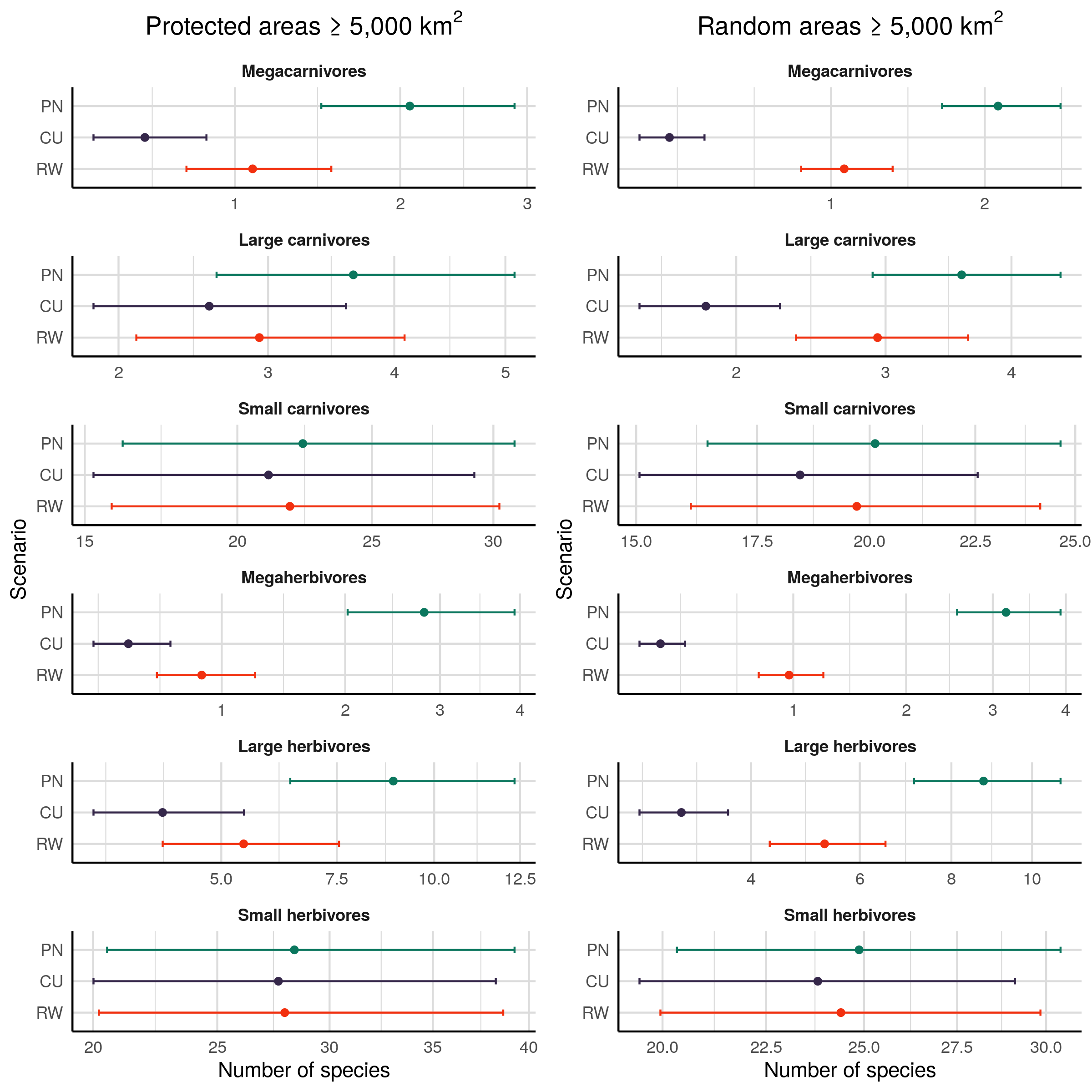


Fig #. Number of species per trophic level for protected areas ≥ 5,000 km2 (A) and for random areas ≥ 5,000 km2 (B) under the three scenario examined: PN, present natural; CU, current; RW, rewilding. In all trophic levels except small herbivores, human-driven extinctions and extirpations have significantly reduced the number of species. A conservative rewilding approach can partly replenish the species pool through reintroduction and introduction of mammals as ecological replacements for globally extinct species, but the number of species in each trophic level cannot be fully restored to natural levels, as many extinct species do not have today functional analogues that are also phylogenetically closely related. Notably, rewilding has higher restoration potential outside protected areas, where the impact of human pressure on trophic level species richness has been particularly severe.

