

# Rewiring food webs in protected areas through trophic rewilding

Globally downgraded food webs in protected areas can be partially rewired through trophic rewilding

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## Keywords

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## Introduction

Protected areas are a key instrument for biodiversity conservation, but generally harbour impoverished faunas and downgraded food webs due to the human-linked prehistoric and historic megafauna extinctions. This trophic downgrading may challenge their functionality, but may be remedied through trophic rewilding, an ecological restoration strategy that uses species introductions to restore top-down trophic interactions. Yet the extent to which extant species can rewire food webs to pre-extinction levels is poorly understood. Using current and estimated natural ranges of all extant and extinct late-Quaternary mammals, we modelled climatic suitability to identify species for reintroductions or introductions as functional analogues to replace closely-related, similar-sized extinct species. We then inferred food webs in large protected areas (PAs) and assessed the consequences of past losses for trophic complexity and the recoveries opportunities through rewilding. Our results show that species richness of high trophic levels has declined following late-Quaternary extinctions and that the number of trophic interactions decreased in PAs on average by 49%. We also found that trophic rewilding would be able to rewire on average 18% of the lost interactions through reintroductions and introductions of functional analogues. Overall, our findings support trophic rewilding as an opportunity to rewire food webs in PAs globally and reinstate lost trophic interactions in degraded ecosystems.

During the last 50,000 years, large-bodied animals (megafauna) have been removed from ecosystems around the world in a size-selective extinction event unique for the last 66 million years<sup>1</sup> (Smith et al. 2018) and strongly linked to the global expansion of modern humans<sup>2</sup> (Sandom et al. 2014)(*Homo sapiens*). These size-biased losses have continued through the Holocene<sup>3,4</sup> (Crees et al. 2014, Teng et al. 2020) and into the present in many areas (Dirzo et al. 2011)<sup>5</sup>, leading to widespread trophic downgrading of ecosystems (Estes et al. 2011, Mendoza et al. 2019)<sup>6,7</sup>. The downsizing of faunas and simplification of food webs have a wide range of ecosystem consequences such as reduced regulatory effects of top-down control and decreased resilience of ecosystems (Estes et al. 2011, Gill 2014)<sup>6,8</sup>. Protected areas (PAs) are a cornerstone for nature conservation. With almost 15% of the terrestrial surface covered<sup>9</sup> (UNEP-WCMC 2018), PAs protect habitats and species from increasing anthropogenic pressure, buffering them from threatening processes (Gaston et al. 2008)<sup>10</sup>. Nevertheless, prehistoric and historic faunal downsizing also affect PAs, potentially reducing their capacity for maintaining biodiversity as well as affected their ecological functioning in varied ways.

Trophic rewilding is a novel restoration strategy that advocates the (re)introduction of

large bodied species to restore trophic top-down trophic interactions and associated tropic cascades to promote self-sustaining biodiverse ecosystems (Svenning et al 2016)<sup>11</sup>. For example, the reintroduction of wolves into Yellowstone National Park in the mid-1990s triggered various direct and indirect effects, as mediated by both mesopredators and cervid prey (Ripple et al. 2014a, Ripple et al. 2014b)<sup>12,13</sup>. Yet, empirical data from rewilding projects are scarce and geographically biased (Tanantzap et al. 2018)<sup>14</sup>, with the scientific literature on rewilding dominated by essays, perspectives and opinion papers (Bakker et al. 2018)<sup>15</sup>. Despite increasing evidence for the restoration potential of rewilding from local studies (Perino et al. 2019)<sup>16</sup>, there is still limited knowledge of the opportunities to rewire ecological networks at a global scale through rewilding.

Macroecology provides a robust framework to assess the potential of trophic rewilding to rewire ecological networks at large scales with deep-time perspectives (Mendoza et al. 2019, Zhang et al. 2017)<sup>7,17</sup>. These approaches can enable comparison of functional similarities between extant and extinct species, and identify functional analogues to replace globally extinct species for rewilding projects (Pires et al. 2017)<sup>18</sup>. Examination of the effects of human-driven extinctions and on biotic interactions is possible, as well as the impacts of rewilding on ecological networks (Yaekel et al. 2014, Pires et al. 2015, Marjakangas et al. 2018)<sup>19–21</sup>. Through combining paleoecological data with macroecologically-grounded reconstructions of interaction networks the consequences of extinctions and the restoration potential of rewilding can be evaluated.

In this study, we investigate the opportunities to rewire terrestrial mammal food webs through rewilding in both large ( $\geq 5,000 \text{ km}^2$ ) PAs with strict International Union for Conservation of Nature (IUCN) category I-II and, for comparison, geographically-unbiased random areas (Fig. 1). We include the latter partly to address the non-random geographic location of PAs and to represent that there may also be opportunities for trophic rewilding outside large PAs (e.g., Pedersen et al. 2020)<sup>22</sup>. We infer food webs under three scenarios: 1) no-extinction, where mammals have not been influenced by human activities through time (following (Faurby et al. 2015, Faurby et al. 2018)<sup>23,24</sup>); 2) current, where mammals are found today, except for introduced ranges; and 3) rewilding, where extant species can be reintroduced to present-natural ranges and extinct species can be replaced by closely-related, similarly-sized functional analogues that have overlapping climatically suitable habitat.

## Results

## Late-Quaternary losses of species and trophic interactions in PAs

Large PAs are globally strongly affected by past size-biased defaunation, with the number of species per trophic levels significantly lower at present than in the no-extinction scenario, except for small herbivores and small carnivores (Table 1). The relative reductions are especially strong for megacarnivores ( $\geq 100$  kg), megaherbivores ( $\geq 1,000$  kg), and large herbivores (45 – 999 kg), while large carnivores (21.5 – 99 kg) were also, but less strongly affected (Table 1, Fig. 2). In our simulated data the numbers of species declined in PAs on average by 41% across all trophic levels. In line with previous evidence (Smith et al. 2018, Sandom et al. 2014, Ripple et al. 2014b)<sup>1,2,13</sup>, we found that much of these decreases were explained by megafaunal losses, particularly of megacarnivores and megaherbivores, with average declines up to 83% (Supplementary Table 3).

Reflecting the strong past size-biased defaunation, in the large PAs, the number of interactions among trophic levels is much reduced under current scenario relative to the no-extinction scenario (Table 2). Notably, all interactions involving megacarnivores are strongly reduced, with the link between large carnivores and large herbivores also strongly reduced, and a smaller reduction in link from large carnivores to small carnivores (Fig. 3). Megaherbivores, being largely immune to predation (Hopcraft et al. 2010), are found to be not involved in any trophic interactions between the mammal trophic groups; hence, their strong species number reduction is not modelled to affect the trophic network. These findings indicate that food webs have been simplified by Late Pleistocene extinctions, with an average loss of interactions between all trophic levels of 49% in PAs. Such declines were due mainly to losses of top-down control interactions of megacarnivores, with average declines in our simulated data as high as 83% (Supplementary Table 4).

