Current Biology

CellPress

Review

Trophic rewilding as a restoration approach under emerging novel biosphere conditions

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https://doi.org/10.1016/j.cub.2024.02.044

SUMMARY

Rewilding is a restoration approach that aims to promote self-regulating complex ecosystems by restoring non-human ecological processes while reducing human control and pressures. Rewilding is forward-looking in that it aims to enhance functionality for biodiversity, accepting and indeed promoting the dynamic nature of ecosystems, rather than fixating on static composition or structure. Rewilding is thus especially relevant in our epoch of increasingly novel biosphere conditions, driven by strong human-induced global change. Here, we explore this hypothesis in the context of trophic rewilding — the restoration of trophic complexity mediated by wild, large-bodied animals, known as 'megafauna'. This focus reflects the strong ecological impacts of large-bodied animals, their widespread loss during the last 50,000 years and their high diversity and ubiquity in the preceding 50 million years. Restoring abundant, diverse, wild-living megafauna is expected to promote vegetation heterogeneity, seed dispersal, nutrient cycling and biotic microhabitats. These are fundamental drivers of biodiversity and ecosystem function and are likely to gain importance for maintaining a biodiverse biosphere under increasingly novel ecological conditions. Non-native megafauna species may contribute to these effects as ecological surrogates of extinct species or by promoting ecological functionality within novel assemblages. Trophic rewilding has strong upscaling potential via population growth and expansion of wild fauna. It is likely to facilitate biotic adaptation to changing climatic conditions and resilience to ecosystem collapse, and to curb some negative impacts of globalization, notably the dominance of invasive alien plants. Finally, we discuss the complexities of realizing the biodiversity benefits that trophic rewilding offers under novel biosphere conditions in a heavily populated world.

Introduction

Rewilding is gaining traction as an approach to restoration based on natural ecological processes. Rewilding can be broadly defined as restoration to promote self-regulating complex ecosystems by restoring non-human ecological processes while reducing human control and pressures[1]. This definition accommodates the diverse range of practical implementations. Rewilding is sometimes perceived as aiming to reconstruct specific past ecosystem states. However, in both formal definitions and practical implementation, rewilding is usually envisioned as a forward-looking, open-ended approach emphasizing the dynamic nature of ecosystems and aimed at promoting trajectories of high functionality for biodiversity rather than maintaining static species composition[2–4]. Taking a historical perspective is nonetheless important to rewilding. First, it is essential to understand how ecosystems functioned over the millions of years during which most current species and their adaptations evolved[5,6]. This knowledge enables us to identify which processes and elements require restoration, for instance depleted megafauna assemblages[7]. Second, the long-term perspective helps avoid shifting baselines, namely the risk of restoring toward already degraded ecosystem states from the recent past. This way, it also directs focus to the problem of negative ecological memory —defined as an ecosystem's accumulated abiotic and biotic material and information legacies from past dynamics — and associated hysteresis[8] in the implementation and evaluation of rewilding actions. Given the dynamic, functional focus of rewilding, the prefix 're-' should therefore be understood to mean 'again' rather than 'back'[9].The focus on functionality also suggests that rewilding is well-suited as an approach to ecosystem management in our current epoch of strong human-induced climate change and other anthropogenic global change, such as influx of alien species through globalization[10]. Rewilding aims to reduce human control on ecosystems, but at least initially some level of human intervention is often necessary. Such interventions can overcome long-lasting negative ecological memory effects from past human activities on ecosystem function and biodiversity[8], such as defaunation or reduced geodiversity. They can also compensate area constraints, for instance via a managed meta-population approach to megafauna species in settings where individual natural areas are too small to sustain long-term minimum viable populations. Abstaining from such active initial restoration efforts may make it impossible to restore ecosystem dynamics with high functionality and associated biodiversity gains[11].

For rewilding to successfully restore ecosystems, multiple interconnected ecological conditions, elements and processes are important, notably connectivity, natural disturbance (e.g., fire regime) and trophic complexity[4], but also area, abiotic heterogeneity and social willingness. In this review, we focus on trophic complexity, as it is often overlooked in contemporary restoration efforts yet has important implications for ecosystem functioning and biodiversity, also in emerging novel ecosystems. We define trophic complexity in terms of the diversity of larger-bodied species and the top-down trophic effects they generate. This focus reflects that species at higher trophic levels are often highly connected in food webs and functionally important to ecosystems[4,12–14]. It also captures the critical functional role of body size in animals[14,15], and the important functional diversity linked to species richness at these trophic levels[14,16]. This definition aligns with that by Bullock and colleagues[17] of ecological complexity as the number of components in a system and their associated number of connections but focusing on megafauna and their ecological connections. Restoration of trophic complexity is the core of trophic rewilding, an ecological restoration strategy that uses species introductions to restore top-down trophic regulation and associated trophic cascades to promote self-regulating biodiverse ecosystems[6]. Active species introduction differentiates trophic rewilding from passive rewilding, where spontaneous species immigration may lead to restoration of trophic complexity. Hybrid forms of active trophic and passive rewilding also exist, for instance when immigration is facilitated via habitat corridors or policy changes, such as hunting regulation. Such facilitation can in fact be considered as active as reintroduction. From a functional perspective, the key point is that trophic complexity is restored, not how this is achieved[5]. However, in modern fragmented and human-dominated landscapes the capacity and opportunity for spontaneous spread varies strongly among large mammal species[18]. In the following we use trophic rewilding in this broader sense, i.e., encompassing all rewilding that restores trophic complexity.

Trophic rewilding is typically focused on large-bodied vertebrate species (megafauna). These species have widely and disproportionally been removed from ecosystems through human activities (defaunation)[19], with severe global losses across the last 50,000–100,000 years and still ongoing[7,20,21]. At the same time, they have potential to play key roles in ecosystems as ecosystem impacts are directly linked to body size[14,15], compounded by the unique functional traits of various megafauna species[14], for instance the different digestive physiology of ruminants and non-ruminants, the trunk of proboscideans or the amphibious adaptations of hippos (*Hippopotamus amphibius*) and water buffalos (*Bubalus* spp.). Moreover, large vertebrates have a deep history of presence and diversity in terrestrial ecosystems, with a continuous span of around 50 million years, dating back to the faunal recovery after the Cretaceous-Paleogene (K-Pg) mass extinction[22,23], suggesting that many other organisms have adapted to, and may even depend on, megafauna[24,25]. In addition, as many megafauna species have gone globally extinct, the use of non-native species as functional analogues and de-domesticated or feral forms is also considered and already implemented in various cases[26–28]. In this review, we focus on terrestrial megafauna. While trophic complexity is also important in marine ecosystems, they are far better spatially connected, reducing the need for active re-introductions.

Actual applications of trophic rewilding must take place within a socio-ecological framework in which social dynamics and equity are crucial factors, as they are in broader restoration and conservation efforts[29–31]. The importance of incorporating social elements into rewilding designs has been emphasized in multiple comprehensive reviews on the subject[2,4]. Reflecting this perspective, continuum approaches have been proposed, where the degree of rewilding implemented is shaped by societal acceptance[2,32]. Notably, a continuum framework for the implementation of trophic rewilding in human-dominated landscapes has been developed, co-produced with managers and other stakeholders[28]. The degree to which ecological functionality is restored will have consequences for biodiversity and ecosystems. Therefore, taking social considerations into account may come with ecological trade-offs, but should nevertheless enhance long-term effectiveness given the need for societal support[30].

