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Trophic rewilding presents regionally specific opportunities for mitigating climate change

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Abstract

Large-bodied mammalian herbivores can influence processes that exacerbate or mitigate climate change. Herbivore impacts are, in turn, influenced by predators that place top-down forcing on prey species within a given body size range. Here, we explore how the functional composition of terrestrial large herbivore and carnivore guilds vary between three mammal distribution scenarios: Present-Natural, Current-Day, and Extant-Native Trophic (ENT) Rewilding. Considering the effects of herbivore species weakly influenced by top-down forcing, we quantify the relative influence keystone large herbivore guilds have on methane emissions, woody vegetation expansion, fire dynamics, large-seed dispersal, and nitrogen and phosphorous transport potential. We find strong regional differences in the number of herbivores under weak top-down regulation between our three scenarios with important implications for how they will influence climate change relevant processes. Under the Present-Natural non-ruminant, megaherbivore, browsers were a particularly important guild across much of the world. Megaherbivore extinction and range contraction and the arrival of livestock means large, ruminant, grazers have become more dominant. ENT Rewilding can restore the Afrotropics and Indo-Malay to the Present-Natural benchmark, but causes top-down forcing of the largest herbivores to become common place elsewhere. ENT Rewilding will reduce methane emissions, but does not maximise Natural Climate Solution potential.

Keywords: climate change; functional ecology; herbivory; macroecology; mammals

Introduction

Large-bodied mammalian herbivores have considerable potential to alter vegetation community structure and composition [1]. The nature of these effects are dependent on the composition of the herbivore guild, the wider community of species they interact with (e.g. predators and parasites), and environmental conditions [2]. Humans have dramatically altered mammalian herbivore and predator assemblages in the late Quaternary [3-6]. One striking change has been the alteration of the predator-prey size structure, which has implications on how mammalian herbivores influence their environment. For example, it has been reported that the loss of megaherbivores (taxa $\geq 1000\text{kg}$), which are relatively free of top-down regulation by predators [7, 8], has resulted in changes in vegetation structure [9, 10], fire dynamics [11, 12], nutrient transport [13], and dispersal of large-seeded species [14]. Trophic rewilding offers to augment these degraded ecological processes by (re)introducing lost species [15]. While the broad aim is to restore autonomous and diverse ecosystems without targeting specific species, habitats, or ecosystem services, recently rewilding has been considered and promoted as a means of mitigating climate change [e.g. 16]. We explore how trophic rewilding may affect the composition of keystone large herbivore guilds and how this might influence climate change.

Predators can alter herbivore ensemble composition, population abundances and individual behaviour [17, 18]. A by-product of these effects is reduced herbivory, particularly in areas where herbivores perceive themselves to be at greater risk of predation [19, 20]. These predator-prey interactions are size dependent as energetic and mechanical constraints limit predators' ability to hunt very large herbivores [21, 22]. Site-scale research in African savannah has demonstrated that megaherbivores, unlike smaller herbivores, do not behave as expected under the landscape of fear [23, 24], and that populations of herbivores weighing more than 150kg tend to be food rather than predator limited [8]. While large herbivore populations can be influenced by disease and targeted

predation on juveniles, this evidence suggests that sufficiently large herbivores are relatively free from strong direct and indirect effects of non-human predation. The presence of these species has implications for ecosystem dynamics, as was seen, for example, in the Serengeti-Mara system where woody expansion was observed after heavy elephant poaching in the Serengeti but not in the better protected Mara [10]. We follow Owen-Smith [7] and refer to this guild as keystone large herbivores.

Throughout most of the Cenozoic, enormous herbivores have occurred on nearly all major continents [25]. In contrast, today they are effectively confined to protected areas within Sub-Saharan Africa and South/South-East Asia as a consequence of the late Quaternary megafauna extinctions [5, 26]. These changes may have resulted in some ecosystems becoming relatively top-down regulated because the largest herbivores are now viable prey for the largest predators. At the same time, by protecting certain domesticated herbivores from predation, pastoral agriculture has created a new guild of large herbivores that can achieve high densities and strongly influence their environment.

As rewilding is process- rather than target-led, and outcomes are the product of complex ecosystem dynamics, it is worth exploring the different ways trophic rewilding might influence ecosystems and climate change. Here, we explore the implications of implementing a specific form of trophic rewilding that uses a Pleistocene benchmark to determine species reintroductions but does not use taxon substitutes to replace extinct species (we refer to it as Extant-Native Trophic Rewilding or ENT Rewilding). This is not a climate mitigation specific rewilding scenario, but one that is in keeping with rewilding being non-target specific. It is also not a proposal to rewild the whole world but presents an opportunity to explore geographical implications of rewilding.

Our aims are to explore: 1) how mammalian predator-prey/herbivore assemblage size structures vary across three mammal distribution scenarios (Present-Natural, Current-Day, and ENT Rewilding); and, 2) how different keystone herbivore ensembles might influence methane emission, woody expansion, fire suppression/promotion, large-seed dispersal, and nutrient transport potential. We conclude by discussing the complex ways in which different herbivore guild compositions might influence climate change.

