

## Introduction



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# Trophic rewilding: impact on ecosystems under global change

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## 1. Introduction

Human-induced global change is increasingly affecting life on our planet, including living conditions for humans themselves as well as the resources we depend on [1,2]. As a result, species diversity is strongly declining [3–5]. The Living Planet Index shows a 58% global decline in populations of amphibians, fish, reptiles, mammals and birds between 1970 and 2012, varying from 36 to 38% in terrestrial and marine ecosystems to 81% in freshwater habitat [6]. Habitat loss or degradation and overexploitation are the main causes of these steep declines. Since the worldwide expansion of modern humans (*Homo sapiens*) began, humans have overexploited vertebrates, with a bias to the largest animals being extirpated first, from the Late Pleistocene extinctions of terrestrial megafauna to the ongoing declines of terrestrial, marine and freshwater large-bodied animals [7–11]. There is increasing evidence that this global wildlife loss, or defaunation, does not only imply the loss of charismatic animals but also the functions they have in ecosystems [12–16]. To restore these missing functions, a novel ecological restoration technique has emerged, referred to as rewilding [17]. Rewilding aims to restore natural processes in ecosystems in general, and often focuses on re-introduction of missing large wildlife species or, in case these went extinct, their proxies [18]. Rewilding is increasingly implemented in practice globally, with a strong emphasis on Europe and the re-introduction of large herbivores [19,20].

## 2. Impacts of rewilding

Rewilding has recently been described as 'a captivating, controversial, twenty-first century concept to address ecological degradation' [20]. Most rewilding initiatives fit the concept of trophic rewilding, defined as an ecological restoration strategy that uses species introductions to restore top-down trophic interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems [18]. If it works, this would both turn around defaunation, by re-introducing missing wildlife, and halt biodiversity declines. Furthermore, rewilding may have positive effects on multiple ecosystem services [21,22]. As such, rewilding is a narrative of hope, which is the captivating part (e.g. [23–25]). The controversial part is that opponents fear that rewilding is the new Pandora's box in conservation and may harm biodiversity, with particular concern about exotic species proliferation as a consequence of rewilding ([26,27]; but see [28] for a response). However, at present, data on the effects of explicit rewilding efforts are scarce and the scientific literature on rewilding is strongly dominated by essays, perspectives and opinion papers [18,20]. At the same time rewilding is increasingly implemented in practice by initiatives such as Rewilding Europe (<http://www.rewildingeurope.com>). Rewilding is also increasingly discussed and implemented in other parts of the world, e.g. Australia [29], oceanic islands in the Pacific [30] and South America [31]. Therefore, there is an urgent need for science to move on from ideological debates to actual data on the impacts of rewilding.

### 3. Obtaining data on rewilding impacts

Whereas data on explicit rewilding projects may be scarce, our understanding of rewilding impacts can be expanded by studying non-intentional rewilding events. Indeed, Tanentzap and Smith [32] demonstrate that the top-down regulation of lower trophic levels is equally strong in trophic rewilding through intentional and non-intentional species introductions. Furthermore, much relevant information exists from studies not explicitly about rewilding. There is, for instance, lots of experience with ecological effects of megafauna reintroductions in South Africa, such as white rhinoceros in Kruger National Park [33], even if these have not been called rewilding projects. Similarly, there is ample experience with impacts of free-ranging horses and bovids in Europe, which could be seen as replacement of the extinct native wild grazer populations, i.e. the aurochs (extinct in 1627) and the tarpan (extinct 1887).

In this issue, we bring together the state-of-the-art of trophic rewilding research, using the multitude of opportunities to obtain data on trophic rewilding impacts as described above. Furthermore, we address the policy and societal sides of trophic rewilding, such as which herbivores can be introduced where and how to measure rewilding success? Importantly, we here synthesize the main outcomes of the impact of trophic rewilding on ecosystems in the light of global change and provide an outlook of the opportunities of trophic rewilding as a new restoration technique as well as research avenues.