Emerging novel biosphere conditions increase the need for trophic rewilding

Biotic assemblages are changing globally at increasing rates driven by a broad range of anthropogenic drivers[33–36], not least reflecting the ‘Great Acceleration’ in socio-economic and human-driven Earth system trends since the 1950s[37]. These biotic shifts even extend to remote areas, such as plant community change on mountain summits[38], and to the functional structure of biotic assemblages, such as accelerating importance of alien species and associated functional restructuring of plant–frugivore networks globally[10]. A principal outcome of this biotic restructuring is the widespread emergence of novel ecosystems[39,40] as a key characteristic of our current human-dominated epoch, the Anthropocene. Novel ecosystems are natural and semi-natural ecosystems, the species composition or ecological functioning of which are without recent historical precedent due to human influence[40]. Importantly, according to this definition of novel ecosystems, their novelty (dissimilarity relative to recent baselines[41]) is self-sustaining and not dependent on ongoing management[40], mirroring a defining aspect of rewilding. Novel ecosystems will likely be the norm by the late 21st century, especially due to increased atmospheric CO_2 levels and climates not seen for millions of years[42,43] (Figure 1), as well as globalized transport of species between distant parts of the world[10,44] (Figure 2). In fact, the Intergovernmental Panel on Climate Change estimates that global anthropogenic warming has already reached levels unprecedented in the Holocene[42].

The remaining wild ecosystems are also affected by reduced area, increased fragmentation[45], changes to key processes, such as fire regimes[46,47], and defaunation[19], all of which generate unprecedented environments and promote novel ecosystems. For example, defaunation is leading to smaller-bodied faunas than seen for at least 30 million years[7], with substantial effects on species composition and ecological functioning[19]. These ongoing fundamental changes are happening in the context of a human population likely to reach a staggering 10 billion people by 2100 (as opposed to 3.7 billion in 1970)[48] and

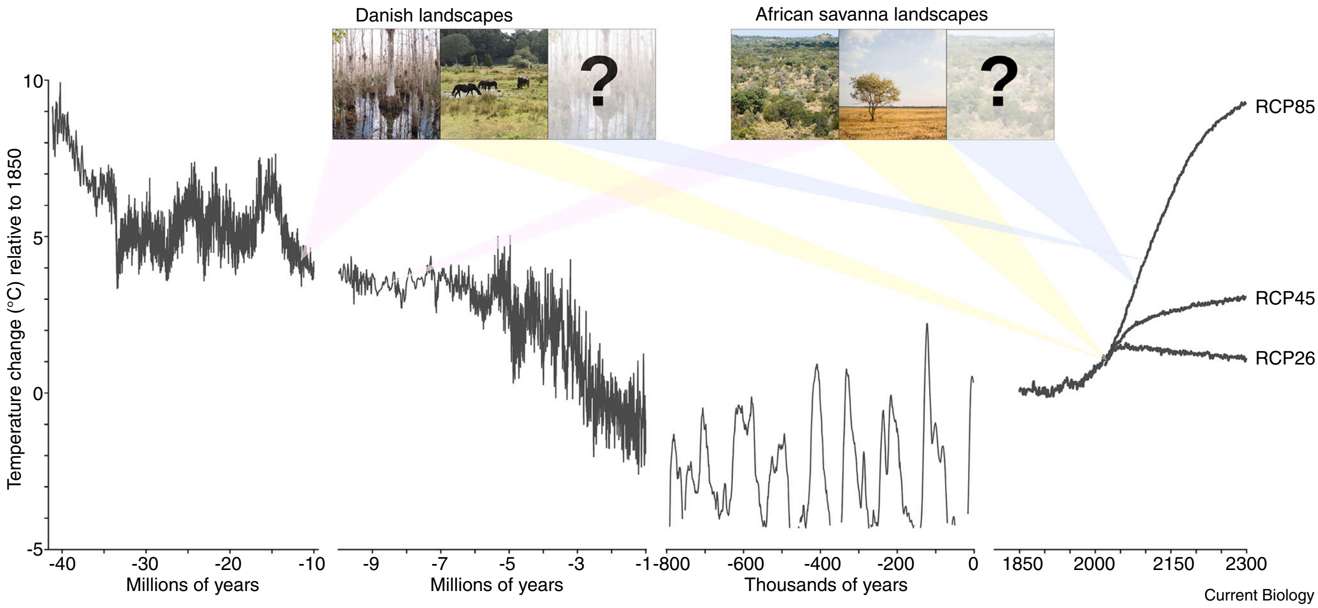

Figure 1. Future climate is likely to cause the global emergence of novel ecosystems.

Future climate is likely to widely become warmer than it has been for millions of years, likely resulting in global biome shifts and novel ecosystem structures. Reconstructed temperature trends for the past 40 million years and projected beyond the present to 2300 under three different climate scenarios[42]. The picture inserts represent vegetation biomes corresponding to the indicated temperature and known natural ecosystems in the past and present, illustrating the stark difference in biome type associated with the temperature shifts expected for the future (photos: Danish landscapes: J.-C. Svenning; African savanna landscapes: left © Chris Eason/Wikimedia commons (CC BY 2.0 DEED) and right © Rodion Kutsaev/Unsplash).

steeply intensifying per capita resource use[49] — dynamics that will further fuel the spread of novel ecosystems worldwide. The expansion of novel ecosystems places their management at the heart of biosphere stewardship.

The ongoing global spread of novel ecosystems is associated with strong risks for Earth's biodiversity, such as climate-driven ecosystem degradation, invasional meltdowns (introduction of one alien species facilitating further invasions, leading to compounding negative ecosystem impacts) and trophic downgrading (ecological consequences of removing apex consumers)[13,36,50,51], all of which could jeopardize biosphere functioning[52–54]. However, novel ecosystems can also have neutral or positive effects on biodiversity and ecosystem services[38,55–59], raising the question whether and how they could affect biodiversity and biosphere functioning on a planetary scale. Could the dynamics of novel ecosystems be steered towards positive outcomes for biodiversity[60] and for people, considering that over one billion people directly depend on nature for their basic needs[61]. In this context, we suggest that trophic rewilding has strong potential as part of a global solution, with scalable benefits to biodiversity and ecosystem functioning also in the context of novel biosphere conditions (Figure 3). We nonetheless recognize and emphasize that limiting anthropogenic warming and associated catastrophic outcomes[62,63] as well as reducing other human pressures on ecosystems are prerequisites for successful ecosystem restoration, as captured in the core conceptualization of rewilding[2,4,6].

Below, we first outline the general ecological effects of trophic rewilding and discuss them in the context of novel biosphere conditions. We then review the upscaling potential in trophic rewilding, its ability to overcome past megafauna losses and its potential to facilitate biotic adaptation and resilience to climate change. Thereafter, we discuss its contribution to climate change adaptation and, potentially, mitigation and to reducing the negative biotic impacts of globalization. Finally, we consider the complexities of implementing trophic rewilding in a heavily human-populated world undergoing strong climatic warming.

Ecological effects of trophic rewilding are likely to benefit biodiversity

The concept of trophic rewilding has been developed to benefit biodiversity by acting on fundamental ecological mechanisms, such as the positive relationships between biodiversity *versus* ecosystem heterogeneity[64] and biodiversity *versus* dispersal[65], and is therefore also expected to remain an effective approach under novel biosphere conditions (Figure 4). Herbivores are particularly important in trophic rewilding as they impact vegetation, which forms the basis of terrestrial food chains, dominates biomass[66] and is often a dominant part of physical habitat structure. Herbivore megafauna strongly affects the structure and energy flows of ecosystems, not least through plant consumption[14], often generating heterogeneity in vegetation structure[67,68]. Additionally, herbivores are important seed dispersers for many plants[69], thus maintaining overall plant diversity[70,71] and persistence of species depending on megafauna-dispersal[24,72,73]. Further, herbivore megafauna affects soils via nutrient dispersal and varied levels of trampling, thus also generating mosaics in soil conditions[68,74]. In general, heterogeneity in vegetation and soil predicts species diversity at local and larger scales[64]; hence, these effects on vegetation and soil represent a general mechanism by which herbivore megafauna may promote biodiversity, also under rising ecological novelty.