Materials and methods

Compilation of species ranges and functional traits

A list of all mammals from the Last Interglacial (~126,000 years ago) to the present-day was obtained from Phylacine v.1.2 [27]. Phylacine v.1.2 also provided estimates for species body mass, the proportion of plant, vertebrate, and invertebrate material in their diet, and their native range in the Present-Natural and the Current-Day. The ranges of livestock species (cattle, buffalo, horses, sheep, goats, pigs) were taken from the Food and Agriculture Organization of the United Nations (FAO) at >5 individuals/km² [28], and their average body mass was sourced from de Magalhaes and Costa [29]. In total, 506 large-bodied (≥ 10 kg) and predominantly herbivorous ($\geq 50\%$ plant diet) species were identified and included in the study. Functional trait data on herbivore digestive physiology and diet were derived from a comprehensive new database compiled by authors (unpublished data; see Appendix B for data on species included in this study). Species range maps were used to create three mammal distribution scenarios: 1) Present-Natural, which included all extant and extinct wild species over their present-natural range, i.e. estimated range where they plausibly would be today without human effects; 2) Current-Day, which included extant wild and livestock species over their present-day range, excluding wild species introduced range ; and 3) ENT Rewilding, present-natural ranges for all extant wild species, including predators, but excludes

livestock. Cow and dromedary were considered to be the sufficiently similar to their ancestral forms and included. All analyses were conducted using Behrman equal-area projections of the globe (cells 9000 km², 1° wide, with widths ranging from 0.75° at the Equator to 9.5° at the poles).

Identifying predators of large herbivores

To address how changes in predator-prey assemblage structure influences the guild of herbivores relatively free from top-down regulation, we identified the maximum size of main prey species for 24 of the largest predatory carnivores. We identified the primary prey (classified as ≥15% occurrence in diet following the lower value given in Sandom et al. 2017b) of 11 extant species, (Table S1). The body mass ratios of extant predator to largest prey are reported in Table S1, and estimated ratios for extinct predators and the red wolf *Canis rufus*, which due to its very small range and critically endangered status has not been studied, in Table S2. For a more detailed explanation of this process please see the Supplementary Methods (Appendix A).

Herbivore functional traits and climate change effects

Each herbivore was placed into one of 12 functional groups, with each group assigned an influence score on the six climate change effect traits based on Cromsigt et al. [31] (detailed for each species in Appendix B). Methane emissions vary with digestive physiology, whereby ruminants emit more methane per capita ($10^{-0.619 + 0.812 \times \log_{10}(\text{BM})^{1.71}}$) than non-ruminants ($10^{-04.564 + 3.278 \times \log_{10}(\text{BM})^{0.592}}$) as given in Hempson et al. [32]. Herbivore ensemble methane emission potential was calculated as the sum of the estimated per capita methane emissions of the species present ($\sum \text{kg species}^{-1} \text{yr}^{-1}$). Herbivore woody expansion suppression potential was assessed by body size (megaherbivores (≥1000 kg) scored +3, large herbivores (100-1000 kg) +2, and medium herbivores (10-100 kg) +1). Ensemble woody expansion suppression was expressed as the sum of the scores of the species present (high values indicating high potential to suppress woody expansion). Herbivore influence

on fire regimes was assigned by feeding guild and body size: browsers promote fire by increasing fuel loads through the creation of woody debris and opening up wooded areas that promote flammable grasses (+3, +2, or +1, for mega, large, and medium body sizes, respectively), whereas grazers generally suppress fire by reducing fuel load (i.e., grasses; -3, -2, or -1, for mega, large, and medium body sizes). Herbivore ensemble effect was estimated as the mean fire effect of the species present (+3: fire promoting, -3: fire suppressing). Large-seeded tree species sequester more carbon and are typically most effectively distributed through greater consumption rate [33] and dispersal distance [34] by megabrowsers (+3) [35]. Large and medium browsers (+2) are also important; grazers (+1) have a lesser effect. Ensemble effect was expressed as the mean large-seed dispersal score of the species present (high values indicate high dispersal potential). Nutrient transport was divided into nitrogen and phosphorous transport. Megaherbivores are also particularly effective at transporting nutrients [13], with megagrazers biased towards nitrogen (+2 nitrogen, +1 phosphorus), while megabrowsers are balanced (+2 nitrogen and phosphorous). Ensemble nitrogen and phosphorous transport potential were expressed as the sum of the scores for the species present (high values indicate greater potential to distribute nitrogen and phosphorous).

To test the sensitivity of our results to errors in body mass estimates and the selection of body mass thresholds for each functional group the analyses of woody expansion, fire suppression, seed dispersal, nitrogen dispersal, and phosphorous dispersal were repeated three times using the following functional group body mass thresholds and compared against the main analysis: 1) meso: 10kg - 80 kg, large: 80kg - 800kg, and mega: ≥ 800 kg; 2) meso: 10kg - 80 kg, large: 80kg - 1250kg, and mega: ≥ 1250 kg; and, 3) meso: 10kg - 125 kg, large: 125kg - 1250kg, and mega: ≥ 1250 kg.

Results

The presence of a large herbivore guild relatively free from top-down forcing was nearly ubiquitous in the Present-Natural (Fig. 1), and predominantly made up of megaherbivores (Fig. S1). Only in central and northern Australia are they absent and this is likely the result of a limited fossil record [36]. The functional composition of keystone large herbivore guild is spatially varied (Fig. S1), with implications for their influence on climate change (Fig. 1). In the Present-Natural, the tropical, subtropical, and temperate grasslands, savannahs, and shrublands, and temperate broadleaf and mixed forests biomes [37] generally supports keystone large herbivore ensembles with greater methane emission, woody suppression, fire promotion, and nitrogen and phosphorous transport potential (Fig. 1). The Indo-Malay also supports large herbivore ensembles with similar climate change effects to these regions, but also the highest large-seed dispersal potential (Fig. 1). The cumulative per capita methane emission potential is particularly high in Europe, Nearctic and Neotropics (Fig. 1), associated with a particularly high richness of megaherbivores (Fig. S1)