The number of interactions among trophic levels decreased between present natural and current conditions in both protected and random areas (Fig. 3). All interactions that involved megacarnivores as predators were severely reduced under current conditions compared to the present natural, with very large effect sizes (Table 2). Predator-prey interactions maintained by large carnivores also decreased between present natural and current conditions, with a large decrease in the number of predator-prey interactions between large herbivores and large carnivores and small reductions in the number of interactions between small mammals and large carnivores. Under the rewilding scenario the number of interactions between trophic levels that have decreased between present natural and current onditions increased with small to large effect sizes, with the only exception being for large herbivore--large carnivores interactions. Rewilding credit did not balance current debt as trophic interactions were not completely restored to present natural levels. The number of large herbivores--large carnivores interactions and all trophic links involving megacarnivores did not increase to present natural levels, with medium to large magnitudes of the difference (Table 2). For trophic level richness, results were qualitatively similar between protected and random areas, but that extinctions debt and rewilding credit were higher in random areas. Rewilding deficit was comparable between protected and random areas, showing that food webs were rewired to similar relative extent in both areas.

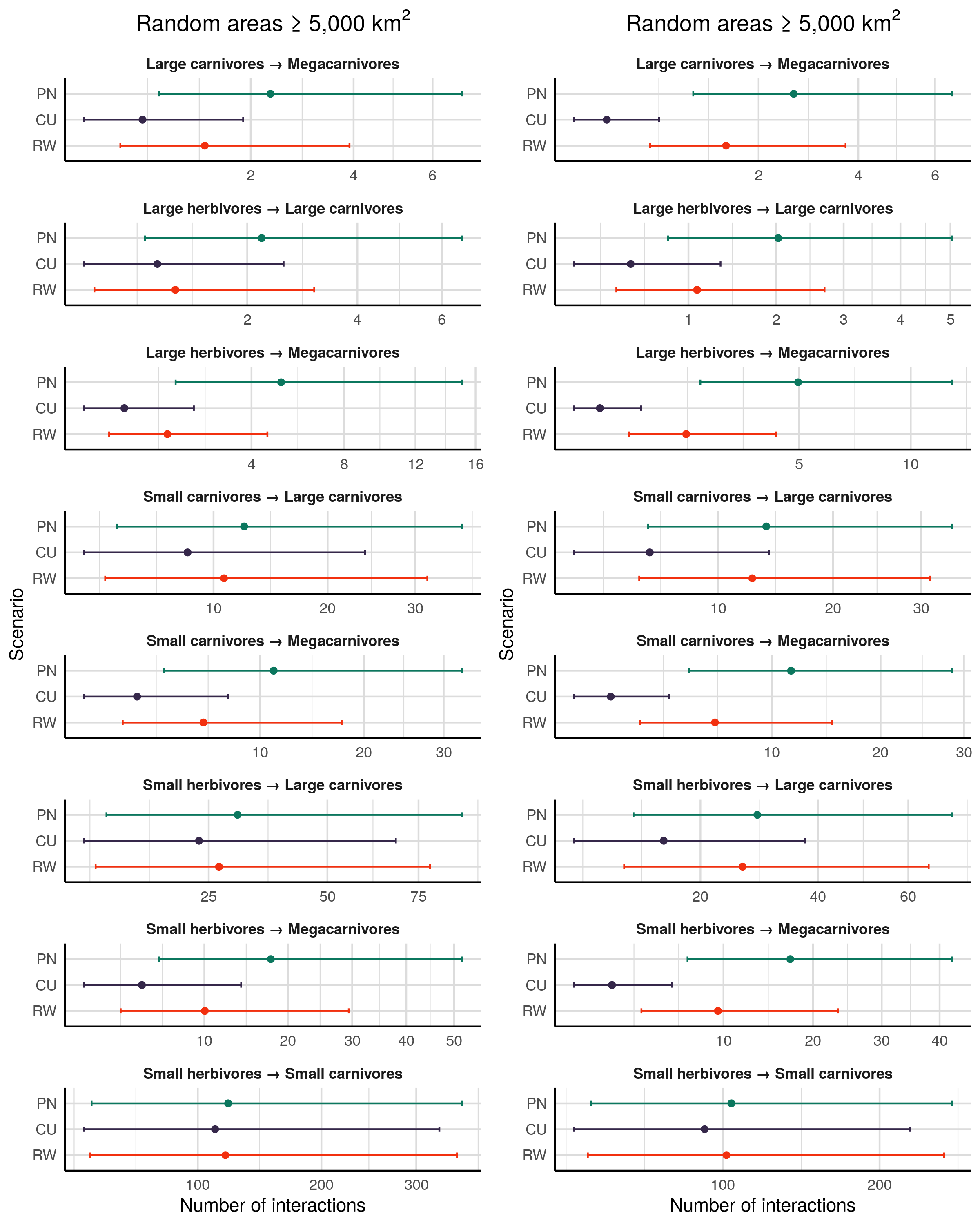


Fig #. Number of predator-prey interactions across trophic levels under each scenarios for protected areas ≥ 5,000 km2 (left) and for random areas ≥ 5,000 km2 (right) under the three scenario examined: PN, present natural; CU, current; RW, rewilding. Top-down interactions promoted by megacarnivores (≥ 100 kg) and large carnivores (≥ 21.5 kg) have been largely removed following Late Pleistocene and late-Quaternary extinctions. Trophic rewilding can restore trophic structure by rewiring food webs with lost or functionally analogue predator-prey interactions. However, a full recovery to pre-human conditions cannot be achieved under the conservative rewilding strategy examined.