The severe losses of megafauna richness and associated trophic processes we found show that food webs have been degraded due to late-Quaternary extinctions and suggest top-down control effects have been severely reduced in large PAs worldwide. These findings are in line with previous studies that found top-down trophic processes and trophic complexity to be severely reduced following late-Quaternary extinctions (Ripple et al. 2014b, Mendoza et al. 2019). Importantly, declines of trophic complexity and associated trophic processes have negative consequences on community dynamics and ecosystem functioning (Estes et al. 2011). For instance, extinction of megacarnivores, which are keystone species regulating densities and behavior of their prey (Ripple et al. 2014b, Atkins et al. 2019)<sup>13,25</sup>, have caused losses of top-down control with cascading effects that altered ecosystems (Estes et al. 2011, Ripple et al. 2014a)<sup>6,12</sup>. Moreover, losses of megaherbivores, which are invulnerable from predation and maintain open vegetation

landscapes (Hopcraft et al. 2010, Bakker et al. 2016), altered ecological processes such as nutrient flow (Le Roux et al. 2018) and caused homogenization of plant communities (Cromsigt et al. 2014, Bakker et al. 2016). Notably, our model quantified only direct predator-prey interactions and our results might underestimate effects of indirect interactions among species, which may lead to trophic cascades affecting communities (Ripple et al. 2014a)<sup>12</sup>.

## Rewiring food webs in PAs through rewilling

Trophic rewilling, as modelled here, would lead to important faunal recoveries for large PAs, with the strongest effects for megacarnivores and megaherbivores, intermediate effects for large herbivores, and no general effects on large carnivores, small carnivores, and small herbivores (Table 1). Specifically, from our simulated data we found that in PAs rewilling would restore the number of species in all trophic levels by 11% of the no-extinction proportions, with recoveries for megafauna being higher: megacarnivores richness increased by 24% and megaherbivores richness by 14% (Supplementary Table 3). These results suggest also that, despite our model does not quantify the interactions between herbivores and plants, the recoveries in the numbers of megaherbivores and large herbivores can partly reinstate herbivore pressure and top-down control on plants, facilitating open vegetation landscapes that host highly-biodiverse communities (Bakker et al. 2016)<sup>26</sup>.

We found that trophic rewilling would partially, but not completely restore food webs to the no-extinction scenario. The relative increase in interactions would be strongest for megacarnivores-large herbivores and megacarnivores-small carnivores, medium for megacarnivores-large carnivores and megacarnivores-small herbivores, and small for large carnivores-small carnivores, while it would not be significant for other interactions (Table 2). In our simulated data for the rewilling scenario, 18% of the lost trophic interactions would be replaced in PAs on average, with recoveries largely concentrated in interactions involving megafauna. For instance, megacarnivores trophic interactions would increase on average by 26% (Supplementary Table 4).

Our results indicate that rewilling has a high potential to rewire food webs in PAs worldwide. In particular, our findings show that predation top-down control, weakened worldwide by human activities (Estes et al. 2011, Ripple et al 2014b), can be partly restored through rewilling to no-extinction levels. Such recoveries would reinstate top-down control on prey densities, likely promoting trophic cascades and increasing the resilience and biodiversity of ecosystems (Atkins et al. 2019, Tylianakis et al 2010). Moreover, recoveries of large herbivore and megaherbivore richness suggest that trophic processes promoted by these trophic levels can be partly restored to no-extinction levels.

Megaherbivores are largely free from predation and facilitate open vegetation landscapes, increase the exchange of nutrients and energy among habitat patches, and create heterogeneous habitats (Cromsigt et al. 2014, Bakker et al. 2016, Le Roux et al. 2018). Recoveries of megaherbivore would thus promote landscape heterogeneity and increase biodiversity of plant communities (Le Roux et al. 2018). Overall, we found strong support for trophic rewilling as a novel restoration approach complementary to traditional conservation and restoration strategies to reinstate trophic complexity and promote biodiverse self-sustaining ecosystems in PAs globally.

## Rewilding food webs globally

In the random areas, we observed similar patterns as for the large PAs, but with stronger effect sizes for both losses due to late-Quaternary extinctions and recoveries through rewilling (Fig. 3 and Supplementary Tables 3 and 4), reflecting strong scope for trophic rewilling here if societal conditions allow. This supports our analyses were not influenced by geographic biases of the current network of PAs, which are located in areas with low human pressure and that poorly cover biodiversity hotspots of mammals (Joppa et al. 2009, Daru et al. 2019). Moreover, these results suggest rewilling would rewire food webs and restore trophic complexity globally, also in areas that are currently non-protected if human-wildlife coexistence can be achieved.

Here, we used a theoretical approach to investigate how late-Quaternary extinctions altered food webs and how rewilling can restore them. However, human-wildlife coexistence is the necessary starting point for rewilling (Perino et al. 2019)<sup>16</sup>. Success of rewilling depends on complex socio-ecological factors, particularly on the support from local communities (Ceausu et al. 2019). For instance, rewilling can cause conflicts with local stakeholders, e.g., due to livestock predation or damages to crops and pastures (Pereira et al., p. 72–74)<sup>33</sup>. People not directly damaged by wildlife can also negatively perceive rewilling projects depending on how they are implemented (Theunissen 2019)<sup>33</sup>. Human-wildlife conflicts can, however, be resolved by identifying benefits and costs of wildlife in a socio-ecological framework (Ceausu et al. 2019), by adopting compensation schemes for damages caused by wildlife (Ravenelle et al. 2017)<sup>35</sup>, and by implementing rewilling with realistic goals (Pedersen et al. 2020)<sup>22</sup>.

Importantly, our results from PAs  $\geq 5,000 \text{ km}^2$  with strict IUCN management category I-II, where anthropogenic activities are more strictly controlled and human pressure is generally low (see Supplementary Information), are representative of regions where human-wildlife coexistence is more likely to be achieved. Rewilling PAs would thus be the first step for restoring food webs and trophic complexity in degraded ecosystems. However, our findings show that similar recovery opportunities would be achieved in

many non-protected areas worldwide. In these cases, facilitating human-wildlife coexistence would allow rewilding to rewire food webs, reinstating lost trophic processes and promoting self-sustaining, biodiverse ecosystems globally (Svenning et al. 2016).

## Discussion

Trophic rewilding is a novel approach proposed to restore species and their ecological functions in degraded ecosystems and promote self-sustaining biodiverse ecosystems (Svenning et al. 2016). Our analyses reveal late-Quaternary extinctions severely degraded food webs worldwide by removing higher trophic levels and their predator-prey interactions, likely weakening top-down control processes (Estes et al. 2011, Ripple et al. 2014b, Atkins 2019). We found that such losses can be largely reversed by a rewilding scenario that minimizes ecological risks and facilitate human-wildlife coexistence. In particular, our results show that the number of species in higher trophic levels, associated with megafauna, and their interactions can be partly restored to no-extinction scenario with medium to strong magnitudes of recoveries. Overall, our findings suggest strong restoration opportunities for food webs and trophic complexity through trophic rewilding globally. This would rewire food webs and increase trophic complexity of terrestrial communities worldwide, reinstating trophic processes and top-down control (Ripple et al. 2014a) and promoting self-sustaining biodiverse ecosystems (Perino et al. 2019).

Despite we found rewilding has high potential to restore food webs to no-extinctions scenario, our results show that complete recoveries cannot be achieved under the conservative rewilding scenario examined here. In particular, replacements of extinct species were restricted to extant species that were phylogenetically closely-related and had similar body sizes. This was to minimize ecological risk of introduction (REF) and to ensure replacement species were functionally similar to extinct ones (Donlan et al. 2006) and had similar role in food webs (Eklöf et al. 2012, Gravel et al. 2013). However, many extinct species did not have any available functional replacement, as closely-related species went all extinct (e.g. Thylacinidae), and could not be replaced (Supplementary Table ... ). Hence, complete restoration of food webs was not possible under these constraints of the conservative rewilding scenario examined here.