In the Current-Day, there are fewer megaherbivores but more meso and large herbivores relatively free from top-down forcing (Fig. S2). The keystone herbivores have the strongest influence on climate change effects in the same regions as the Present-Natural, but with important differences. In the savannahs of the Afrotropics and in the Indo-Malay, methane emission and woody suppression potential are patchier and more intense (Fig. 1). The loss of the megaherbivores in Europe, the Nearctic, and Neotropics means the cumulative per capita methane emissions of the species present is considerably lower in the Current-Day compared to the Present-Natural (Fig. 1). Large herbivore potential influence on the other climate change effect traits has generally less intense and patchier in the Current-Day compared to the Present-Natural (Fig. 1)

ENT Rewilding reduces the richness and distribution of the small and medium sized herbivores relatively free from top-down forcing and restores the megaherbivore guilds within Afrotropics and Indo-Malay (Fig. S4). These changes have the potential to largely restore keystone herbivore

potential to influence climate effect traits in the Afrotropics and Indo-Malay (Fig. 1 & S3). In Australia, herbivore influence on climate effect traits remain comparable to the Current-Day and stronger than the Present-Natural (Fig. S3). In all other biogeographic realms, ENT Rewilding causes further reduction or total removal in keystone herbivore's potential to influence climate effect traits, in most cases causing further deviation from the Present-Natural benchmark (Fig. 1 & S3).

The influence of entire large herbivore ensembles on climate effects, regardless of whether they are likely to be relatively free from top-down control or not, largely mirrors the results we have reported for herbivores likely to be relatively free of top-down forcing (Fig. S5). Fire is the exception, with more ameliorated effects when considering all large herbivores.

The sensitivity analysis revealed that our results were not sensitive to changing the functional group body mass thresholds, albeit with some variation in Saharan Africa and Saudi Arabia (Fig. S6-S8), and to a lesser extent eastern and southern Afrotropics in the most extreme sensitivity test (Fig. S8).

Discussion

Our results highlight how predator-prey assemblage size structures differ between the Present-Natural, Current-day, and ENT Rewilding scenarios. In turn, the functional composition of keystone herbivore ensembles also varies. Critically, geography has important implications for how ENT Rewilding is likely to affect climate change effect traits. ENT Rewilding can largely restore the keystone large herbivore guild to a Present-Natural benchmark in the Afrotropics and Indo-Malay but results in even greater deviations in the other realms. The likely implications these changes could have for climate change mitigation are discussed below.

The loss of the largest wild herbivores (such as proboscideans and giant ground sloths) and the survival of medium-sized carnivores and herbivores have altered predator-prey food web structure

and thus the pervasiveness of potential top-down regulation. Outside the Afrotropics and Indo-Malay realms, there are few places today where wild large herbivores are relatively free from top-down regulation. Exceptions include the eastern Nearctic, western Palaearctic and Saharan Africa, where the extirpation of medium-sized predators has released surviving medium-sized herbivores from potential top-down regulation. Importantly, however, this excludes human hunting. Human top-down forcing of large herbivore populations in North America and Europe has reduced considerably in the last 75-150 years [38]. As a result, medium-sized herbivore populations, particularly deer, have expanded dramatically [38, 39]. Humans also influence predator population dynamics, and predator persecution may prevent predators from achieving the densities needed to exert strong top-down forcing [4, 40]. This might imply that there are wild medium-sized herbivores relatively free from top-down regulation in regions not reported here. While there has been a stark reduction in the number of wild herbivores influenced by top-down regulation, the expansion of livestock has increased the number of medium and large ruminant grazers protected from top-down regulation over large parts of the world.

We have explored how the functional composition of keystone herbivore ensembles could vary across the world. How these variations influence climate change, however, depends on the local environments that herbivores interact with. Methane emissions will be greatest where megaherbivores and ruminants occur at the highest densities. This will be in regions where primary productivity is high and accessible. As species richness is also expected to be higher in these regions [41], our results should capture some of the relative macroscale variation for wild species. Methane emissions will also be high where people manage the environment to maximise ruminant livestock stocking densities, which is not captured by our results, but have been mapped previously [28, 42]. ENT Rewilding will result in the lowest methane emissions where keystone herbivores are not present or are not megaherbivores or ruminants; the Neotropics in particular. Reductions in

methane emissions is also expected in the Nearctic and western Palaearctic (Europe) as rewilded wild keystone large herbivore density is expected to be lower than Current-Day livestock density in these regions.

The degree to which herbivores will influence woody expansion will be strongly influenced by local environmental conditions. Bond [43] suggests that a large part of the world is covered by environmental conditions where vegetation structure is uncertain, dynamic, and particularly susceptible to the synergistic influence of herbivores and fire. These regions are thought to cover much of the western Palaearctic, central and eastern Nearctic, southern and eastern Neotropics, the non-forested areas of the Afrotropical and Indo-Malay realms, and the fringes of Australia. These regions would also support diverse large herbivore guilds during the Present-Natural [44], and support high livestock density currently [28, 42]. Diverse and abundant keystone large herbivore guilds may be an important reason why these regions contain a heterogeneous mix of open grasslands, savannah, and more closed woodland, though the eastern Nearctic is a notable exception with generally higher tree cover [45]. This may be a result of field abandonment in the second-half of the 19th Century when people were still exerting strong top-down forcing of herbivore populations [38, 46]. Woody expansion in savannah biomes is currently prevalent across the Neotropics, Afrotropics, and, to a lesser extent, Australia, and may be associated with the depletion in the keystone large herbivore guilds along with increased CO₂ availability and human fire suppression [47]. These examples may provide insight into possible woody expansion expected from ENT Rewilding in grasslands, savannahs, and pastureland of the Neotropic, Palaearctic, and Nearctic realms. In the Neotropics, all native-extant herbivores are expected to be viable primary prey for jaguar and puma. In the Palaearctic and Nearctic, the only species large enough to be relatively free from top-down forcing are bison and cows, and as grazers are likely to have a lesser ability to suppress woody expansion [48].