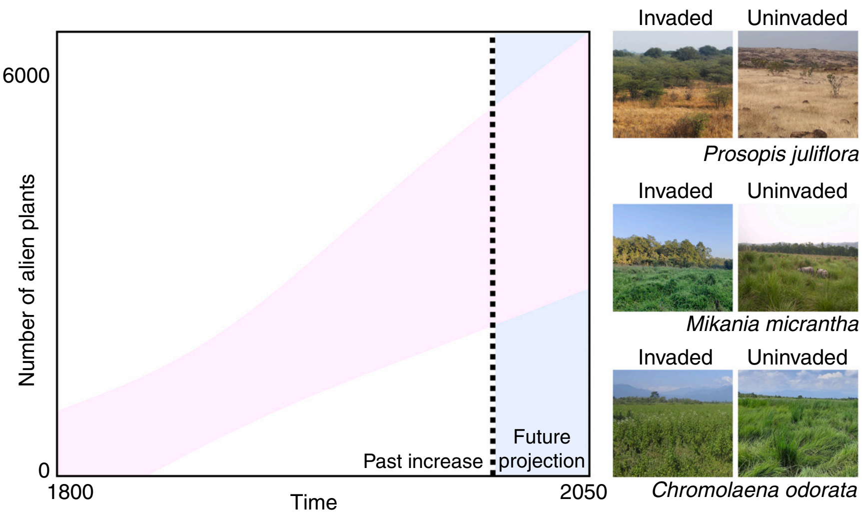

Figure 2. Historical and projected future increase in alien vascular plant species per continent.
The number and abundance of alien plant species at local to continental scales have been increasing steeply since the 1800s and are projected to continue to increase into the future[10,44]. This invasion progression speaks to the inevitability of novel species assemblages, hereunder the risk of dominance by one or a few alien species to the detriment of local biodiversity. Photo inserts compare ecosystems heavily invaded by invasive plants (left) with the same ecosystem in its uninvaded state (right) in India (photos: *Prosopis juliflora* by Rajat Rastogi (left) and Ninad Mungi (right); *Mikania micrantha* by Ninad Mungi (left) and © Meg and Rahul/ Flickr.com (right); *Chromolaena odorata* by Alolika Sinha).

Large herbivores also generate a variety of microhabitats for many other species. These include the herbivores' own bodies, which host a variety of direct and indirect parasites and commensals. Likewise, their feces harbor a rich diversity of dung-dependent invertebrates and fungi, and their carcasses provide for decomposer species, from invertebrates to large scavenger birds and mammals[24]. As herbivores vary in ecological traits[75,76], a more functionally diverse fauna should have greater and more varied impacts on ecosystems and species diversity[14,67,77]. It is important to recognize that different megafauna herbivore species have different effects on vegetation and biodiversity[14]. There are differences according to feeding ecology, such as browsers, mixed-feeders or grazers, and according to digestive systems; for example, hindgut fermenters, such as horses, typically have higher daily movement rates and dietary niches than ruminants, such as cattle, while both are considered grazers[14,78–80]. Additionally, subtle dietary differences among functionally similar species, even in relatively intact assemblages, suggest that higher herbivore richness will affect more plant species and increase food-web links[16,80]. Additionally, there can be marked differences in dung-associated arthropod communities even among similar-sized herbivore species[78]. Movement rates and the capacity to consume larger, coarse, and more lignified plant parts strongly increase with body size[14,69,81], with megaherbivores such as elephants having particularly strong capacity to open up woody vegetation[82,83]. Altogether, given these different effects, larger herbivore species are expected to have more potential to positively affect biodiversity than smaller species. High abundances of smaller mesoherbivores — with body weights ranging from about 5 to 100 kg — in simplified assemblages increase the risk of losses in preferred food plant species than more diverse faunas, as illustrated by deer overabundance reducing plant diversity[84,85]. Indeed, herbivore assemblages characterized by smaller, selective feeders tend to lead to a reduction in local plant diversity, while those dominated by larger, bulk-feeding species tend to increase it[86].

Carnivores may enhance the positive effects of herbivores, notably in terms of promoting heterogeneity in vegetation and other factors. Carnivores can modulate numbers and space use of herbivore species, for instance by causing prey species to avoid areas of high predation risk due to dense vegetation ('landscape of fear'), which may in turn affect herbivore pressure and vegetation dynamics[87–89]. These direct and indirect effects are well documented for mesoherbivores, such as deer[87,90]. Still, the role of carnivores in shaping the ecological effects of herbivores is more nuanced[14]. Importantly, effects linked to carnivores are often complemented or even overshadowed by bottom-up and abiotic stress effects[90,91]. Megaherbivores (>1000 kg) are not top-down regulated[83] and the same is often true for large (≥500 kg) herbivores such as bison and African buffalo[90,92,93]. Ungulates undertaking large migrations are also often limited by food rather than predation[94], and the same can be true for certain non-migratory mesoherbivores that are dangerous and have high reproductive rates, such as wild boar[90].

Apart from their interplay with herbivores, large carnivores often suppress mesopredators, which may lead to increased abundance of the latter's prey species[95,96] including mesoherbivores, such as pronghorn (*Antilocapra americana*)[97]. In fact, such suppression may even occur between large carnivore species, such as tigers strongly suppressing wolf abundance in northeastern Asia, resulting in lower overall predation pressure in tiger territories and probably increasing the abundance of herbivores[98]. Furthermore, studies from both Africa and North America show that large carnivore restoration is not associated with a smaller total biomass of large and medium-sized herbivores, but rather with shifts toward less predation-prone big herbivores, such as rhinos and big bovids[93,99]. As their landscape use is driven less by predator avoidance rather than resource availability[100,101], this is likely to affect the spatial patterning in herbivory levels. These considerations suggest that perceptions — as for example seen in the public discourse on the wolves in Yellowstone — of widespread down-regulation of herbivore density by predation are unsupported, and that the assumed low natural numbers of herbivores in, for instance, Europe and North America are similarly misconceived[102]. Rather, large carnivores are likely to promote overall biodiversity by a more complex set of mechanisms, namely limiting mesopredator and mesoherbivore abundance and enhancing spatial heterogeneity in mesoherbivore impact[12], while promoting the biggest herbivore species.