### 4. Effects on biodiversity and invasive species

Trophic rewilding potentially has positive effects on biodiversity, and could thus mitigate the biodiversity crisis, but data to test this are very limited. Van Klink and WallisDeVries [34] review the evidence of the impacts of rewilding with large herbivores on arthropods, the most species-rich group of eukaryotic organisms, but rarely considered in rewilding. They found that systematic monitoring is rare and that a comparison with a relevant control treatment is usually lacking. Still, they can conclude that at moderate densities large herbivores increase grassland arthropod diversity, whereas they decrease diversity at high densities [34]. These results are largely in line with large herbivore impact on arthropod diversity in non-rewilding areas [35]. In wetlands, Eurasian beavers (*Castor fiber*) strongly affect wetland plants and wetland ecosystem functioning [13]. Beavers are increasingly being introduced in the context of rewilding projects [36], but empirical evidence of their effects is often lacking. Willby *et al.* [37] show that by creating within-habitat heterogeneity beavers increase plants diversity, whereas they increase the abundance, but not the diversity of aquatic beetles. By creating heterogeneity within ponds, beavers likely contribute to increased biodiversity across scales [38].

A concern of trophic rewilding is the impact on invasive species. Derham *et al.* [39] show three cases in which rewilding native carnivores helps suppressing invasive smaller carnivores and releasing native prey species; in contrast rewilding a meso-herbivore (Tule elk *Cervus canadensis nannodes*) sometimes slows down grassland plant invasions, sometimes not. Trophic rewilding can work to prevent biological invasions, mitigate their impacts and promote the coexistence of newcomer species

with long-time residents. However, the conditions for success will vary from case to case and will be hard to predict. In this respect trophic rewilding shows parallels with invasion biology itself [39].

### 5. Can trophic rewilding serve as a climate change mitigation strategy?

Large herbivores can interact with climate change in a number of direct and indirect ways [40,41]. In the Arctic, caribou or reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) are the only large herbivores. With rising temperature, thermophilic plant species are invading the tundra and these are preferred by the herbivores. Therefore, reindeer and muskoxen are able to maintain the present vegetation composition even in a warmer climate [42]. Furthermore, they prevent woody plant encroachment with increasing temperatures, which in turn leads to a higher albedo [43], with a cooling effect. Large herbivores may increase soil carbon sequestration, when they consolidate the persistence of the permafrost [44]; however, this is at present uncertain [41]. Andriuzzi & Wall [45] also indicate uncertainty and major knowledge gaps about the impact of large herbivores on soil responses and feedbacks. Despite this uncertainty, rewilding the Arctic with a larger density and diversity of large herbivores may mitigate the impact of temperature rise in this region [40,41]. In tropical rainforest, defaunation leads to lower dispersal of tree species with megafaunal fruits, which have a higher wood density and, therefore, contribute strongly to carbon storage in tropical forests [16,46]. Rewilding with large herbivores could thus increase the carbon storage potential of the forest [40]. In rangelands, greenhouse gas emissions could be strongly reduced when ruminant livestock are replaced by non-ruminant wildlife [40,47]. Cromsigt *et al.* [40] argue that trophic rewilding as a climate change mitigation strategy should focus on restoring populations of large (greater than 100 kg) non-ruminant herbivores. Furthermore, trophic rewilding should be integrated into intergovernmental climate change mitigation funding schemes to allow wide enough implementation of rewilding to make a difference.

Trophic rewilding can mitigate the incidence of wildfires which may be increasing in areas which are more prone to droughts as a result of climate change [48]. Especially large grazers are suitable for this purpose, as they consume large amounts of potential fuel, whereas browsers increase the fuel load by consuming woody plants, not herbaceous plants. The frequency and intensity of fires, in turn, has a myriad of effects on climate, but the net effect remains uncertain [40].

### 6. Which animals to introduce where in trophic rewilding

To introduce species into systems to restore extinct top-down interactions requires knowledge of their former distribution as well as their diet. As historic and pre-historic human-driven extinctions have reshaped global patterns of mammal diversity [49], it is unsure where these animals may be able to live under current climate conditions, and thus which sites are suitable for trophic rewilding. Furthermore, these anthropogenic range contractions bias species climate change