Woody expansion into non-woodland communities results in carbon sequestration into woody biomass, but the net climate change effects are also dependent on changes in soil organic carbon (SOC), fire dynamics, and albedo [31]. Reforestation is estimated to offer the greatest 'Natural Climate Solution', with potential to mitigate climate change by the equivalent of sequestering over 10 petagrams of CO₂ equivalent per year in 2030 [49]. Much of this reforestation (woody expansion) potential occurs in what is today is pastureland, but were hotspots of species rich keystone herbivore guilds in the Present-Natural, with high woody suppression potential. In the Afrotropics and Indo-Malay, ENT Rewilding restores keystone herbivore guilds with the potential suppress woody expansion and so limit associated climate change mitigation potential. In contrast, ENT Rewilding is predicted to create conditions more suitable to allow woody expansion in the pasturelands of the Neotropics, Nearctic, and Palearctic by removing livestock and restoring predators with the potential to exert top-down forcing on all or nearly all extant herbivores. However, extensive woody expansion in these regions may come at the opportunity cost of restoring more diverse habitat for biodiversity conservation [50].

The loss of the particularly speciose megabrowser guilds of the Last Interglacial may be reducing fire promotion potential in the Current-Day. However, evidence from Last Glacial lake cores associates the loss of large herbivores with enhanced fire regimes [11, 12], highlighting that the combined effect of grazers and browsers can still result in fire suppression [51]. The increased prevalence of grazers in current grasslands increases fire suppression. ENT Rewilding causes the Afrotropics and Indo-Malay realm to return to a fire promoting state, although as stated above grazers can suppress fire regardless of browser activity in some circumstances[52]. In the Palearctic and Nearctic the remaining grazers could drive greater fire suppression. It is worth noting that in the

Palearctic and Nearctic and especially in the Neotropics, the large keystone herbivore guilds are depleted, which may result in the accumulation of larger fuel loads and more fire.

In higher latitudes, woodland cover has lower albedo compared to alternative land cover, thus, woody expansion increases local radiative forcing [53]. There are also uncertainties about the implications of woody expansion on Soil Organic Carbon (SOC) as some studies estimate SOC losses in response to woody expansion into grassland communities in wetter areas (Jackson et al. 2002). All taken together, it is challenging to determine the net effects of woody expansion on climate change. But, ENT Rewilding has the greatest potential to suppress woody expansion in the Afrotropics and Indo-Malay because the keystone herbivore guilds are most intact in these realms, reducing climate change mitigation potential in the region. In contrast, ENT Rewilding in pasturelands, grasslands and savannahs of the Neotropics increases the likelihood of woody expansion, as it will in the Nearctic and Palaeartic. It is worth noting ENT Rewilding has lower potential to suppress woody expansion in the temperate and boreal regions where it is most uncertain what the net effects for climate change will be.

Megaherbivores, especially browsers, are particularly important for nutrient transport and large-seeded species dispersal [13, 14, 54], although smaller species, including livestock, have important roles to play as well [54]. Restoring megaherbivores to their former ranges in the Afrotropics and Indo-Malay realm could be important in restoring transportation processes important for recovering deforested native-woodland sites, while the other realms will remain denuded. However, for ENT Rewilding to be effective in restoring these processes, the conservation of extensive core areas must be a priority [55], as well as the promotion of coexistence strategies where large herbivores, predators, and humans share space effectively. Where large-seeded species dispersal can be improved through trophic rewilding it is expected that carbon sequestration will increase by increasing the prevalence of these carbon rich tree species [14].

Our ENT Rewilding is relatively consistent with the focus of institutions such as the Rewilding Institute and Rewilding Europe, which support the reintroduction or natural expansion of large native mammals [56, 57]. Rewilding Australia is also promoting actions relevant to our ENT Rewilding scenario in Australia, including native species reintroductions and non-native species removal [58]. However, rewilding at smaller scales typically limits the opportunities to restore large predators and so more emphasis is placed on large herbivores [59]. Interestingly, these examples increase the number of large herbivores relatively free from top-down regulation, unless people regulate them in an effort to mimic predation. This increases the similarity between predator-prey assemblage structure to the Present-Natural benchmark, although the composition of the resulting keystone herbivore guild is quite different with large ruminants typically replacing megaherbivores. A huge variety of rewilding relevant projects are underway across the world [15, 60], and inadvertent passive rewilding such as land abandonment as result of social change is also occurring [61]. Diverse rewilding approaches presents an important opportunity to study how these complex ecosystems behave to provide a better understanding of how rewilding might influence people, nature, and climate change.