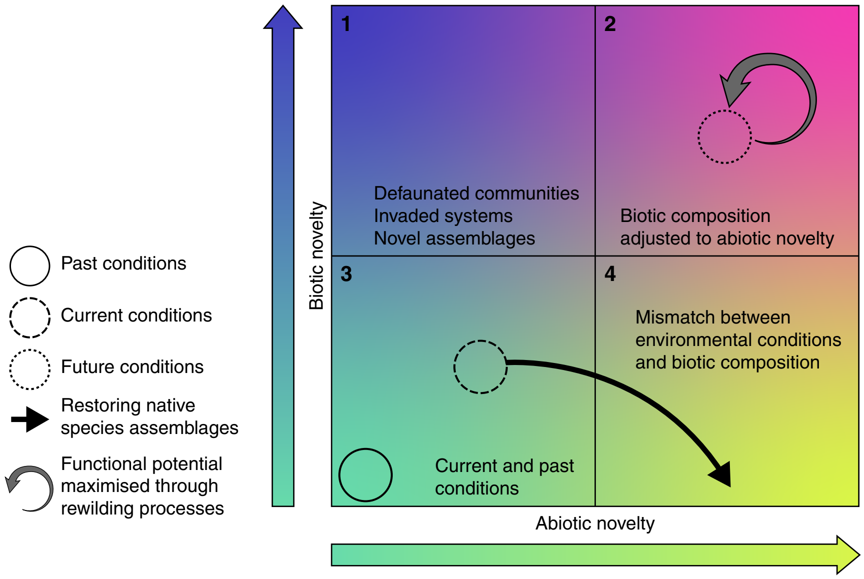

Figure 3. Trophic rewilding as part of a global solution to ecological risks from rising biosphere novelty.
Processes, such as alien species invasions and defaunation, give rise to ecosystems with novel biotic composition, ranging in form from heavily invaded systems with single species dominance to diverse and functioning communities without historical precedent (quadrant 1). Given the inevitability of strong future climate change, to maintain ecosystem functioning biotic composition should be allowed to keep pace with abiotic novelty (quadrant 2). Traditional restoration practices, which typically focus on restoring species assemblages to fixed, often historical states, will lead to a mismatch between future environmental conditions and biotic composition (quadrant 4). However, trophic rewilding could potentially enhance the functional potential of emerging novel ecosystems by re-establishing key ecological processes and structures (such as dispersal, disturbance, and ecological heterogeneity), thereby minimizing the risk of undesirable biotic novelty such as single-species dominance or ecosystem breakdowns.

An important point for trophic rewilding is that megafauna effects often interact with geodiversity, which refers to heterogeneity in abiotic elements and processes[103], such as flood dynamics of rivers, which in themselves are also expected to increase species diversity[64]. Notably, megafauna create[74] and respond to geodiversity[104]. Importantly, via faunal responses to terrain and hydrology, these factors may promote heterogeneity in herbivory types and levels and thereby lead to heterogeneity in vegetation[105]. Furthermore, through their movement patterns herbivores may generate heterogeneity in soil conditions, such as mosaics of soil compaction and turbation[74], albeit especially the largest species may also homogenize soil conditions at certain scales[101]. In addition, carnivores and omnivores may also shape spatial nutrient cycling patterns e.g., cougars generating nutrient hotspots at preferred hunting spots via carcass deposition[106]. The interaction of megafauna with geodiversity suggests that high geodiversity generally should benefit the biodiversity outcomes of trophic rewilding, also under ecological novelty. Therefore, it should be advantageous to restore or even create geodiversity in rewilding areas, for instance by restoring natural river dynamics. A related action would be to allow connectivity between terrestrial and marine ecosystems, which also may have strong effects on trophic interactions and nutrient movement (Figure 4)[107,108].

Non-native megafauna and trophic rewilding

In the context of trophic rewilding under novel biosphere conditions, it is worth considering the role of non-native species — a designation best seen as gradual[109]. In fact, they can be among the most abundant megafauna present, though often underreported, as for instance feral pigs or wild boar (*Sus scrofa*), feral horses and donkeys (*Equus* spp.) as well as axis deer (*Axis axis*) in various parts of the Americas[110]. Given the ecological effects of large herbivores discussed above, it is expected that non-native megafauna species are likely to often benefit biodiversity, especially when embedded in functionally diverse assemblages and in regions that historically hosted a diverse megafauna.

Perceived problems around impacts of non-native megafauna are widely reported. However, many studies are from regions without functionally similar present or past native megafauna[111,112], livestock systems where effects are strongly shaped by husbandry practices[14], or simplified faunas that lack bigger herbivores or large carnivores[113]. Moreover, the focus on negative impacts in the literature may also be affected by bias in study design and interpretation, as discussed for the invasion biology literature overall[114]. In fact, functional traits of non-native large herbivores generally contribute to restoring functional trait composition of herbivore assemblages towards the pre-extinction Pleistocene baseline[115]. This supports the expectation of overall positive effects as the majority of native species must have been exposed to, or even shaped by, similar forms of herbivory for most of their evolutionary lifespan. In the case of the African, Eurasian and American continents it is also important that they have been well connected for megafauna across the last 20–30 million years[116,117], owing to their high mobility across frequent land bridges. Hence, megafauna exchanges between these regions are not expected to carry big risks for regional biodiversity, at least not across large spatial scales and longer periods. In line with these considerations, non-native megafauna in modern-day ecosystems do indeed sometimes generate ecosystem heterogeneity, resources and habitat (for instance, well-digging by feral donkeys in American deserts[118]), and promote biodiversity (for instance, positive livestock effects on plants and macroinvertebrates in the Andes[119]). Further, a global meta-analysis found that the degree of nativeness of large herbivores did not shape their effect on plant abundance and diversity, which instead was linked to herbivore functional traits[86].

Due to the late-Quaternary global extinction of a large proportion of megafauna species[6], non-native megafauna species are in fact being considered for active introductions in