**Figure 1.** Examples of how to collect data in trophic rewilding research. (a,b) Using enclosures to study the impact of the presence of large herbivores in rewilding projects. (a) Enclosure in the Lauwersmeer, The Netherlands, where Konik horses and bovids are used as proxies for extinct native horses and bovids and maintain short lawn grasses, whereas upon exclusion of the large herbivores inside the enclosure a tall wetland reed (*Phragmites australis*) vegetation emerges. (b) Enclosure on the island of Tiengemeten, The Netherlands, where Scottish highland cattle prevent the encroachment of woody plants; inside the enclosure willow species have established. (c,d) Using collars to track animal movement and quantify areas used with high and low intensity. (c) Eurasian elk (*Alces alces*) in a rewilding project in the largest raised bog area in Denmark, Lille Vildmose (Little Wild Bog). (d) Tapir (*Tapirus terrestris*) with young from the Iberá Rewilding Program, Argentina [64]. Photo credits: (a,b) E.S.B and (c,d) J.-C.S. (Online version in colour.)

forecasts [50]. Using species distribution modelling Jarvie & Svenning [51] demonstrate that for 17 large-bodied mammalian taxa near-future climate change should not generally prohibit the implementation of megafauna-based trophic rewilding, reflecting the broad environmental tolerances of many megafauna species. However, this may be different for ectotherms, which in contrast to mammalian megafauna, need to be able to thermoregulate efficiently. Extant giant tortoises are used as substitutes for their extinct relatives in trophic rewilding projects on oceanic islands to restore their role of ecosystem engineers [52]. In these seasonally dry environments, mitigation measures may be needed to allow the tortoises to successfully maintain their water balance and execute their role in seed dispersal, nutrient cycling and herbivory at the landscape scale [53]. In the boreal forest, moose (*Alces americanus*) fulfil an important role in fertilizing the forest with nitrogen, the limiting plant nutrient, by transporting nitrogen across the aquatic-terrestrial ecotone [54]. If moose were to follow the boreal-deciduous forest ecotone, which moves north with increasing temperatures [55], deer would replace moose, but these are much less effective as nutrient transporters [54].

Then, when the climate is suitable, how to identify areas that would profit most from restoration of trophic interactions? Marjakangas *et al.* [56] use species distribution

modelling in combination with occurrence data and species interaction records to quantify the potential to restore seed-dispersal interactions through rewilding in the Brazilian Atlantic forest, a biodiversity hotspot strongly impoverished in large animals [16]. By ranking bird and mammal species based on their seed-dispersal potential they identify which species can best be used. More species-rich and larger forest fragments have many more interactions to cash in on than the deteriorated ones, hence could be prioritized for re-introductions of missing seed dispersers [56].

The traits of the animals and plants involved in the interaction that should be restored are central to these types of analyses, as well as the pre-human distribution of the plants and animals. However, when it comes to grassland conservation Fuhlendorf *et al.* [57] argue that an essential component is missing, namely the role of humans. As evidenced by the degradation that included the loss of large native herbivores and replacement with domestic livestock [58], a focus on restoring an appropriate herbivore for a restoration context is important for both the conservation of the herbivore species, as well as their recognized role in conserving biodiversity broadly [59]. Future grassland conservation efforts including the decision which herbivores to use, must depend on the development of a model that better integrates societal, economic and policy objectives

global trends	problems	potential of large-scale trophic rewilding
changing land-use: a. urbanisation  b. intensification of agriculture  c. large-scale abandonment of marginal farmland	a. people increasingly separated from nature and wildness  b. biodiversity crisis  c. lost income in rural areas	a. attractive for urban people  b. opens opportunities for new societal partners  c. new 'nature-based economies' (a.o. wildlife tourism)
biodiversity decline	nature management increasingly more intensive and expensive and not always effective	focus on natural processes lowers costs and increases biodiversity
defaunation	loss of species and ecosystem functions	conserving species; restoring ecosystem functions
wildlife comebacks in some places	human-wildlife conflicts in fragmented habitats	increases connectivity among and within nature reserves
climate change	more flooding, droughts, fires, shrub or woody encroachment	mitigation of climate change; even more so when combined with adaptive water and land management; increasing ecosystem resilience

**Figure 2.** Scheme with outlook of potential of trophic rewilding under global change for nature and society. The potential of large-scale trophic rewilding in relation to global trends and problems offers new research avenues for ecology, sociology and economy. (Online version in colour.)

and recognizes climate change, fragmentation and humans as an integral part of grassland ecosystems [57].