We acknowledge that this exploratory study comes with a number of caveats. A central one with regard to predator-prey size structures concerns estimates of the effect of predation on juveniles. Predation on adult individuals of megaherbivores will likely be rare, but it is difficult to determine the natural frequency of such predation on juveniles and if such predation will allow top-down regulation. Van Valkenburgh et al. [62] suggest that such predation might have been fairly common, arguing for top-down regulation of slow breeding Pleistocene megafauna in North America. There are several records of lions taking relatively large numbers of juvenile elephants [e.g. 63], but lions and elephants co-exist across much of their ranges and because regular predation is not seen today, it could suggest it was not a general pattern in the Pleistocene either. Dietary

isotopic studies further do not support widespread predation on mammoths or other proboscideans [64]. This does not mean that there were not be packs of extinct lions or saber-tooth cats specializing on proboscideans [65], but it at least suggests that there is no reason to assume that predation on extinct proboscideans should be any more important than predation on extant African elephants is today.

Trophic rewilding seeks to restore ecosystem complexity, which is thought could have beneficial biodiversity and ecosystem service outcomes. Because these outcomes are the result of complex ecological processes, they are likely to vary in time and space. Climate change presents a substantial challenge to people and nature today, so it is prudent to consider the likely consequences of a proposed land use change. We have highlighted that ENT Rewilding presents climate change mitigation opportunities such as an expected reduction in methane emission potential and carbon sequestration through potential woody expansion in the Neotropics, Nearctic, and Palearctic. But, rewilding does not aim to deliver specific benefits and our results highlight that ENT Rewilding is unlikely to maximise Natural Climate Solutions. The strengths of a rewilding approach often lie in diversifying the range outcomes delivered. Rewilding may offer an important complimentary strategy to Natural Climate Solutions to ensure other nature-based benefits to biodiversity conservation and society are also delivered.

Contributions

CS and SF conceived the idea and led the writing. SF, EL, and OM led the analysis and produced the figures. SDS, EL, JR, OM compiled data. All authors contributed to editing of the text.

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The datasets supporting this article have been uploaded as part of the supplementary material.

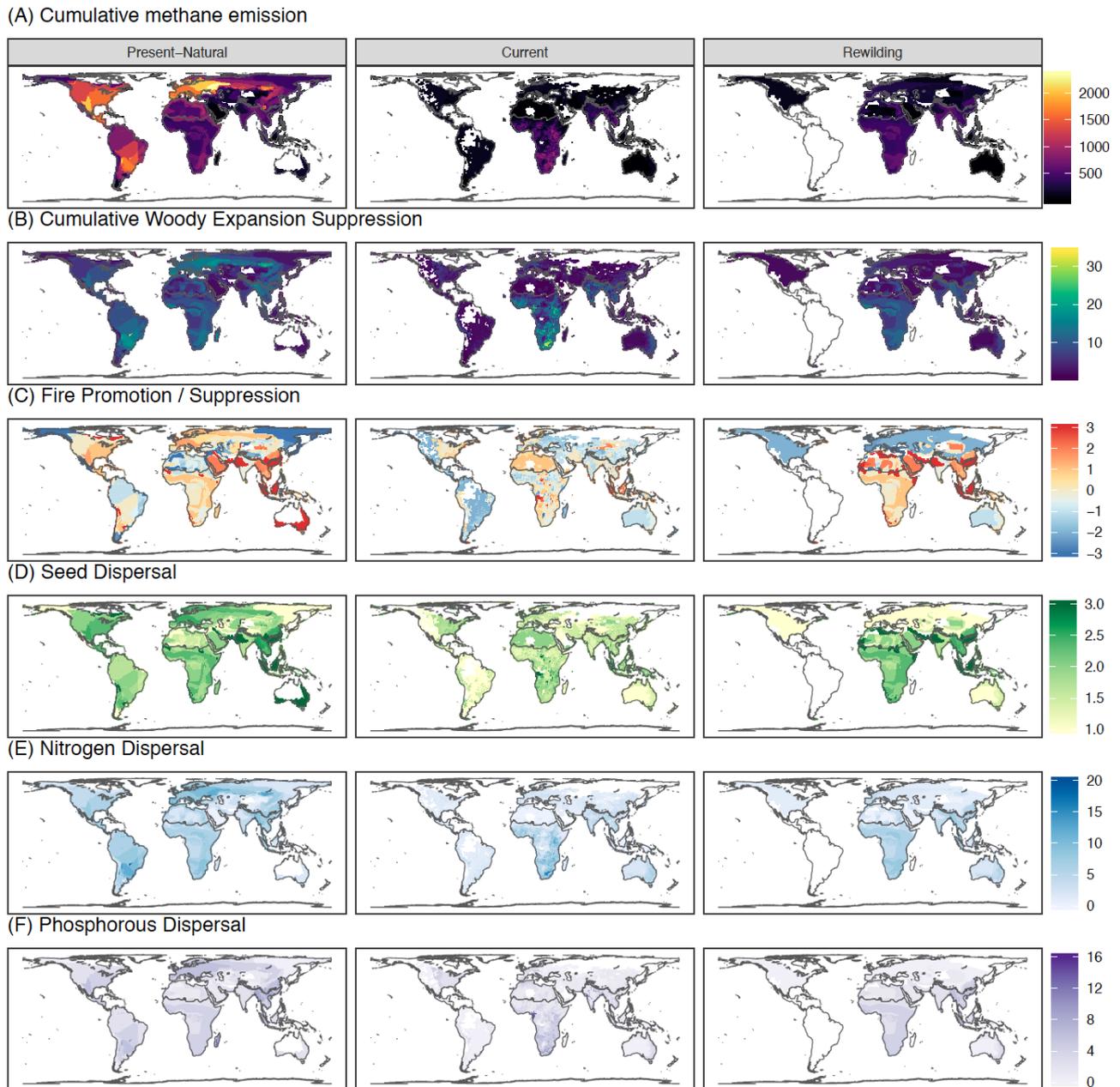


Fig. 1. The relative contribution large herbivores ensembles that are relatively free from top-down have on six ecological processes relevant to climate change across three scenarios: 1) Present-Natural, Current-Day, and ENT Rewilding. A) total per capita methane production from a herbivore ensemble ($\sum \text{kg species}^{-1} \text{ yr}^{-1}$). B) The effect of the herbivore ensemble on fire regimes was estimates as the mean fire effect of species per ensemble (+3: fire promoting, -3: fire suppressing). C) Woody expansion suppression was expressed as the sum of the relative effectiveness at