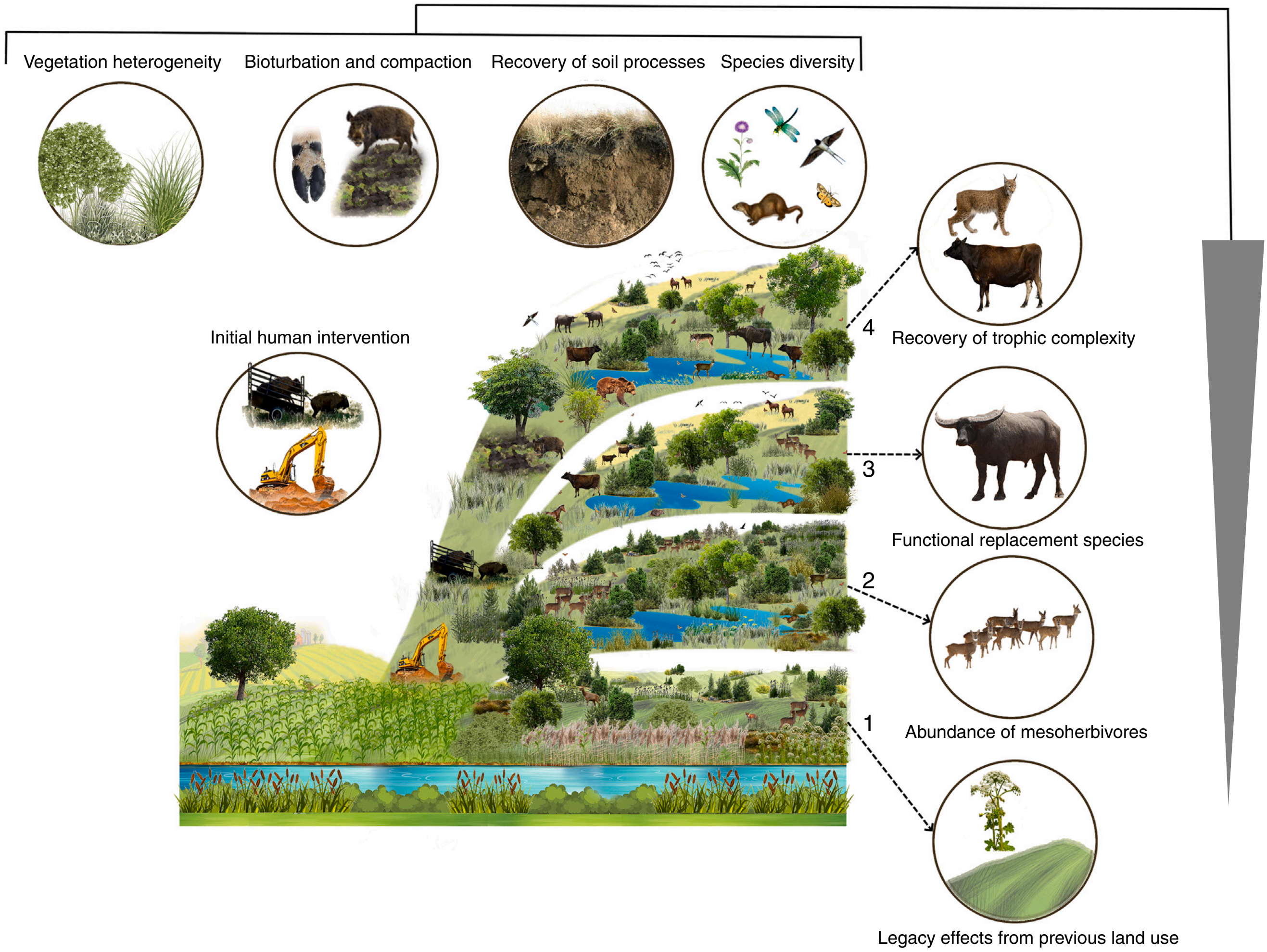

Figure 4. Restoring megafauna-related trophic complexity is important for effective rewilding.
Rewilding as a restoration approach aims to promote functional, biodiverse and complex ecosystems through the re-establishment of natural ecological processes, with trophic rewilding focusing on the restoration of trophic complexity notably as mediated by large animals. Its implementation can be achieved in increasingly more ambitious ways with each additional tier more likely to achieve the self-regulating complex ecosystems sought. At its most basic, passive rewilding (1) essentially involves land abandonment followed by the spontaneous resurgence of some animal populations. This non-interventionist approach is likely to retain many negative legacy effects of previous land uses and may be insufficient to restore ecosystem functionality (e.g., lack of a functional herbivore fauna may facilitate dominance by competitive alien plants). Some degree of human intervention, such as restoring natural river flows (2), may enhance functionality and biodiversity value, but the depauperate surrounding species pools will constrain biotic recovery and functionality, e.g., with faunal recovery restricted to smaller species. Under trophic rewilding, a more ambitious initial intervention, such as the reintroduction of extirpated, large-bodied herbivores (at times using functional replacement species) (3) and the reassembly of complete trophic levels, including carnivores (4), is more likely to initiate essential ecological processes such as dispersal, herbivory pressure on low-quality food plants, and spatial variability in herbivory and disturbances. Such faunal restoration is likely to exhibit synergy with restoration of geodiversity such as natural river dynamics. These effects are likely to be effective also under novel biosphere conditions.

trophic rewilding and in some cases already being used; for instance, Asian water buffaloes (*Bubalus bubalis*) are being introduced in Europe[28] to have a large semi-aquatic bulk-feeder to provide herbivory also in wet landscapes. In this case, the species has long history as a domestic species in the region, minimizing the risk of unforeseen negative ecological effects. By contrast, entirely new introductions of non-native species should go through carefully controlled initial screening phases. Risk of unintended invasion is comparatively low for large-bodied species that are typically easier to find and control than insects, mesopredators or plants and the risk can be further mitigated by selecting trial sites that would facilitate control if needed. Extra care should be taken on isolated oceanic islands that did not harbor mammalian megafauna prior to human arrival[112]. However, even here carefully selected alien substitute species can have positive effects, for instance, substituting extinct native tortoise and flightless birds with introduced tortoises[120]. Overall, we believe the current evidence is not fit to dismiss non-native megafauna in ecosystem restoration, whether by chance or on purpose[121] but rather indicates much positive potential. We suggest that a rebalancing of the research focus on these introduced species will facilitate discerning generalities from context dependencies and potential biases.

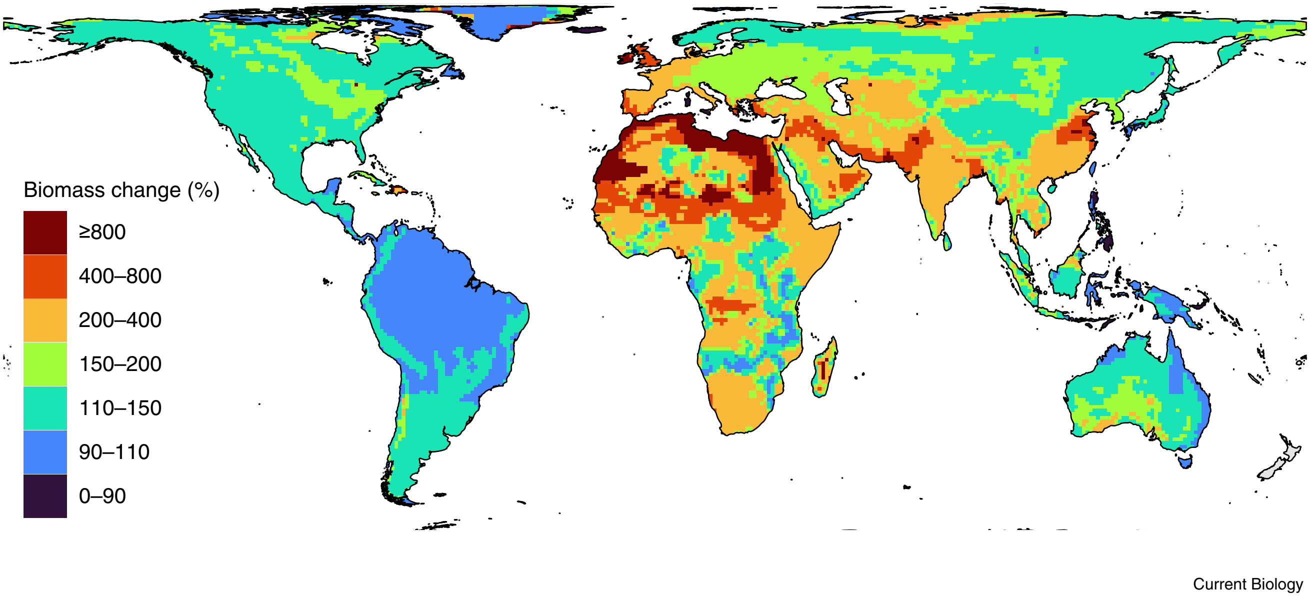

Figure 5. Potential increase in mammal community biomass by restoring extant species to their native ranges.
If still extant mammal species are restored to their natural distribution, this could strongly increase average community body mass (weighted by animal density) and the many associated functions; multiplicative increase in biomass if extant terrestrial mammals were reestablished in their present-natural ranges (natural ranges without human impacts now or in the past) relative to their current native distributions. Biomass is estimated as estimated species body mass times estimated natural population density. Extant species include IUCN extinct in the wild status as well as *Bos primigenius* and *Camelus dromedarius*, where domesticated forms could be introduced as the wild form but excludes modern humans (*Homo sapiens*). Terrestrial excludes bats, whales, pinnipeds, and sea cows, and two marine non-pinniped carnivores (sea otter, *Enhydra lutris*; marine otter, *Lontra felina*). Average refers to geometric means of 3000 sums of sampled mass distributions for all species in a grid cell (data from[196,197]).

Upscaling trophic rewilding

To realize its potential effects on biodiversity, ecosystem functioning and ecosystem services, any restoration approach needs to be scalable to large areas. Species diversity is strongly dependent on area. Decline in suitable habitat area is the major cause of species loss, through immediate as well as delayed effects, so-called ‘extinction debt’[122]. Biotic community and population dynamics as well as many ecosystem processes depend on dispersal processes within larger landscapes, as conceptualized in the metacommunity and meta-ecosystem concepts[123,124]. Further, any ecosystem-based contributions to climate change mitigation need to be effective across large areas to substantially affect global climate[125]. The overarching importance of area is highlighted by ambitious area-based conservation and restoration targets, and fortunately there is also major potential to make the space available[126].