In some cases, species are re-expanding to their natural ranges and passive rewilding has already started. In Europe, for instance, land abandoned has increased in recent decades (Verburg and Overmars 2009), promoting wildlife's comeback (Chapron et al. 2014, Ceausu et al. 2015). Traditional conservation and restoration approaches, which require large amount of resources and are limited to relatively small spatial scales, are unlikely to be effective measures to protect and restore ecosystems (Pereira and Navarro 2015). Our

results show that, in such cases where wildlife is re-expanding into abandoned landscape, rewilding would already be a viable and pragmatic alternative or complementary strategy to more traditional conservation and restoration approaches (Perino et al. 2019).

In conclusion, our study shows that late-Quaternary extinctions severely degraded food webs, but that rewilding can partly rewire food webs and restore trophic interactions globally. Hence, our findings support trophic rewilding as a promising, novel restoration strategy to re-establish in defaunated ecosystems important ecological functions, such as top-down control and trophic complexity (Estes et al. 2011, Ripple et al. 2014a, b). Measures to facilitate human-wildlife coexistence and mitigate negative impacts of wildlife for local communities are needed to promote rewilding with realistic goals (Ceausu et al. 2019, Pedersen et al. 2020). In some areas, such as large PAs I-II and abandoned landscapes where wildlife is re-expanding, rewilding is possibly already a viable alternative to traditional restoration strategies (Pereira and Navarro 2015). In a time of widespread biodiversity changes and trophic downgrading as today (Estes et al. 2011, Mendoza et al. 2019), rewilding could be a much needed approach to restore degraded ecosystems to self-sustaining biodiverse states (Svenning et al. 2016, Perino et al. 2019).

# Methods

## Overview

Our methodology follows four distinct steps: 1) we ran correlative species distribution models (SDMs) for extant terrestrial mammals to estimate their climatically suitable habitats; 2) we modelled reintroductions of extant terrestrial mammals and identified extant mammals that can be used to replace closely-related, similarly-sized extinct species in climatically suitable habitats; 3) we reconstructed food webs within protected and random areas for the present-natural, current, and rewilling scenarios; and 4) we contrasted the food webs of the three scenarios and investigated whether rewilling can rewire current food webs to present-natural conditions. These four steps are summarised below; more details are provided in the supplementary material.

Expanding upon the terminology of Genes et al. (2017), we quantified: a) current debt, the number of species and interactions lost due to Late Pleistocene extinctions; b) rewilling credit, the number of species and interactions restored under the rewilling scenario; and c) rewilling deficit, the extent of past losses not restored by rewilling. After quantifying current debt, rewilling credit and rewilling deficit, we assessed whether rewilling credit can balance current debt or if a rewilling deficit remained as food webs were not restored to present-natural conditions.

## Species distribution models

Correlative SDMs are currently the main tools used to derive spatially explicit predictions of environmental suitability for species (Elith and Leathwick 2009). They typically achieve this through identification of statistical relationships between species observations and environmental descriptors, and are then projected onto landscapes that fall within the species ‘environmental envelope’ (Guisan and Thuiller 2005). Following previous studies (Jarvie and Svenning 2018, Monsarrat et al. 2019), we used current and present-natural range maps from the PHYLACINE database (Faurby et al. 2018) to overcome biases when running SDMs due to anthropogenic range contraction of species (Faurby and Araújo 2018). PHYLACINE current ranges were generated from the IUCN range maps for current, natural, and reintroduced ranges only (IUCN 2019) By using both current and present-natural ranges we thus limited biases in species occurrence records due to anthropogenic modification of species distribution ranges (Faurby and Araújo 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 and were derived using known historic distributions of species, fossil co-occurrence data, and known range modifications caused by humans (Faurby and Svenning 2015). We generated presence locations for extant terrestrial mammals 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 2019). Elevation was determined for presence locations using the EarthEnv-DEM90 digital elevation model (Robinson et al. 2014). We did not model species with less than 10 presence locations, thus excluding 76 species with restricted ranges. In total, we modelled 4,130 of the 4,206 living terrestrial mammals.

As environmental predictors for the SDMs, we used four bioclimatic variables from the WorldClim v.2 database: 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 species' distributions (Guisan et al. 2017). The four variables were downloaded at 2.5 arc-minute resolution (Fick and Hijmans 2017) and reprojected to a 5 km resolution using bilinear interpolation with a Behrmann equal-area projection. To minimize potential issues with multi-collinearity, we ensured that the variance inflation factor among the climatic variables was below 4 (O'Brien 2007).

To model the climatic suitability of terrestrial mammals, we fitted maximum entropy (Maxent) models as implemented in the maxnet R package (Phillips et al. 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 et al. 2013). Maxent models were fitted with the default settings, besides disabling threshold features to avoid locally overfitted response curves (Merow et al. 2013) and increasing the number of randomly sampled background records from 10,000 up to a maximum of 100,000 to ensure greater representation of environmental space (Guevara et al. 2018). For the background area, we calculated species-specific buffers from combined current and present natural ranges to reflect the dispersal abilities of each species (Barve et al. 2011). Following previous studies (Poo-Muñoz et al. 2014, Hof et al. 2018), we calculated the buffer size as the maximum distance from the centroid to the edge of the largest continuous range (see Supplementary Fig. 1 for an example).

We assessed the predictive performance of Maxent SDMs through five-fold cross validation using the average Continuous Boyce Index (CBI; Hirzel et al. 2006), which indicates how much models discriminate against random expectation, and the average Area Under the Curve (AUC) of the Receiver Operating Clot (ROC; Swets 1988), which indicates how well models differentiate between presences and pseudo-absences regardless of the degree of difference between them. Values of CBI 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 to 1, where values  $\leq 0.5$  are models with discrimination no better than random to 1 for models with perfect discrimination (Fielding and Bell 1997). Model fit was inspected by five-fold cross validation of the average omission rate based on the minimum training presence value ( $OR_{MTP}$ ; Radosavljevic and Anderson 2014). The values of  $OR_{MTP}$  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 (Maximum Sensitivity and Specificity; MSS), which is a more reliable than other threshold metrics when only presence data are available (Liu et al. 2016). We also assessed the

performance of SDMs by comparing our projected binary suitability maps with the introduced ranges of 136 species obtained from Lundgren et al. (2018; n = 22 species) and the IUCN (IUCN 2019; n = 114 species). The introduced ranges were not used to generate presence records to train the SDMs. For three species found in both datasets (*Cervus elaphus*, *Ovibos moschatus*, and *Rangifer tarandus*), we assessed performance of SDMs using only the ranges from Lundgren et al. (2018).

Predictive performance of the SDMs was on average very high to excellent (mean CBI = 0.87; mean AUC = 0.85), while model overfitting was generally low (mean OR<sub>MTP</sub> = 0.07). The SDMs predicted on average 62% of introduced ranges (Supplementary Fig. 2). See Supplementary Table 1 and Supplementary Fig. 2 for further details on predictive performance of SDMs. These results indicate that SDMs give reliable projections of climatically suitable habitat for terrestrial mammals.