suppressing woody vegetation of the species present (high values indicate high potential to suppress woody expansion). D) The total effect on seed dispersal was expressed as the ensembles average potential to disperse large-seeded plants (high values indicate high potential to disperse large seeded species). E & F) Nitrogen and phosphorous transport potential was expressed as the sum of the potential contribution of each species in each ensemble (high values indicate greater potential to distribute nitrogen and phosphorous).

References

- [1] Bakker, E. S., Gill, J. L., Johnson, C. N., Vera, F. W. M., Sandom, C. J., Asner, G. P. & Svenning, J. C. 2016 Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. *P Natl Acad Sci USA* **113**, 847-855. (DOI:10.1073/pnas.1502545112).
- [2] Pausas, J. G. & Bond, W. J. 2018 Humboldt and the reinvention of nature. *J. Ecol.* (DOI:10.1111/1365-2745.13109).
- [3] Sandom, C. J., Faurby, S., Sandel, B. & Svenning, J.-C. 2014 Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20133254.
- [4] Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M. P., et al. 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 151-162. (DOI:10.1126/Science.1241484).
- [5] Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., Hayward, M. W., Kerley, G. I. H., Levi, T., Lindsey, P. A., et al. 2015 Collapse of the world's largest herbivores. *Science Advances* **1**, e1400103.
- [6] Sandom, C. J., Faurby, S., Svenning, J. C., Burnham, D., Dickman, A., Hinks, A., Macdonald, E. A., Ripple, W., Williams, J. & Macdonald, D. 2017 Learning from the past to prepare for the future: felids face continued threat from declining prey. *Ecography*.
- [7] Owen-Smith, N. 1987 Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* **13**, 351-362.
- [8] Sinclair, A., Mduma, S. & Brashares, J. S. 2003 Patterns of predation in a diverse predator-prey system. *Nature* **425**, 288-290.
- [9] Sandom, C. J., Ejrnaes, R., Hansen, M. D. D. & Svenning, J. C. 2014 High herbivore density associated with vegetation diversity in interglacial ecosystems. *P Natl Acad Sci USA* **111**, 4162-4167. (DOI:10.1073/pnas.1311014111).
- [10] Sinclair, A. R. E., Mduma, S. A. R., Hopcraft, J. G. C., Fryxell, J. M., Hilborn, R. & Thirgood, S. 2007 Long-term ecosystem dynamics in the Serengeti: Lessons for conservation. *Conserv Biol* **21**, 580-590. (DOI:10.1111/j.1523-1739.2007.00699.x).
- [11] Rule, S., Brook, B. W., Haberle, S. G., Turney, C. S., Kershaw, A. P. & Johnson, C. N. 2012 The aftermath of megafaunal extinction: ecosystem transformation in Pleistocene Australia. *Science* **335**, 1483-1486.
- [12] Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B. & Robinson, G. S. 2009 Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100-1103.
- [13] Doughty, C. E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E. S., Malhi, Y., Dunning, J. B. & Svenning, J. C. 2016 Global nutrient transport in a world of giants. *P Natl Acad Sci USA* **113**, 868-873. (DOI:10.1073/pnas.1502549112).