Realizing the potential of area-based conservation and restoration approaches requires that areas are functional for biodiversity and support resilient ecosystems with persistent climate benefits; this means that ecosystems should remain functional also under emerging novel biosphere conditions. To upscale restoration efforts, trophic rewilding has two major advantages: it involves reinstating general megafauna-linked processes[14], which are expected to remain effective under novel conditions; and it can be upscaled via spontaneous rapid population increases and spatial expansions in megafauna species. There are many real-world examples illustrating the potential for massive megafauna recoveries as soon as human pressures are removed, as long as the animals are in the system already or are introduced. One impressive case is the massive post-war comeback of megafauna and their ecological effects in Gorongosa National Park in Mozambique[127]. Another is the fast population growth of reintroduced populations of muskox (*Ovibos moschatus*) in various parts of northern Eurasia[128]. Just restoring still extant large-mammal species to their natural distribution could strongly increase average community body mass (weighted by animal density) and the many associated functions (Figure 5), illustrating the strong potential to reinstate megafauna-linked processes at least partially. More complete functional restoration would depend on the use of approaches such as functional replacements and acceptance of already established non-natives[115] and would be especially needed in regions having suffered severe global extinctions of their megafauna species[76].

Long before trophic rewilding was considered, anthropogenic extirpation of megafauna prompted efforts to restore the individual species themselves. Upscaling these efforts is important both from the functional perspective of trophic rewilding and to safeguard Earth’s megafauna biodiversity under rising biosphere novelty. Given the potential severity of future climate stress[129] along with human fragmentation of megafauna habitats[18], assisted movement will likely remain an important tool, as already envisioned in trophic rewilding[6], and this may well need to include translocation outside the conventionally recognized native range, potentially even to new geographic regions[115]. Nevertheless, even with such translocation, megafauna populations are likely to often encounter novel ecosystem conditions. Fortunately, there are many examples of megafauna populations thriving under novel conditions due to introductions outside their native range unrelated to rewilding, such as feral horses in South American tropical savannas[130] and hippos (*Hippopotamus amphibius*) in South American river ecosystems[131]. These examples also suggest that already established alien populations in some cases may play important roles in the conservation of megafauna species under future novel biosphere conditions. The same applies to feral populations, not least species that are completely extinct in the wild or have lost much of their gene pools. A few megafauna species such as Eurasian ox (*Bos primigenius*) only survive as domestic and feral populations, but are far from extinct, with extant populations harboring high, ancient genetic diversity[132]. Further species such as horse (*Equus ferus*) and donkey (*E. africanus*) have substantial genetic diversity within the domestic and feral populations outside remnant wild populations[133,134]. Inclusion of feral populations of such species in trophic rewilding is important for the re-establishment of these species as functional evolutionary entities in nature, which requires establishment of long-term viable populations under natural selection. Smaller rewilding-inspired projects often include animals managed as domestic animals or even only sterilized animals, which offers limited or no contribution in this regard. This underscores the need for larger areas and megafauna populations and compensatory strategies in the case of small, fragmented populations, e.g., managed meta-population approach[135]. In summary, upscaling trophic rewilding efforts via the re-establishment of large populations of species otherwise rare or extinct in the wild is ecologically important and will also contribute to safeguarding megafauna biodiversity in the long-term.

Trophic rewilding to facilitate biotic adaptation and resilience to climate change

Restoring wild megafauna has potential to promote biotic adaptation and resilience to climate change via two main mechanisms: promoting plant dispersal and generating environmental heterogeneity. As primary producers and the main biomass component[66], plants play a crucial role in the response of terrestrial ecosystems to climate change. A key factor in the adaptive response to climate change is dispersal, as it enables species to move to track suitable climate conditions. This is also true for plants, even though their established individuals are sessile. At least 50% of species of seed plants are dispersed by animals, with dispersal distance strongly increasing with animal body size and a positive effect of gut passage on germination[81]. Consequently, past and current defaunation is estimated to have strongly reduced overall plant dispersal and the ability of plant species to track current climate change[81]. Consequently, many plant species suffer strong dispersal limitations in current anthropogenic landscapes, such as in Europe, limiting their ability to thrive in current landscapes and to colonize restored natural areas[70,136]. Through restoring large animals and their important dispersal function, trophic rewilding is expected to facilitate biotic adaptation and resilience to climate change, allowing both colonization of new areas and recolonization after disturbance, for instance after extreme climate events.

Trophic rewilding is also expected to promote biotic adaptation and resilience to climate change via positive effects of megafauna on environmental heterogeneity[68]. Such heterogeneity promotes a larger species pool[64] with a greater variety of niche requirements. This in turn promotes adaptation and resilience at the community and ecosystem levels. Species may respond differently to climate change while providing functional redundancy. Additionally, heterogeneity can provide source populations within landscapes for tracking spatial climate shifts and facilitate recolonization after diebacks. By promoting vegetation heterogeneity, megafauna may promote microclimatic variability, helping populations of individual species to adapt to climate change in terms of modulating direct climate effects. For mobile species, vegetation heterogeneity also facilitates behavioral adaptation at the individual level to climate change, for instance by avoiding thermal stress[137]. Furthermore, megafauna may also help other species survive indirect climate effects, such as climate-driven vegetation change. For example, by maintaining areas of open habitat in arctic landscapes undergoing warming, large herbivores help shade-intolerant tundra plants survive[138].

Trophic rewilding for climate change mitigation

There are five main pathways through which the restoration of large, wild populations of large herbivores has the potential to contribute to climate change mitigation over the long term: reducing catastrophic fires, enhancing stable carbon accumulation in forests and soils, facilitating ecosystem adaptation to climate change (as discussed above), maintaining carbon sequestration and promoting high-albedo land cover[125].

Warming temperatures and associated drying are driving a rise in fire risk, especially of high-intensity fires in forested regions. Fires are a natural disturbance phenomenon with positive ecological functions over large parts of the world, but high-intensity fires in high-biomass ecosystems may lead to large losses of established vegetation, with immediate strong carbon releases and (temporarily) reduced capacity to sequester carbon, as large trees sequester carbon more efficiently than smaller trees[139]. In ecosystems in which fire is not endemic, such as most tropical forests, fire can have strong negative impacts on biodiversity. Furthermore, shifts toward more intense fire regimes may transform high-biomass vegetation such as forest and woodland into more open systems, with permanently reduced carbon sequestration[140]. Large herbivores consume vegetation and may thus limit the build-up of flammable plant biomass, reducing ecosystem flammability, fuel load and fuel continuity[14]. There is evidence that prehistoric declines in megafauna have elicited more intense fire regimes[141,142]. There are also contemporary examples of large herbivores reducing fire in the landscape[14], such as white rhinos (*Ceratotherium simum*) generating grazing lawns that function as natural fire breaks reducing fire spread and size in savannas[143] or grazing livestock nearly excluding fire from rangelands[47]. There is increasing interest in trophic rewilding to achieve reduced fire risk, but the generality of such effects remains an open question[144].

Herbivory is expected to reduce carbon sequestration by reducing vegetation biomass[14,68]. Nevertheless, reductions in above-ground carbon sequestration may sometimes be fully compensated for by increased sequestration below-ground, as reported from savanna woodland in Namibia[145]. Importantly, below-ground pools may be more persistent due to reduced risk of release due to disturbances, such as fire[146]. Moreover, process-based modelling suggests that forest elephants (*Loxodonta cyclotis*) promote trees with high wood density via dispersal of their large seeds and preferential herbivory on more palatable low-density species, thereby promoting higher carbon sequestration within these dense forest ecosystems in Africa[147]. However, there are large uncertainties regarding the net impact of animals on total ecosystem carbon, with potential effects likely varying substantially across species and environmental contexts[148,149]. Abundant, diverse megafaunas are expected to facilitate ecosystem adaptation to climate change by promoting plant migration and generating high levels of local microclimatic variability (as discussed above). Hence, re-establishing abundant, diverse megafauna should reduce risks of ecosystem breakdowns and associated carbon releases.