Table 2: Differences between regression coefficients estimates from generalised linear mixed models for the number of predator-prey interactions between trophic levels : present natural, current, and rewilding. The differences were obtained by performing multiple pair-wise contrasts accounting for variation across Ecozones and food webs. Superscripts show the p-value of the contrasts adjusted with the Bonferroni correction and subscripts show the effect size of the change (Cohen's *d* (J. Cohen, 1988; Sawilowsky, 2009)).

| Prey | Predator | Present natural - Current | Current - Rewilding | Present natural - Rewilding |
| --- | --- | --- | --- | --- |
|  |  | **Protected areas** |  |  |
| Large carnivores | Megacarnivores | 1.300.00very large | -0.730.00medium | 0.560.00medium |
| Large herbivores | Megacarnivores | 1.920.00very large | -0.740.00medium | 1.190.00large |
| Small carnivores | Megacarnivores | 1.450.00very large | -0.840.00large | 0.620.00medium |
| Small herbivores | Megacarnivores | 1.310.00very large | -0.740.00medium | 0.570.00medium |
| Large herbivores | Large carnivores | 0.930.00large | -0.190.17very small | 0.740.00medium |
| Small carnivores | Large carnivores | 0.410.00small | -0.270.00small | 0.140.07very small |
| Small herbivores | Large carnivores | 0.260.00small | -0.140.04very small | 0.120.09very small |
| Small herbivores | Small carnivores | 0.080.37very small | -0.060.67very small | 0.021.00very small |
|  |  | **Random areas** |  |  |
| Large carnivores | Megacarnivores | 2.260.00huge | -1.700.00very large | 0.560.00medium |
| Large herbivores | Megacarnivores | 2.670.00huge | -1.600.00very large | 1.080.00large |
| Small carnivores | Megacarnivores | 2.050.00huge | -1.420.00very large | 0.630.00medium |
| Small herbivores | Megacarnivores | 1.990.00very large | -1.400.00very large | 0.590.00medium |
| Large herbivores | Large carnivores | 1.340.00very large | -0.720.00medium | 0.630.00medium |
| Small carnivores | Large carnivores | 0.890.00large | -0.800.00large | 0.090.56very small |
| Small herbivores | Large carnivores | 0.640.00medium | -0.550.00medium | 0.090.51very small |
| Small herbivores | Small carnivores | 0.140.05very small | -0.120.15very small | 0.031.00very small |