- [14] Doughty, C. E., Wolf, A., Morueta-Holme, N., Jorgensen, P. M., Sandel, B., Violle, C., Boyle, B., Kraft, N. J. B., Peet, R. K., Enquist, B. J., et al. 2016 Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography* **39**, 194-203. (DOI:10.1111/ecog.01587).
- [15] Svenning, J. C., Pedersen, P. B. M., Donlan, C. J., Ejrnaes, R., Faurby, S., Galetti, M., Hansen, D. M., Sandel, B., Sandom, C. J., Terborgh, J. W., et al. 2016 Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *P Natl Acad Sci USA* **113**, 898-906. (DOI:10.1073/pnas.1502556112).
- [16] Bakker, E. S. & Svenning, J. C. 2018 Trophic rewilding: impact on ecosystems under global change. *Philos T R Soc B* **373**. (DOI:10.1098/rstb.2017.0432).
- [17] Connell, J. H. 1975 Some mechanisms producing structure in natural communities; a model and evidence from field experiments. In *Ecology and Evolution of Communities* (eds. M. L. Cody & J. M. Diamond), pp. 460-491. Cambridge, Belknap Press.
- [18] Ripple, W. J. & Beschta, R. L. 2004 Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? *Bioscience* **54**, 755-766. (DOI:doi:10.1641/0006-3568).
- [19] Bleicher, S. S. 2017 The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ* **5**. (DOI:10.7717/peerj.3772).
- [20] Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. & Brashares, J. S. 2019 Landscapes of Fear: Spatial Patterns of Risk Perception and Response. *Trends Ecol Evol* **34**, 355-368. (DOI:<https://www.sciencedirect.com/science/article/pii/S0169534719300199>).
- [21] Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. 1999 Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**, 442-442. (DOI:Doi 10.1038/46607).
- [22] Carbone, C., Teacher, A. & Rowcliffe, J. M. 2007 The costs of carnivory. *PLoS Biol.* **5**, e22.
- [23] Le Roux, E., Kerley, G. I. H. & Cromsigt, J. P. G. M. 2018 Megaherbivores Modify Trophic Cascades Triggered by Fear of Predation in an African Savanna Ecosystem. *Curr Biol* **28**, 2493-+. (DOI:10.1016/j.cub.2018.05.088).
- [24] Riginos, C. 2015 Climate and the landscape of fear in an African savanna. *Journal of Animal Ecology* **84**, 124-133. (DOI:10.1111/1365-2656.12262).
- [25] Smith, F. A., Boyer, A. G., Brown, J. H., Costa, D. P., Dayan, T., Ernest, S. K. M., Evans, A. R., Fortelius, M., Gittleman, J. L., Hamilton, M. J., et al. 2010 The Evolution of Maximum Body Size of Terrestrial Mammals. *Science* **330**, 1216-1219. (DOI:10.1126/science.1194830).
- [26] Barnosky, A. D., Koch, P. L., Feranec, R. S., Wing, S. L. & Shabel, A. B. 2004 Assessing the causes of Late Pleistocene extinctions on the continents. *Science* **306**, 70-75. (DOI:Doi 10.1126/Science.1101476).
- [27] Faurby, S., Davis, M., Pedersen, R. O., Schowaneck, S. D., Antonelli, A. & Svenning, J. C. 2018 PHYLOCINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. *Ecology* **99**, 2626-2626. (DOI:10.1002/ecy.2443).
- [28] Gilbert, M., Nicolas, G., Cinardi, G., Van Boeckel, T. P., Vanwambeke, S. O., Wint, G. R. W. & Robinson, T. P. 2018 Global distribution data for cattle, buffaloes, horses, sheep, goats, pigs, chickens and ducks in 2010. *Sci Data* **5**. (DOI:10.1038/sdata.2018.227).
- [29] de Magalhaes, J. P. & Costa, J. 2009 A database of vertebrate longevity records and their relation to other life-history traits. *J Evolution Biol* **22**, 1770-1774. (DOI:10.1111/j.1420-9101.2009.01783.x).
- [30] Sandom, C. J., Williams, J., Burnham, D., Dickman, A. J., Hinks, A. E., Macdonald, E. A. & Macdonald, D. W. 2017 Deconstructed cat communities: Quantifying the threat to felids from prey defaunation. *Diversity and Distributions* **23**, 667-679. (DOI:10.1111/ddi.12558).
- [31] Cromsigt, J. P. G. M., te Beest, M., Kerley, G. I. H., Landman, M., le Roux, E. & Smith, F. A. 2018 Trophic rewilding as a climate change mitigation strategy? *Philos T R Soc B* **373**. (DOI:10.1098/rstb.2017.0440).
- [32] Hempson, G. P., Archibald, S. & Bond, W. J. 2017 The consequences of replacing wildlife with livestock in Africa. *Sci Rep-Uk* **7**. (DOI:10.1038/s41598-017-17348-4).
- [33] Shipley, L. A., Gross, J. E., Spalinger, D. E., Hobbs, N. T. & Wunder, B. A. 1994 The Scaling of Intake Rate in Mammalian Herbivores. *Am Nat* **143**, 1055-1082. (DOI:Doi 10.1086/285648).
- [34] Jetz, W., Carbone, C., Fulford, J. & Brown, J. H. 2004 The scaling of animal space use. *Science* **306**, 266-268. (DOI:DOI 10.1126/science.1102138).