Large herbivores may also affect the climate via their effect on land cover albedo[125]. Forests generally have low albedo, while grassy and herbaceous vegetation and bare ground have high albedo, providing a cooling effect. In some circumstances such as boreal forest, their low albedo may exceed their carbon sequestration benefit in terms of climate forcing[150]. By promoting more open high-albedo conditions, large herbivores may thereby contribute to reducing warming, an effect that has especially received attention with respect to arctic and boreal ecosystems and that needs further investigation[125].

In summary, there are several mechanisms through which trophic rewilding has potential to contribute to climate mitigation in natural ecosystems, but the empirical support for these mechanisms varies. For example, animal impacts on fire regimes have been more extensively studied and show more consistent results compared to animal impacts on carbon sequestration. The empirical work on the latter is still in its early stages, with sometimes conflicting results and many open questions[14,151,152]. At a more general level, it is clear that converting vast tracks of marginal or unneeded agricultural lands to a (semi-) natural state is likely to contribute considerably to climate change mitigation[126]. Still, to have substantial and timely impact on the climate system, trophic rewilding would indeed need to take place across large proportions of the land surface at short to medium timescales[125]. So, while the potential for climate benefits from trophic rewilding is encouraging, it should not distract from reducing greenhouse gas emissions and phasing out fossil fuels.

Trophic rewilding may reduce the negative impacts of invasive species

In addition to climate change, the emergence of novel biosphere conditions is also driven by globalization as humans spread organisms around the word, reshaping global and local biotic interactions at accelerating rates[10]. Biological invasions are widely perceived as a major threat to biodiversity[36], albeit with some controversy[114]. This spread of organisms is likely to keep intensifying across the coming decades[44,153]. Invasions by alien plants (sensu[154]) are an important driver of the emergence of novel ecosystems and broadly considered a risk to native biodiversity. This reflects that vascular plants form the biomass backbone of most terrestrial ecosystems[66] and strongly affect the biodiversity of other organisms[155,156]. Many studies report negative effects of alien plants on native plants[157]. At the same time, positive relations between species richness of native and alien plants are common[58,158] and effects on ecosystem services are heterogeneous[159]. Furthermore, the dominance of some alien plant species may become reduced over time[160]. Alien plant invasions also affect non-plant organisms[161,162], sometimes with positive feedback between alien plants and non-native species from other organism groups[10,163].

Restoring megafauna may in various settings reduce the dominance of alien plants and mitigate their effects on native biodiversity. A recent, extensive study[164] assessed the relationships between megaherbivores, native plants and alien plants across 12 ecoregions in India. It found a strong, negative relationship between the abundance of megaherbivores (gaur (*Bos gaurus*) and bigger species) and alien plant abundance whereas richness of native plant species was increased. This relationship was strongest at medium net primary productivity and megaherbivore density close to ecological carrying capacity. Another remarkable example comes from a protected savanna area in Mozambique, where recovery of large herbivores led to strong control of an invasive shrub (*Mimosa pigra*) through herbivory pressure[127]. Furthermore, reintroduction of elk (*Cervus canadensis*) similarly suppressed annual alien plants in a California grassland area[165], and cattle grazing in Serbian floodplain woodland strongly reduced an invasive shrub[166]. Further case studies also support that ungulates can suppress invasive plants[167–169]. However, there are also instances where large herbivores promote alien plants[170] or reduce some alien plants but promote others[171]. It is a long-standing idea in invasion biology that high native species richness reduces the invasion success of potential invaders[172], notably through competitively limiting niche space availability[173], but also through trophic interactions[163]. Support for such biotic resistance by native plants has varied[58,174] likely due to scale- and context-dependence[175], where herbivory may be an important factor[176,177].

We suggest that large herbivores may play a general key role in generating biotic resistance towards invasive alien plants. The reason is that invasive alien plants have general ecological characteristics that should make them susceptible to suppression by megafauna, notably adaptations for fast growth[178,179], which typically come with lower resistance against herbivores[180,181]. Large herbivores would be expected to seek out less defended alien plants or simply encounter dominant alien plants more frequently, resulting in a higher herbivory pressure on these plants[182,183], decreasing their competitive ability relative to other plants and maintaining plant diversity in many settings[164,183]. However, large herbivores may also promote alien plants via enhancing their dispersal[184]. In addition, there are clearly also alien plants that do not fit the general pattern and are indeed herbivory-tolerant, and such species may become so abundant that they lower the capacity of large herbivores to down-regulate them[164]. So, an important outstanding question is the extent to which these effects are overcome by the expected general limitations from megafauna herbivory on most alien plant species.

For invasive alien animals, the expectations and the evidence for the effects of restoring trophic complexity are less clear than for invasive plants. One expected general type of effect is mesopredator suppression by large carnivores. Comeback of the native Eurasian otter (*Lutra lutra*) may suppress invasive American mink (*Neovison vison*) in parts of Europe[185], but the overall effect is not clear[186]. Predation by wolves causes substantial mortality in introduced racoon dogs (*Nyctereutes procyonoides*) in some areas of Europe[187]. Perhaps the clearest case is the suppression of invasive mesopredators in Australia by dingoes

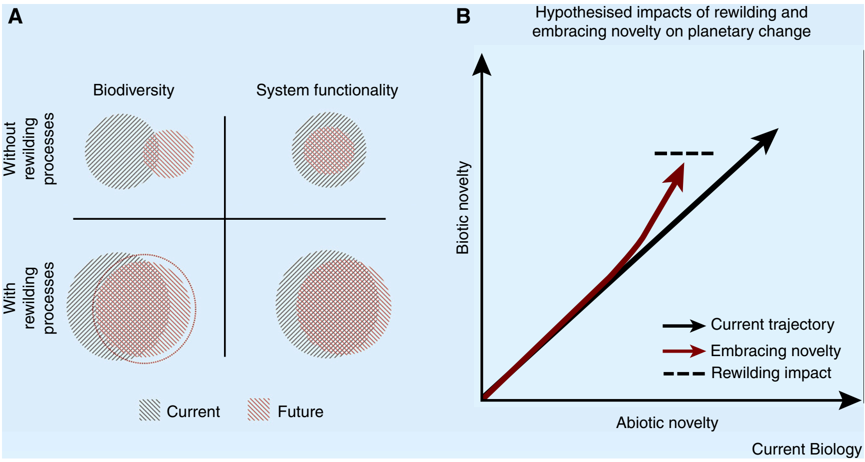

Figure 6. Trophic rewilding may mitigate negative effects of rising biosphere novelty.
(A) Anticipated declines in biodiversity and system functionality under increasing future biosphere novelty can potentially be mitigated through trophic rewilding by triggering processes that create niche space and facilitate species' adaptation to environmental change. Immigrating new alien and neonative[198] species may also compensate for the loss of native biodiversity (indicated by the dotted circle). Under trophic rewilding, the benefit to native biodiversity means that changes in species composition will likely be less, with new species constituting a smaller fraction of future communities. This is in contrast to the scenario without trophic rewilding, where a less diverse, more novel community is expected, often with a few dominant species controlling the limited niche space (e.g., driven by warming[199] or alien invasions[164]). (B) Climate change and other anthropogenic impacts are creating a more abiotically novel planet. Biotic novelty is following suit, both in direct response to the changing abiotic conditions and because of anthropogenic drivers such as globalization and associated alien species introductions. We hypothesize that, by embracing biotic novelty, we can preserve essential natural processes and interactions that will serve to curb abiotic novelty (e.g., grazers reducing fuel loads to maintain regular fire regimes and, if scaled up, climate change[125]). Simultaneously, the ecological impacts of a trophically complex animal community achieved through trophic rewilding will serve to curtail the unwanted outcomes of novelty (e.g., single species dominance). This will again benefit the native community and limit biotic novelty.