Table 2: Differences between regression coefficients estimates of the number of predator-prey interactions between trophic levels among scenarios. Differences were obtained performing multiple pair-wise contrasts accounting for variation across Ecozones and food webs. Superscripts show the p-value of the contrasts adjusted with the Bonferroni correction and subscripts show the effect size of the change (Cohen's *d* (J. Cohen, 1988; Sawilowsky, 2009)).

# Discussion

During the last 50,000 years, the expansion of modern humans have been associated with species’ extinctions and extirpations, with a large-bodied size selectivity (Martin, 1984; F. A. Smith et al., 2018). These extinctions degraded ecological networks by removing predator-prey interactions that control ecosystems' trophic structure (Malhi et al., 2016). A recently proposed approach to restore ecosystems and rewire ecological networks is trophic rewilding, the (re)introduction of species to promote biodiverse, self-sustaining ecosystems (Perino et al., 2019; Svenning et al., 2016). Empirical studies at a local scale suggest rewilding can be an effective strategy for biodiversity conservation and ecosystem restoration, e.g. by maintaining semi-open landscapes and reinstating lost ecological interactions (Garrido et al., 2019; Genes et al., 2019; Riesch, Tonn, Meißner, Balkenhol, & Isselstein, 2019). However, the potential of rewilding to restore ecological networks to present-natural levels at a global scale has not been investigated so far. We fill this knowledge gap by taking a deep-time, large scale perspective on trophic rewilding. Our results suggest that rewilding can rewire food webs, but that full restoration is not possible under a conservative rewilding scenario that minimises ecological risks and human-wildlife coexistence and conflict.

Our findings show that trophic levels of large body-size species were, not surprisingly, the most affected by human pressure. Previous studies corroborate these findings by … The number of megacarnivores and megaherbivores significantly reduced due to extinctions, followed by large carnivores and large herbivores that also had significant but relatively smaller decreases in numbers. As a consequence of these species' losses, trophic interactions maintained by higher trophic levels were pruned away, the top-down control of higher to lower trophic levels decreased, and ecosystem trophic structure got degraded. Importantly, as trophic complexity is necessary for self-sustaining biodiverse ecosystems (Perino et al., 2019), the removal of … food webs complexity and community trophic structure likely jeopardises stability and resilience of ecosystems (Estes et al., 2011).

We found that trophic level richness and interactions debts due to past extinctions can, in part, be balanced by rewilding credit. The reintroduction of species into their present natural ranges together with replacement of globally extinct species with functional analogues increased the number of species in affected trophic levels with medium to large effect sizes, showing intermediate-high potential for recovery. Although the number of trophic interactions for trophic levels significantly impacted by extinctions increased, this was not to pre-human levels. Our findings therefore highlight the potential of a conservative rewilding scenario to restore food webs to more self-sustaining, biodiverse states. Full restoration to pre-human levels, however, cannot be achieved under this rewilding scenario, where replacement of extinct species was phylogenetically constrained.

Our results also show that extinction debt and rewilding credit are higher in large random areas than in large protected areas with strict IUCN management (Ia, Ib, and II). Although human land-use is concentrated in highly productive areas that potentially host higher biodiversity and species richness (Venter et al., 2018), the network of protected areas has limited coverage for current mammalian biodiversity hotspots (Daru et al., 2019). As a consequence, current extinction debt is lower in protected areas than random areas, where human pressure caused larger losses of species and interactions and degraded ecosystems more severely. The consequence of this is because random areas have higher potential species richness and trophic complexity than protected areas, rewilding credit and restoration potential are higher in the counter-factual random areas than in protected areas. This suggests trophic rewilding will rewire food webs most effectively outside the current network of large protected areas. Importantly, rewilding deficit is comparable between protected and random areas, showing a similar relative potential of rewilding to restore trophic structure of ecosystems. Even if losses and recoveries are higher in random areas than in protected areas, the relative level of restoration that can be achieved via trophic rewilding are comparable. These results highlight the importance of rewilding strategies targeting also regions outside the protected area network, where (re)introductions of mammals will rewire food webs to pre-human conditions to larger extents and greatly restore ecosystems trophic structure.