- [35] Blake, S., Deem, S. L., Mossimbo, E., Maisels, F. & Walsh, P. 2009 Forest Elephants: Tree Planters of the Congo. *Biotropica* **41**, 459-468. (DOI:10.1111/j.1744-7429.2009.00512.x).
- [36] Rodriguez-Rey, M., Herrando-Perez, S., Brook, B. W., Saltre, F., Alroy, J., Beeton, N., Bird, M. I., Cooper, A., Gillespie, R., Jacobs, Z., et al. 2016 A comprehensive database of quality-rated fossil ages for Sahul's Quaternary vertebrates. *Sci Data* **3**. (DOI:10.1038/sdata.2016.53).
- [37] Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., et al. 2001 Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* **51**, 933-938. (DOI:Doi 10.1641/0006-3568).
- [38] Cote, S. D., Rooney, T. P., Tremblay, J. P., Dussault, C. & Waller, D. M. 2004 Ecological impacts of deer overabundance. *Annu Rev Ecol Evol S* **35**, 113-147. (DOI:Doi 10.1146/Annurev.Ecolsys.35.021103.105725).
- [39] Deinet, S., Ieronymidou, C., McRae, L., Burfield, I. J., Foppen, R., Collen, B. & Böhm, M. 2013 Wildlife comeback in Europe: The recovery of selected mammal and bird species. (Zoological Society of London).
- [40] Bull, J. W., Ejrnaes, R., Macdonald, D. W., Svenning, J. C. & Sandom, C. J. 2019 Fences can support restoration in human-dominated ecosystems when rewilding with large predators. *Restoration Ecology* **27**, 198-209. (DOI:10.1111/rec.12830).
- [41] Schipper, J. & Chanson, J. S. & Chiozza, F. & Cox, N. A. & Hoffmann, M. & Katariya, V. & Lamoreux, J. & Rodrigues, A. S. L. & Stuart, S. N. & Temple, H. J., et al. 2008 The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* **322**, 225-230. (DOI:10.1126/science.1165115).
- [42] Robinson, T. P., Wint, G. R. W., Conchedda, G., Van Boeckel, T. P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S. I. & Gilbert, M. 2014 Mapping the Global Distribution of Livestock. *Plos One* **9**. (DOI:10.1371/journal.pone.0096084).
- [43] Bond, W. J. 2005 Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science* **16**, 261-266. (DOI:Doi 10.1658/1100-9233).
- [44] Faurby, S. & Svenning, J. C. 2015 Historic and prehistoric human-driven extinctions have reshaped global mammal diversity patterns. *Diversity and Distributions* **21**, 1155-1166. (DOI:10.1111/ddi.12369).
- [45] Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., et al. 2013 High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* **342**, 850-853. (DOI:10.1126/science.1244693).
- [46] Foster, D. R. 1992 Land-Use History (1730-1990) and Vegetation Dynamics in Central New-England, USA. *J. Ecol.* **80**, 753-772. (DOI:Doi 10.2307/2260864).
- [47] Stevens, N., Lehmann, C. E. R., Murphy, B. P. & Durigan, G. 2017 Savanna woody encroachment is widespread across three continents. *Global Change Biol.* **23**, 235-244. (DOI:10.1111/gcb.13409).
- [48] Archer, S. R., Andersen, E. M., Predick, K. I., Schwinning, S., Steidl, R. J. & Woods, S. R. 2017 Woody plant encroachment: causes and consequences. In *Rangeland systems* (pp. 25-84, Springer, Cham).
- [49] Griscom, B. W., Adams, J., Ellis, P. W., Houghton, R. A., Lomax, G., Miteva, D. A., Schlesinger, W. H., Shoch, D., Siikamaki, J. V., Smith, P., et al. 2017 Natural climate solutions. *P Natl Acad Sci USA* **114**, 11645-11650. (DOI:10.1073/pnas.1710465114).
- [50] Veldman, J. W., Overbeck, G. E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G. W., Durigan, G., Buisson, E., Putz, F. E. & Bond, W. J. 2015 Where Tree Planting and Forest Expansion are Bad for Biodiversity and Ecosystem Services. *Bioscience* **65**, 1011-1018. (DOI:10.1093/biosci/biv118).
- [51] Kimuyu, D. M., Sensenig, R. L., Riginos, C., Veblen, K. E. & Young, T. P. 2014 Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna. *Ecological Applications* **24**, 741-749. (DOI:Doi 10.1890/13-1135.1).
- [52] Holdo, R. M., Holt, R. D. & Fryxell, J. M. 2009 Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecological Applications* **19**, 95-109.
- [53] Bonan, G. B. 2008 Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science* **320**, 1444-1449. (DOI:10.1126/science.1155121).
- [54] Pires, M. M., Galetti, M., Donatti, C. I., Pizo, M. A., Dirzo, R. & Guimaraes, P. R. 2014 Reconstructing past ecological networks: the reconfiguration of seed-dispersal interactions after megafaunal extinction. *Oecologia* **175**, 1247-1256. (DOI:Doi 10.1007/S00442-014-2971-1).

- [55] Peres, C. A. 2005 Why we need megareserves in Amazonia. *Conserv Biol* **19**, 728-733. (DOI:DOI 10.1111/j.1523-1739.2005.00691.x).
- [56] Rewilding Europe. 2019 Our Story: Making Europe a Wilder Place. <https://rewildingeuropa.com/our-story/>.
- [57] Parsons, D., Soulè, M., Miller, B. & Foreman, D. 2018 The Rewilding Institute's Vision and Work. <https://rewilding.org/about-tri/vision/>.
- [58] Rewilding Australia. 2018 Rewilding Australia. <https://rewildingaustralia.org.au>.
- [59] Sandom, C. J. & Wynne-Jones, S. 2019 Rewilding a country: Britain as a case study. In *Rewilding* (eds. N. Pettorelli, S. Durant & J. Du Toit), pp. 222-247. Cambridge, Cambridge University Press.
- [60] Pettorelli, N., Barlow, J., Stephens, P. A., Durant, S. M., Connor, B., Buhne, H. S. T., Sandom, C. J., Wentworth, J. & du Toit, J. T. 2018 Making rewilding fit for policy. *J Appl Ecol* **55**, 1114-1125. (DOI:10.1111/1365-2664.13082).
- [61] Carver, S. 2019 Rewilding through land abandonment. In *Rewilding* (eds. N. Pettorelli, S. M. Durant & J. Du Toit), pp. 99-122. Cambridge, Cambridge University Press.
- [62] Van Valkenburgh, B., Hayward, M. W., Ripple, W. J., Meloro, C. & Roth, V. L. 2015 The impact of large terrestrial carnivores on Pleistocene ecosystems. *Proceedings of the National Academy of Sciences*, 201502554.
- [63] Loveridge, A. J., Hunt, J. E., Murindagomo, F. & Macdonald, D. W. 2006 Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *J Zool* **270**, 523-530. (DOI:10.1111/j.1469-7998.2006.00181.x).
- [64] Bocherens, H. 2015 Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. *Quaternary Sci Rev* **117**, 42-71.
- [65] Marean, C. W. & Ehrhardt, C. L. 1995 Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. *J Hum Evol* **29**, 515-547. (DOI:DOI 10.1006/jhev.1995.1074).