(*Canis lupus dingo*), especially for foxes (*Vulpes vulpes*)[188], albeit even this case remains questioned[189]. Linking to our earlier discussion on non-native megafauna, it is noteworthy that the dingo is itself an introduction, albeit several millennia old. There are also cases where restoring of trophic complexity down-regulates other types of alien vertebrates. Notably, pine marten (*Martes martes*) recoveries in the British Isles have resulted in strong predation-driven population declines in the introduced grey squirrel (*Sciurus carolinensis*)[190]. Integrating this case with other empirical evidence and theory, it has been proposed that restoration of vertebrate predator populations offers a general solution to vertebrate invasive species management[190]. Overall, such effects are indeed expected under trophic rewilding for mesopredators, mesoherbivores and smaller species, given the high exposure to predation many such species are exposed to in megafauna-rich ecosystems.

Complexities of trophic rewilding in a human-dominated, rapidly warming world

Trophic rewilding will have to be implemented under conditions of an increasing human population with rising resource needs and intensifying anthropogenic warming. Coexistence of people and wild megafauna is a challenging issue due to loss and fragmentation of wildlife habitats, damage to crops and property, and risks to human safety. Mitigating these problems requires careful attention to socio-ecological context, e.g., how benefits and disservices from megafauna are distributed[191]. While the coexistence of people with megafauna will be one key issue, another is the availability of areas in which trophic rewilding in any form can be implemented. Here, it is worth noting that shifting diets in the richer countries towards a more sustainable, plant-rich diet would mean that large agricultural areas would no longer be needed for animal feed production and could become available for rewilding[126]. Hence, despite a growing human population, there is much scope for sparing large proportions of Earth's land area for biodiversity and natural ecosystems. As mentioned earlier, this in itself would have substantial climate change mitigation benefits[126]. However, implementing trophic rewilding across these areas would enhance their value for biodiversity and, potentially, also for climate change mitigation. Furthermore, incorporating wild species into low-intensity production landscapes may offer some of the same benefits, e.g., as seen in certain pastoralist systems where wildlife–livestock coexistence is facilitated via managed, rotational grazing[192]. This illustrates the practicality of continuum approaches to trophic rewilding (Figure 4), expanding its applicability in the Anthropocene[2,4,28], albeit trade-offs between social considerations and ecological functionality also need to be recognized. Planning and implementation of trophic rewilding in the contexts of both land sparing and sharing should more generally consider social processes and equity, not least to facilitate long-term societal support[30]. Realizing the potential of trophic rewilding at scale on a densely populated planet clearly comes with many complexities that deserve a diversified interdisciplinary research agenda.

Strong climatic warming is forecast under even moderate business-as-usual scenarios, that is, assuming that current policy commitments will be kept[42,62]. This will affect the possibilities for trophic rewilding in many indirect ways, for instance by affecting general societal functioning or driving human migration and settlement patterns. However, warming will also affect trophic rewilding more directly through effects of climate change on the animals that are at the center of trophic rewilding. Large mammals have a lower risk of hyperthermia and dehydration, but often also have less ability to exploit climatic microrefugia[137]. Still, the greater mobility associated with larger body mass increases adaptive response capacity towards climate-related stress at landscape scales given the environment is suitably heterogenous[193]. Overall, there is considerable uncertainty about how megafauna species will respond to future climate change[137]. Perhaps the most critical issue here is how extreme warming at low latitudes, beyond recent temperatures on the planet, will affect megafauna physiologically and ecologically, for instance if major ecosystems break down from climatic stress, as feared for substantial parts of the Amazon rainforest[194]. Having functionally intact, diverse megafaunas should enhance the potential to successfully realize trophic rewilding also in a warming world. However, there are clearly many open questions on how ecosystems with or without trophic rewilding will function in a future world with warmer climates and higher CO_2 levels than in the last several million years or more[42].

Future potential and research needs for trophic rewilding

Rewilding is gaining popularity as a restoration approach that aims to restore self-regulating complex ecosystems by reintroducing non-human ecological elements and reducing human pressure. It often involves human intervention in the initial phases to compensate for past human activities that have negatively impacted biodiversity and ecosystem function. Importantly, rather than reconstructing fixed past ecosystem states, rewilding is forward-looking and focuses on promoting dynamic ecosystems with high functionality for biodiversity (Figure 6). As a key element in rewilding, trophic rewilding focuses on restoring trophic complexity through species introductions to restore top-down trophic interactions. It has the potential to benefit biodiversity and ecosystem functioning under emerging novel biosphere conditions. Notably, restoration of abundant, diverse megafaunas is expected to promote vegetation and soil heterogeneity, seed dispersal and nutrient cycling and generate a range of biotic microhabitats (Figure 6). Non-native megafauna species, often abundant in present-day ecosystems, may contribute to these effects in appropriate settings. At the same time, the complexities of implementing trophic rewilding in a human-dominated world undergoing strong climatic warming have to be acknowledged, highlighting the need for careful design, implementation and governance to address socio-ecological challenges and the direct and indirect effects of climate change on megafauna.

Trophic rewilding is also a strategy to enhance biological adaptation to climate change and, potentially, climate change mitigation, although considerably more empirical support is needed, particularly with regards to the net effects of large mammals on carbon sequestration. Dispersal is a key factor in the adaptive response of ecosystems to climate change, with large animals facilitating plant dispersal. Restoring large animals and their dispersal function through trophic rewilding is expected to aid plant colonization of new areas and recolonization after disturbance. Furthermore, environmental heterogeneity is important for biotic adaptation and resilience and is expected to be generally enhanced by the modulation of vegetation structure by large herbivores and associated microclimatic variability. Additionally, trophic rewilding has potential to help mitigate climate change over the long term by reducing risks of ecosystem breakdowns from climatic stress, but also through reducing catastrophic fires, potentially promoting carbon accumulation in soils and certain vegetation types, and increasing land cover albedo in various settings (Figure 6). Biotic globalization is another anthropogenic pressure of our epoch, which trophic rewilding may help address. Notably, restoring large herbivores has potential to down-regulate invasive alien plants to the benefit of overall biodiversity (Figure 6).

Although the body of knowledge encompassing these themes is expanding, there remains a need for much more research[6,14]. Notably, it is important to increase our mechanistic understanding and improve our capacity for generalization regarding the effects of trophic rewilding. Key issues include the roles of functional diversity in megafauna and plants, the interactions with climate-driven dynamics and biological invasions, and potential contributions to climate change mitigation. Similarly, it is also critical to enhance our understanding of trophic rewilding in its varied socio-ecological contexts, including feedbacks with political dynamics[195]. To progress on these themes a broad range of approaches from theoretical and macroecological to experimental and from biological to sociological are needed, applied to a wide variety of contexts. Overall, such work is central for refining approaches and strategies for trophic rewilding as a major restoration approach under the emerging novel biosphere conditions of the Anthropocene.

ACKNOWLEDGEMENTS

This work was supported by the Center for Ecological Dynamics in a Novel Biosphere (ECONOVO), funded by Danish National Research Foundation (grant DNRF173 to J.-C.S.), VILLUM FONDEN via J.-C.S.' VILLUM Investigator project "Biodiversity Dynamics in a Changing World" (grant 16549), and the Independent Research Fund Denmark | Natural Sciences via J.-C.S.' MegaComplexity project (grant 0135-00225B). E.L.R. considers this work a contribution to the Independent Research Fund Denmark | Green Transition Grant 1127-00046B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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