## Selection of rewilding candidates

To select rewilding candidates, two steps were followed: 1) we modelled reintroductions of extant terrestrial mammals into their present-natural ranges; 2) we identified extant mammals that can be used as functional analogues to replace closely-related, similarly-sized extinct species in climatically suitable habitats. Reintroductions of extant mammals were always prioritised over introductions of functional analogues, as moving species outside their indigenous range is inherently riskier than reintroduction due to unforeseeable uncertainties and ecological risks (Fernández et al. 2017). We further constrained functional analogues to come from the same family and to be within 50% of the body mass range of the extinct species, with two exceptions: 1) extinct megaherbivore  $\geq 1,000$  kg (Malhi et al., 2016) from the Proboscidea order were allowed to be replaced by the two extant elephants (*Elephas maximus* and *Loxodonta africana*). The rationale being that extant elephants are often considered as functional analogues of extinct megaherbivore proboscidean in many areas of the globe (Donlan 2005, Donlan et al. 2006, Svenning 2007), due to their general phenotypic similarity (large body size, tusks, trunk) and because they promote similar key ecosystem processes, e.g., nutrient cycles and vegetation clearing (Janzen and Martin 1982, Donlan et al. 2006). 2) Extinct Felidae and Ursidae megacarnivores  $\geq 100$  kg (Malhi et al. 2016) were allowed to be replaced by extant megacarnivores within the same family because they play an integral part of a complete animal community, influencing ecosystems by regulating the abundance and activity of large herbivores that are smaller than megaherbivores, either through direct predation or by behavioural changes induced by generation and shaping of “landscapes of fear” (Laundré et al. 2010). For functional analogues, we examined each biogeographic realm separately due to these being areas where ecological and evolutionary processes operate strongly (Olson et al. 2001, Olson and Dinerstein 2002). We excluded Antarctica because no terrestrial mammal lives there and Oceania because no terrestrial protected areas  $\geq 5,000$  km<sup>2</sup> with strictly managed IUCN categorisation are found there (Figure 1).

To avoid negative impacts from introductions of functional analogues into present-natural ranges of similarly-sized – i.e., within 50% of the body mass – extant species of the same taxonomic

group, we excluded the functional analogue to prevent potential issue due to competition between two species (Linnell and Strand 2000). For the remaining functional analogues, we selected the species that had the largest climatically suitable range overlapping within the present-natural range of the extinct species in each biogeographic realm. We did not select species for rewilding that violated any of the above conditions. See Supplementary Fig. 3 for a schematic representation for the selection of functional analogue. In total, we found 94 living species that can act as functional analogues to replace 127 of the 334 terrestrial mammals extinct during the Late Pleistocene (Supplementary Table #).

## Reconstructed food webs in both large protected areas and random areas

To investigate the potential of rewilding to rewire terrestrial mammal food webs, we reconstructed food webs in large protected areas and geographically-unbiased random areas at a global scale. We selected protected areas with a strict IUCN management categories (Ia: strict nature reserves; Ib: wilderness areas; and II: national parks) as they represent sites where trophic rewilding is likely more feasible today, being geographically isolated and with generally less human pressurestrictly-controlled human access (Dudley et al. 2013). We selected large protected areas to be  $\geq 5,000 \text{ km}^2$  as this size should be sufficient for viable, biodiverse megafauna populations to exist (Woodroffe and Ginsberg 1998, Cantú-Salazar and Gaston 2010, Ripple et al. 2015). The  $\geq 5,000 \text{ km}^2$  area is also a pragmatic trade-off between a possibly optimistic cut-off of, e.g.,  $100 \text{ km}^2$  (Ripple et al. 2015) and an overly-conservative cut-off, e.g.,  $25,000 \text{ km}^2$  (Cantú-Salazar and Gaston 2010). For the protected areas, we used spatial geometries from the World Database of Protected Area (WDPA; UNEP-WCMC & IUCN 2019, downloaded June 2019). Following previous global studies (Runge et al. 2015), we excluded protected areas without detailed geographic information, with unknown management status, UNESCO Biosphere Reserves, marine-only sites as well as the marine portion of coastal sites, and not considered protected areas internationally. We then dissolved adjacent geometries, assigning overlapping areas the strictest IUCN category of all protected areas in that location following WDPA best practice guidelines (<https://www.protectedplanet.net/c/calculating-protected-area-coverage>), before excluding areas with extent  $< 5,000 \text{ km}^2$ . We found 209 protected areas that met our requirements (Fig. 1).

Because protected areas  $\geq 5,000 \text{ km}^2$  with strict IUCN management categories are unevenly distributed on the continents (Fig. 5) and poorly overlap with current mammal biodiversity hotspots (Joppa and Pfaff 2009, Daru et al. 2019), we assessed the potential of rewilding to rewire food webs in random areas that did not have the geographic biases of protected areas (Fig. 1). We thus quantified current debts, rewilding credit and deficit in areas randomly scattered across Earth's terrestrial surface to investigate if results from protected areas were affected by their geographic biases. To do this, we randomly generated 37 areas of 40 km radius (area  $\sim 5,026 \text{ km}^2$ ) within each biogeographic realms – large terrestrial land masses that delineate areas where ecological and evolutionary processes operate most strongly (Olson et al. 2001, Olson and Dinerstein 2002). We excluded from our analyses the Antarctic realm, as no terrestrial mammal

have ever lived there, and the Oceania realm, as there were no large protected areas that met our requirements. For the Palearctic realm, we generated 15 of the 37 random areas within Europe excluding Russia; this was to more adequately represent both extinction patterns and rewilding opportunities. As random areas were used to assess the effects of past losses and the restoration potential of rewilding without geographic biases, we did not impose further restrictions. Random areas could thus be located in places where rewilding might be unlikely, e.g., area with high human densities. The results from random areas are useful for highlighting possible biases in the analysis of protected areas, but do not reflect real-world applications of rewilding when considered alone. In total, we found 206 random areas for which we could reconstruct food webs, excluding 16 areas that did not have terrestrial mammals or for which predator-prey interactions could not be inferred.

To reconstruct the predator-prey communities for the three scenarios, we used the current and present-natural ranges maps from the PHYLACINE database (Faurby et al. 2018) and the binary climatic suitability maps for the selected rewilding candidates. For the present-natural scenario, we used for extant and extinct species the present-natural ranges; for the current scenario, we used for extant species the current range maps; and for the rewilding scenario, we used for extant species the current range maps, the present-natural range maps that we assumed to be the indigenous range for a reintroduction, and the rewilding range maps for the functional analogues that replaced closely-related, similarly sized extinct species. The rewilding scenario were always constrained to areas where extant species were found to be climatically suitable (see Supplementary Fig. 4 for an example).

Food webs were inferred to describe ecological networks of direct predator-prey interactions for each protected and random areas by combining a phylogenetic method with a trait-based approach (Pomeranz et al. 2019). Phylogeny has been shown to be a good predictor of trophic interactions (Eklöf et al. 2012), as closely related species share similar resources (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), and assigned each known interaction between a prey and a predator to all species of the respective families. Data of predator-prey interactions was obtained from the ECOWeB database (Cohen 2010), the Global Biotic Interactions database (GLOBI; Poelen et al. 2014), and two food webs (Baskerville et al. 2011, De Visser et al. 2011). We then used a trait-based approach to remove interactions inferred using phylogeny that were not supported by macroecological evidence (Pomeranz et al. 2019). This trait-based approach uses the relationship between the body mass of prey and predators, which structures trophic interactions in food webs (Williams and Martinez 2000, Owen-Smith and Mills 2008, Segura et al. 2016). Following previous studies (Gravel et al. 2013, Pomeranz et al. 2019), we used the range within the 10% and the 90% regression quantiles to obtain dietary niches of carnivores, i.e. the body mass range of their prey. Phylogenetically inferred predator-prey interactions outside the dietary niche were removed from the food webs.

After food webs were inferred, we used the herbivore-carnivore definition of Malhi et al. (2016) to assign species to a trophic level according to their diet and body mass, as this reflects the trophic and ecological role of species. For carnivores, we divided them into three trophic levels: i)

megacarnivores  $\geq 100$  kg, which are generally apex predators that 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 et al. 1999). For herbivores, we also used three trophic levels: i) megaherbivores  $\geq 1,000$  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 by all carnivore trophic levels (Hopcraft, Olff, & Sinclair, 2010).