Rewilding may increase the … human-wildlife coexistence and conflict in many areas, especially outside the network of protected areas, and society will play an important role in rewilding implementation and success (Perino et al., 2019). Rewilding may cause economic losses to some local stakeholders via predation on livestock or damages to crops and pastures. Moreover, people not directly damaged by wildlife can negatively perceive rewilding projects depending on how rewilding is implemented (Theunissen, 2019). Nevertheless, negative effects of rewilding can be mitigated by the adoption of compensation schemes by governmental agencies (Navarro & Pereira, 2015) and by aligning scientific, managers, and people's conception of nature with rewilding goals (Theunissen, 2019). In particular, identifying benefits and costs of wildlife in a socio-ecological framework can highlight possible actions to remedy unwanted outcomes of rewilding initiatives (Ceauşu, Graves, Killion, Svenning, & Carter, 2019). Also, the goals of traditional ecosystem conservation and restoration strategies and rewilding may not be so different as perceived (Van Meerbeek, Muys, Schowanek, & Svenning, 2019), and looking for a common ground and mutual understanding among scientific community, practitioners, and local communities will determine whether rewilding will be successful (R. M. Anderson et al., 2019).

In conclusion, our study shows that trophic complexity has been severely degraded worldwide and that a conservative rewilding strategy can partly, but not completely, restore trophic complexity in ecosystems. To rewire food webs to pre-human conditions, rewilding needs to be taken with a bolder approach. In particular, we simulated a conservative rewilding scenario with strict phylogenetic constraints; by focusing on species' functional traits rather than phylogenetic relationships, a larger number of extinct species can probably be replaced, raising the potential of rewilding to rewire food webs. Rewilding will probably be a controversial topic for long time and its implementation needs further improvements to secure the long-term restoration goals (Root-Bernstein, Gooden, & Boyes, 2018). This does not mean however that rewilding should be ostracised as a failing or unnecessary restoration strategy, but rather that policy makers, societal agencies, managers, and ecologists need to discuss and improve why and how rewilding is implemented. New opportunities for implementing rewilding are occurring at local to regional scales, as recently shown by the return of wildlife in abandoned agricultural areas in Europe (Ceausu et al., 2015; Chapron et al., 2014). Human intervention at these large scales will unlikely be possible because of limited funding and resources, if and how rewilding is adopted will determine whether trophic complexity is restored or not in ecosystems. Overall, our findings show that a conservative rewilding strategy is a good starting point to restore ecosystems' trophic structure, but that rewilding cannot be so conservative and its restrictions need to be relaxed if the long-term goal is to achieve self-sustaining biodiverse ecosystems.

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# Data accessibility

All data used was open access. Predator-prey interactions were obtained from the ECOWeB and GLOBI databases (J. E. Cohen, 2010; Poelen et al., 2014), and from two published savanna food webs (Baskerville et al., 2011; Visser et al., 2011). Body mass and current and present-natural ranges were obtained from the PHYLACINE 1.2 database (Faurby et al., 2018). We used climate data from the Worldclim 2.0 database (Fick & Hijmans, 2017), elevation data from the EarthEnv-DEM90 digital elevation model (Robinson, Regetz, & Guralnick, 2014), and the Ecozone shapefile from the WWF (Olson & Dinerstein, 2002).

# Author contribution

EB conceived and developed the study, performed the analyses, and drafted the manuscript.

SJ and JCS conceived and developed the study, interpreted the results, and helped revise the manuscript. All authors gave final approval for publication.EB conceived the idea, performed the analyses, and prepared the manuscript for submission.

# Competing interests

We have no competing interests.

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