## 7. How to study rewilding impacts?

From the studies presented in this issue, a number of different ways emerge to evaluate the impact of trophic rewilding. It is essential to compare the state of the rewilding area with a non-rewilding situation at a given time and as they develop [34]. This is a challenge in many cases, as rewilding projects are commonly not designed as scientific experiments, but in practice rather a certain site is selected where subsequently animals are released, and/or other restoration actions are implemented. Sometimes some additional land use is also continued or implemented. A classical before/after comparison can be used in some cases to evaluate the change in state. This has for instance been done to evaluate the impact of the release of wolves in Yellowstone National Park and the subsequent impact on elk and tree density in the landscape [60,61]. However, a site may be subject to autonomous changes over time, which may interfere with assessing the effects of rewilding. Furthermore, certain measures may be necessary to implement trophic rewilding, such as altering the fencing around the site, changing the hydrology of the site to give more room to natural water level dynamics, or taking it out of former agricultural use, which may alter the site irrespective of the (re-) introduction of animals [62]. Lastly, and most often, before-rewilding data may simply not be available. In such cases, one can attempt to find neighbouring similar sites, which are not subject to rewilding, to allow a paired comparison. This can be challenging as well, as often sites differ in more aspects than the rewilding management and the site subject to rewilding may be chosen because it was different from other sites to begin with. Still, variations on this theme are

possible, as similar sites with different densities of introduced animals may be suitable for comparison of the impact of the animals. The more sites, the more robust the analysis (see for instance [63]). Another way to evaluate the impact of trophic rewilding is to use enclosures, e.g. fenced areas inside the rewilding site where the animals have no access (figure 1*a,b*). In this way, the impact of the animals can be deduced from the differences in site characteristics in the presence of the animals and inside the enclosures [13,14]. When no such comparisons are possible, then animal movement within a site, using GPS collars, can be used to identify low- and high-impact areas (figure 1*c,d*).

## 8. How to evaluate rewilding progress?

Trophic rewilding can be seen as a form of open-ended management [65], as it focuses on promoting natural processes rather than pre-determined targets [62]. However, this may falsely suggest that rewilding is without ambition and measurable output as a classical evaluation of targets is not possible in open-ended management. To overcome this challenge Torres *et al.* [66] developed a rewilding scale, through which rewilding progress can be measured. The rewilding scale evaluates the recovery of processes and their natural dynamics based on decreasing human influence on ecological processes and increasing ecological integrity of the ecosystem [66]. Instead of achieving the highest score *per se*, a gradual increase in naturalness of the ecosystem over time could be a suitable goal of local management.

## 9. Opportunities for trophic rewilding

Ecosystems worldwide are increasingly affected by human-induced global change, including over-exploitation of living

systems, temperature rise, eutrophication and exotic species proliferation, resulting in a biodiversity crisis [6]. Furthermore, human societies increasingly experience disasters as an increase in flooding events and wildfires, with further increases likely in the near future [67,68]. Therefore, new thinking is needed to address these pressing societal and biodiversity conservation challenges. Rewilding could potentially offer such a new way of thinking, as it is a future-oriented process-oriented and non-static restoration strategy [62] (figure 2). Through its focus on natural processes, rewilding advocates new ways of land management, focused on restoring diversity-maintaining autonomous mechanisms in nature. By restoring more complete ecosystems, trophic rewilding—if successful—could (i) confer greater robustness (resistance or resilience) to the pressures from global change and (ii) by restoring (more) self-managing ecosystems help reduce needs for people and domestic animals for ongoing management, which overall should release economic and human resources for other uses. By combining functions such as water storage capacity and giving room to natural processes, rewilding could contribute to finding solutions for flooding and drought problems as well as increase biodiversity. Such examples are now becoming available (e.g. [62]). Furthermore, rewilding aims to pursue both

fundamental aims of restoration – biodiversity conservation and wildness, which has a lot of value to many people [25,69].

Trophic rewilding can potentially provide solutions to problems which are the result of current global trends (figure 2). This special issue is an overview of where we stand at the moment. There are promising examples of climate change mitigation, of mitigation of invasive species and mitigation of biodiversity decline. But all authors agree that we are in strong need of more data, for which we hope this theme issue will serve as an inspiration and motivation. Furthermore, it becomes increasingly clear how trophic rewilding is a highly interdisciplinary field, where scientists in ecology, sociology and economy are all involved (see figure 2 and [40,57,62]).

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**Competing interests.** We declare we have no competing interests.

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