## Statistical analyses

For the three food web scenarios, we calculated for each protected and random area the number of species present in each trophic level and the number of predator-prey interactions connecting trophic levels. We then fitted generalised linear mixed models (GLMMs) using the protected and random areas as replicate sample units to compare the changes between scenarios. Specifically, we estimated: current debts, i.e. the differences between current and present-natural; rewilding credit, i.e. the differences between rewilding and current; and rewilding deficit, i.e. the differences between rewilding and present-natural. We selected the error distribution for the GLMMs based on the response data type and to remedy overdispersion (Zuur et al. 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, trophic levels involved in the link, and their interaction. Because preliminary analyses including protected and random areas as categorical predictors in the GLMMs showed random areas had in general lower numbers of species and interactions than protected areas ( $P < 0.05$ ), we analysed protected and random areas separately. For both GLMMs, we used the random effects food web ID and biogeographic realm. We assessed significance among scenarios by performing pair-wise contrasts with Bonferroni correction, with overall significance set at  $P < 0.05$ . We checked model assumptions were met for GLMMs through inspection of the residuals (Zuur et al. 2009). We assessed GLMMs goodness-of-fit by calculating the marginal  $R^2$ , the proportion of variance in the data explained by only the fixed effects, and the conditional  $R^2$ , the proportion of variance in the data explained by both fixed and random effects (Nakagawa & Schielzeth 2013). GLMMs had in general very good fit, explaining on average 67% of the variance in the data when only fixed effect was considered and 95% of the variance when also the random effect was included.

To assess if significant results were also ecologically meaningful (Nakagawa & Schielzeth, 2010), we used the Cohen's  $d$  effect size, which quantifies the standardized difference between model estimates (Cohen 1988). Following Cohen (1988) and using the expanded guidelines from Sawilowsky (2009), the effect sizes we used were: very small ( $d = 0.00$ – $0.19$ ), small ( $d = 0.20$ – $0.49$ ), medium effect ( $d = 0.50$ – $0.79$ ), large ( $d = 0.80$ – $1.19$ ), very large ( $d = 1.20$ – $1.99$ ), and huge ( $d \geq 2.00$ ).

Data processing and analyses were performed in the R programming language v. 3.6.1 (R Core Team, 2018). We ran Maxent SDMs using the package (Phillips et al. 2017) and performed quantile regression using the package quantreg (Koenker 2019). All spatial analyses were

conducted using the Behrmann cylindrical equal-area projection, with maps displayed in the Molleweide projection.

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## Data accessibility

All data used was open access. Predator-prey interactions were generated from Baskerville et al. (2011), Visser et al. (2011), and the ECOWeB and GLOBI databases (J. E. Cohen, 2010; Poelen et al., 2014), Body mass and range maps were from PHYLACINE 1.2 (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 et al., 2014), and the biogeographic realms shapefile from the WWF (Olson et al. 2001).

## Author contribution

EB conceived and developed the study, performed analyses, and drafted the manuscript. SJ and JCS conceived and developed the study, interpreted the results, and helped revise the manuscript.

## Competing interests

We have no competing interests.

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**Table 1: Trophic level richness estimates.** Standardized differences between model estimates for the number of species per trophic level from generalized linear mixed models (GLMMs) among the scenarios: no-extinction, current, and rewilding. Cohen's  $d$  are standardized differences between model estimates.  $P$  are the statistical significances of the contrast (set at  $P < 0.01$ ) adjusted with Bonferroni correction. Effect sizes indicate the magnitude of the change and illustrate the ecological importance of the standardized differences. GLMMs accounted for the variability across food web sites and biogeographic realms.

Trophic level	No-extinction – current			Rewilding – current			No-extinction– rewilding		
	Cohen's $d$	$P$	Effect size	Cohen's $d$	$P$	Effect size	Cohen's $d$	$P$	Effect size
<b>Protected areas</b>									
Megacarnivores ( $\geq 100$ kg)	1.24	< 0.01	very large	0.60	< 0.01	medium	0.64	< 0.01	medium
Megaherbivores ( $\geq 1,000$ kg)	1.79	< 0.01	very large	0.61	< 0.01	medium	1.18	< 0.01	large
Large carnivores (21.5–99 kg)	0.35	< 0.01	small	0.13	0.06	very small	0.22	< 0.01	small
Large herbivores (45–999 kg)	0.82	< 0.01	large	0.33	< 0.01	small	0.49	< 0.01	small
Small carnivores ( $< 21.5$ kg)	0.06	0.01	very small	0.04	0.19	very small	0.02	0.79	very small
Small herbivores ( $< 45$ kg)	0.03	0.40	very small	0.01	1.00	very small	0.02	< 0.01	very small
<b>Random areas</b>									
Megacarnivores ( $\geq 100$ kg)	1.89	<0.01	very large	1.21	<0.01	very large	0.67	<0.01	medium
Megaherbivores ( $\geq 1,000$ kg)	2.49	<0.01	huge	1.31	<0.01	very large	1.19	<0.01	large
Large carnivores (21.5–99 kg)	0.68	<0.01	medium	0.48	<0.01	small	0.20	<0.01	small
Large herbivores (45–999 kg)	1.10	<0.01	large	0.59	<0.01	medium	0.50	<0.01	medium
Small carnivores ( $< 21.5$ kg)	0.09	<0.01	very small	0.07	0.01	very small	0.02	0.92	very small
Small herbivores ( $< 45$ kg)	0.04	0.06	very small	0.02	0.57	very small	0.02	0.91	very small

**Table 2: Estimates of the number of interactions between trophic levels.** Standardized differences between model estimates for the number of species per trophic level from generalized linear mixed models (GLMMs) among the scenarios: no-extinction, current, and rewilding. Cohen's  $d$  are standardized differences between model estimates.  $P$  are the statistical significances of the contrast (set at  $P < 0.01$ ) adjusted with Bonferroni correction. Effect sizes indicate the magnitude of the change and illustrate the ecological importance of the standardized differences. GLMMs accounted for the variability across food web sites and biogeographic realms. For the definitions of trophic levels see caption of Fig. 1.

Predator	Prey	Present-natural – current			Rewilding – current			Present-natural – rewilding		
		Cohen's $d$	$P$	Effect size	Cohen's $d$	$P$	Effect size	Cohen's $d$	$P$	Effect size
<b>Protected areas</b>										
Megacarnivores	large carnivores	1.30	< 0.01	very large	0.73	< 0.01	medium	0.56	< 0.01	medium
	large herbivores	1.92	< 0.01	very large	0.74	< 0.01	medium	1.19	< 0.01	large
	small carnivores	1.45	< 0.01	very large	0.84	< 0.01	large	0.62	< 0.01	medium
	small herbivores	1.31	< 0.01	very large	0.74	< 0.01	medium	0.57	< 0.01	medium
Large carnivores	large herbivores	0.93	< 0.01	large	0.19	< 0.01	very small	0.74	< 0.01	medium
	small carnivores	0.41	< 0.01	small	0.27	< 0.01	small	0.14	0.07	very small
	small herbivores	0.26	< 0.01	small	0.14	0.04	very small	0.14	0.07	very small
Small carnivores	small herbivores	0.08	0.37	very small	0.06	0.67	very small	0.02	1.00	very small
<b>Random areas</b>										
Megacarnivores	large carnivores	2.26	< 0.01	huge	1.70	< 0.01	very large	0.56	< 0.01	medium
	large herbivores	2.67	< 0.01	huge	1.60	< 0.01	very large	1.08	< 0.01	large
	small carnivores	2.05	< 0.01	huge	1.42	< 0.01	very large	0.63	< 0.01	medium
	small herbivores	1.99	< 0.01	very large	1.40	< 0.01	very large	0.59	< 0.01	medium
Large carnivores	large herbivores	1.34	< 0.01	very large	0.72	< 0.01	medium	0.63	< 0.01	medium
	small carnivores	0.89	< 0.01	large	0.80	< 0.01	large	0.09	0.56	very small
	small herbivores	0.64	< 0.01	medium	0.55	< 0.01	medium	0.09	0.51	very small
Small carnivores	small herbivores	0.14	0.05	very small	0.12	0.15	very small	0.03	1.00	very small

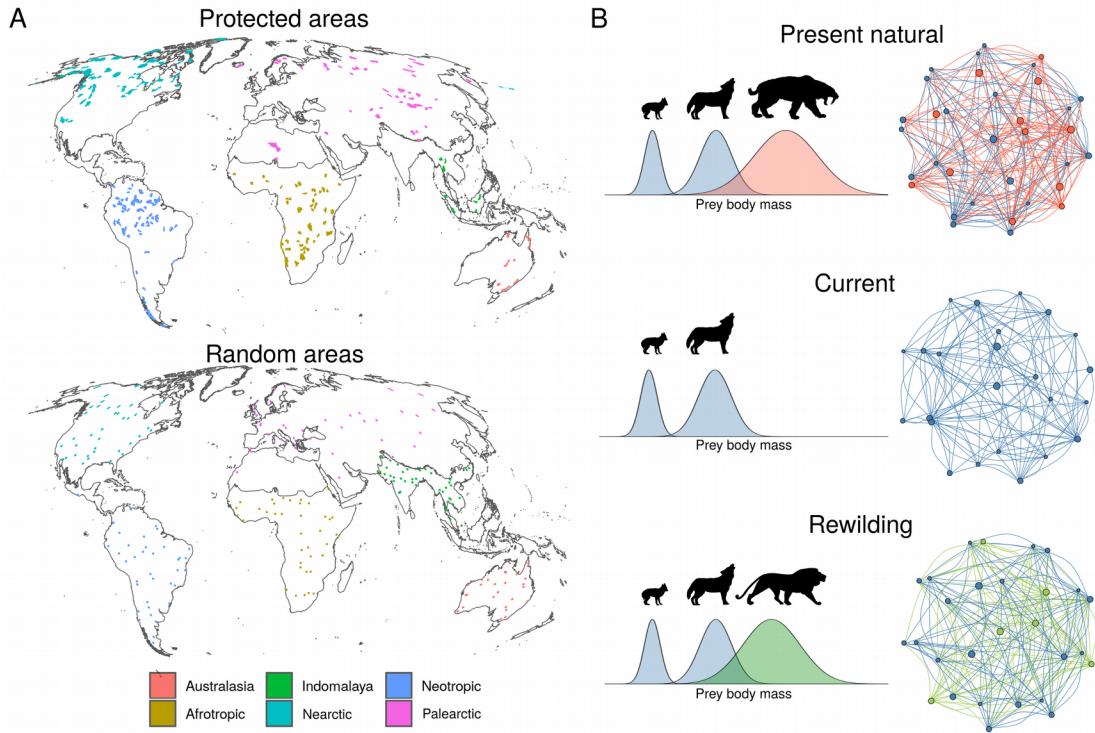


Fig. 1. Conceptual representation of rewiring food webs via trophic rewilding. A) The protected areas and random areas  $\geq 5,000 \text{ km}^2$  are coloured by the six biogeographic realms considered for trophic rewilding of terrestrial mammals. We excluded Antarctica because no terrestrial mammals live there and Oceania because no terrestrial protected areas larger than  $\geq 5,000 \text{ km}^2$  are found there. B) Network representation of food webs assessed using reconstructions of species assemblages and interactions under three modelling scenarios: present natural (communities in the absence of human), current (present day communities), rewilding (communities given reintroduction of living mammals and introduction of functional analogues for extant mammals). Species are shown as circles and predator-prey interactions as lines. Red color show the species and interaction that are lost in current conditions. Green color show the species reintroduced or replaced by functional analogues and the interactions rewired. Blue color show species and interactions common to all scenarios.

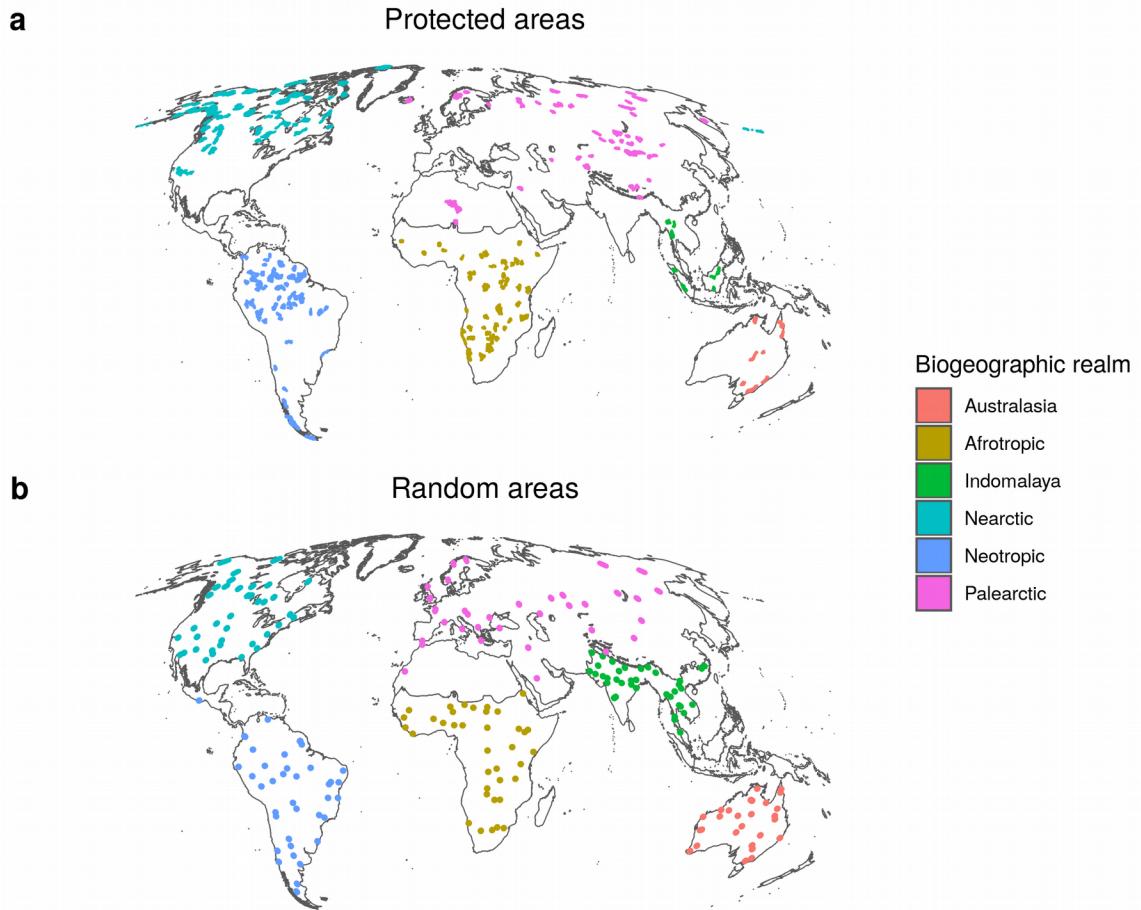


Fig. 1: Map of large protected and random areas  $\geq 5,000 \text{ km}^2$  for trophic rewilding in each Biogeographic realm (colours). **a**, Protected areas with strict IUCN management categories I–II. We excluded Antarctica because no terrestrial mammals live there and Oceania because no terrestrial protected areas larger than  $\geq 5,000 \text{ km}^2$  are found there. **b**, Areas  $\approx 5,026 \text{ km}^2$  generated at random for each Biogeographic realm, used to assess if trophic rewilding was affected by geographic biases of the protected areas. Random areas are displayed larger than their real extent for easier visualization.

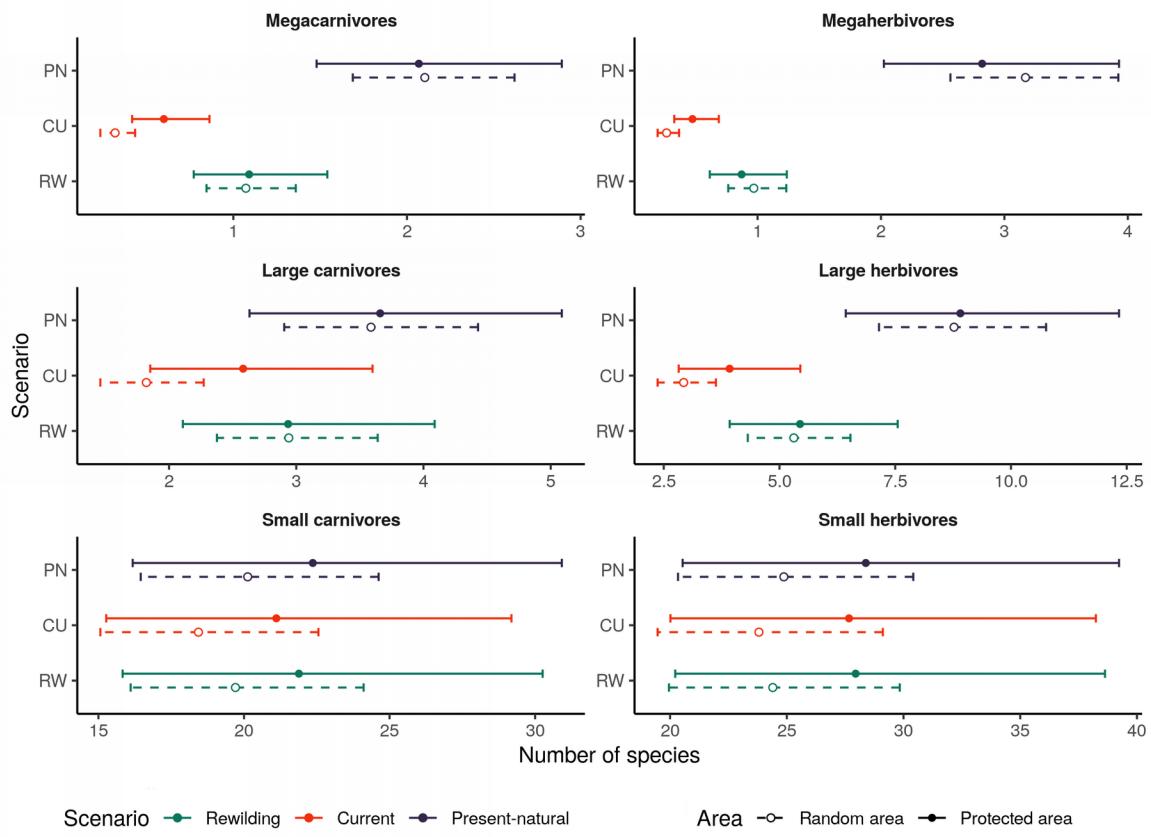


Figure 2: Model estimates of the number of species per trophic level from generalised linear mixed models (GLMMs) for three scenarios: PN, present-natural (blue); CU, current (red); and RW, rewilding (green). Circles show the estimated means from the GLMMs and lines the 95% confidence intervals for protected areas (closed circle and solid lines) and for random areas (open circle and dashed lines). The GLMMs accounted for variation across biogeographic realms and food webs. Trophic levels were defined following of Malhi et al. (2016) as: megacarnivores ( $\geq 100$  kg), large carnivores (21.5–99 kg), small carnivores ( $< 21.5$  kg), megaherbivores ( $\geq 1,000$  kg), large herbivores (45–999 kg), and small herbivores ( $< 45$  kg).

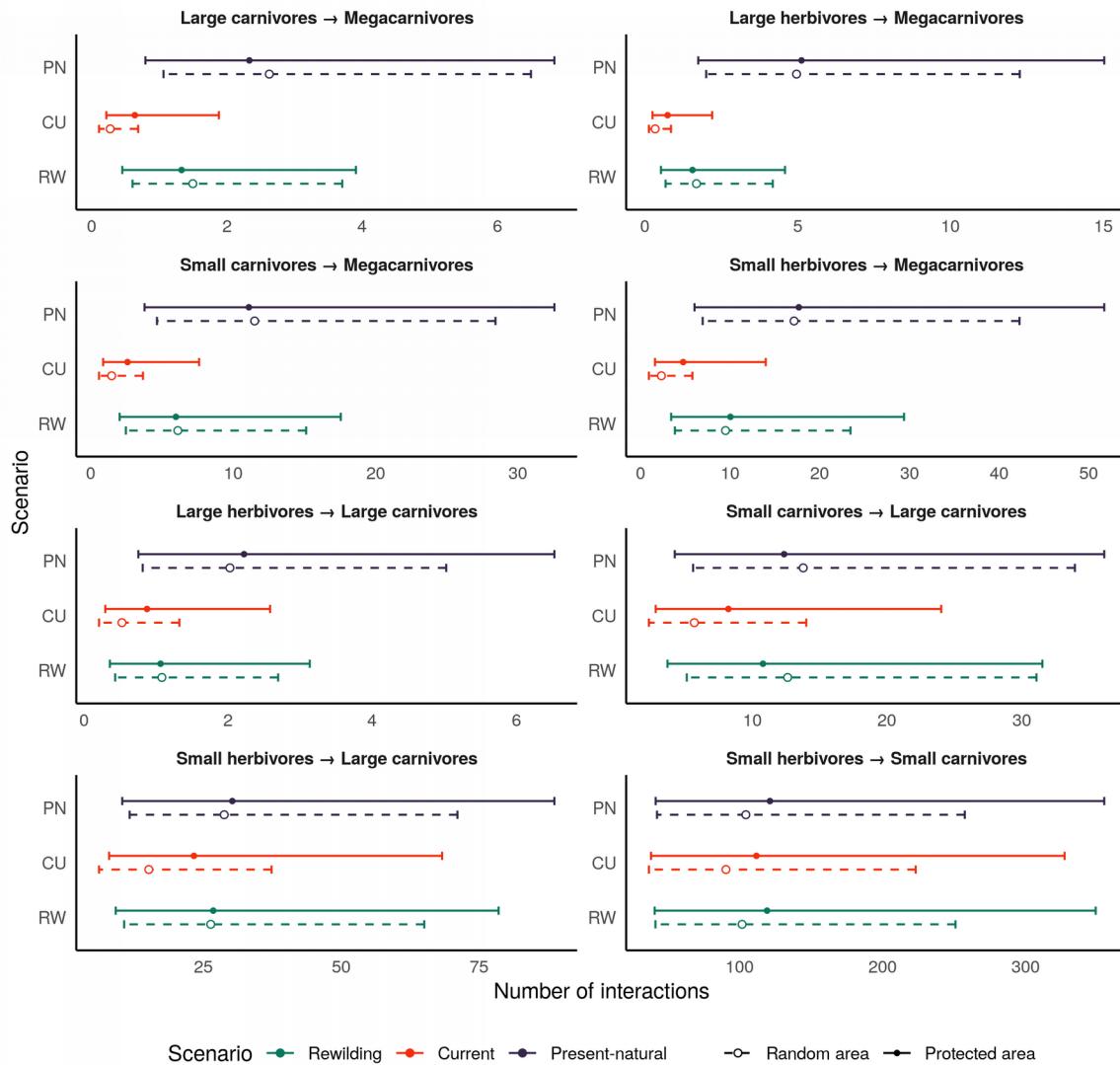


Figure 3. Model estimates of the number of predator-prey interactions between each trophic level from generalised linear mixed models (GLMMs) for three scenarios: PN, present-natural (blue); CU, current (red); RW, rewilding (green). Circles show the estimated means and lines the 95% confidence intervals for protected areas (closed circle and solid lines) and for random areas (open circle and dashed lines). The GLMMs accounted for variation across biogeographic realms and food webs. For the definitions of trophic levels see the caption of Fig. 1. Megaherbivores were free from predation in all food webs.

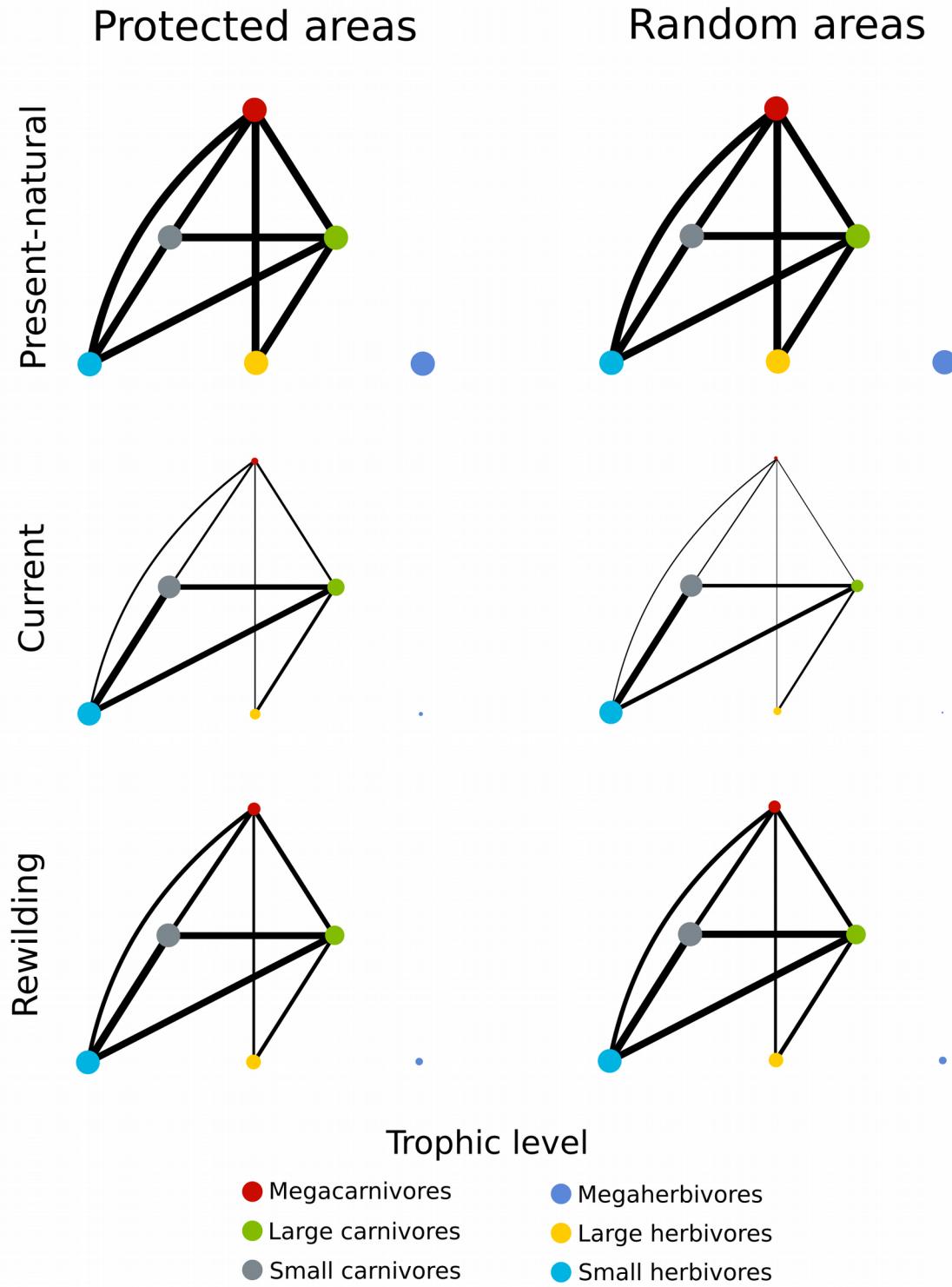


Figure 4: Network representation of the mean estimates from GLMMs for the food webs in the three scenarios. Circles are trophic levels and lines the predator-prey interactions. Circles and lines are normalised for the present-natural values, our reference baseline. Circle colours show

the trophic levels.

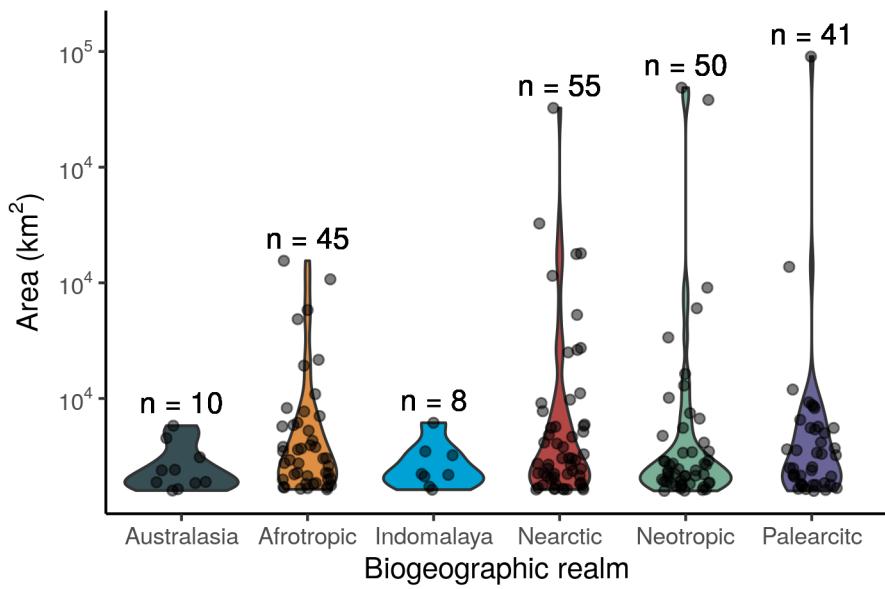


Figure 5: Area size of the protected areas studied for the six biogeographic realm. The violin plots show the distribution of area size per realm and the points the individual protected areas, with the number (n) of area per realm displayed.

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