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REWILDING AND THE RISK OF CREATING NEW, UNWANTED ECOLOGICAL INTERACTIONS

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1. Introduction

We are currently experiencing unprecedented environmental changes driven by anthropogenic activities with consequences that include soil erosion, nutrient enrichment, population and species extinctions, and species invasions (Corlett 2015). These rapid changes generate uncertainties that may compromise the goals and priorities of conservation and management efforts (Wiens & Hobbs 2015), including rewilding attempts.

Some conservationists, including rewilding advocates, subscribe to the ideal that natural processes should be allowed to take their course without human intervention. Others believe that such an approach is too risky so it is more appropriate to actively manage nature (Corlett 2016). However, rewilding outcomes may become more unpredictable because of uncertainties in future conditions (e.g., climate change, land conversion etc) and increased frequency of extreme events. In this chapter, we focus on how trophic and passive rewilding initiatives may intensify the risk of unwanted ecological effects. We do not address potential economic and societal implications of rewilding initiatives because there are covered in other chapters (see chapters X). In addition, we show that biological communities can be understood only by considering their evolutionary history, and we warn that ignoring this point in rewilding projects could ultimately risk failure.

2.2 Trophic rewilding

Rewilding (Soulè & Noss 1998, chapter 5) is aimed at restoring and protecting natural processes in specific wild areas, providing connectivity between such areas, and protecting or reintroducing keystone species ("trophic rewilding"). Trophic rewilding aims at restoring top-down interactions and associated trophic cascades through the reintroduction of species lost to the environment, with the ultimate goal of promoting a self-regulating ecosystem (Svenning et al. 2016, chapter 5). Unwanted effects of

trophic rewilding can be broadly classified into three main categories: ecological, human, and economic (but see Nogués-Bravo et al. 2016 for a more detailed discussion of the far-reaching consequences of rewilding). Here, we will briefly review potential unwanted ecological effects caused by the reintroduction of both top predators and herbivores within rewilding initiatives.

2.1 Top predators

Rewilding initiatives are usually based on the reintroduction of large predators because their relationships with species at lower trophic levels maintain stability of their ecosystems (Corlett 2016). This approach is especially useful when a species is known to have widespread effects over an area and change its ecology, as was the case with grey wolves (*Canis lupus*) in Yellowstone National Park, a case study that has become known globally and acts as a flagship in favour of trophic rewilding using top predators. However, the unprecedented impact that wolves have had on the park's ecology and geography highlights the need to understand better the uncertainty surrounding rewilding initiatives and the importance to reflect upon potential undesirable outcomes thereof (Paine et al. 1998). In their review paper on "ecological surprises", Doak and collaborators (2008) showcase some unintended consequences of trophic rewilding. For instance, the reintroduction of rock lobsters (*Jasus lalandii*) to a seamount off the western coast of South Africa provides one of the most astonishing examples of predator–prey role reversals (Barkai & McQuaid 1988). For reasons that remain uncertain, lobsters disappeared from Marcus Island in the early 1970s. As a result of this, predatory whelk populations apparently increased substantially following the lobsters' disappearance since lobsters preyed on the whelks. To re-establish the species, 1,000 lobsters were reintroduced but were immediately attacked and consumed by the now overabundant whelks, their previous prey; a week later, no live lobsters could be found at Marcus Island (Barkai & McQuaid 1988). Ecological surprises are inescapable given the panoply of ways species interact with one another

(Berger et al. 2001; Laundré et al. 2001; Sterner & Elser 2002; Hansen et al. 2007). Despite this, virtually none of these potential interactions are typically incorporated into broad community predictions in the trophic rewilding of predators (Doak et al. 2008). Although evidence has been collected showing the negative consequences of large-bodied species defaunation, the reverse (i.e., the restoration of ecosystem functions after these species return) has been assessed less often (Fernández et al. 2017). Potential repercussions include changes in local diversity and ecosystem functioning (defined as the collective life activities of plants, animals, and microbes and the effects these activities have on the physical and chemical conditions of the environment), and the possibility of catastrophic disease transmission (e.g., Daszak et al. 2000). For example, large carnivores typically depress mesopredator abundance, thus potentially favouring their rodent prey and, under some conditions, potentially increasing the incidence of various zoonotic diseases (e.g., Ostfeld & Holt 2004). Moreover, trophic rewilding experiments do not normally consider potential interactions with undiscovered species, although it is possible that some small, undiscovered prey (e.g., insects) might support many species in an ecosystem.

Even though the expectation with the reintroduction of predators is that they will trigger top-down cascading effects, under certain ecological conditions heterogeneity at any trophic level can affect levels above or below. For instance, in northern Utah, USA, Bridgeland and collaborators (2010) showed experimentally that an arthropod community structure on a foundation riparian tree mediated the ability of insectivorous birds (top predators) to influence tree growth. These authors found that abiotic growing conditions affected tree growth and herbivore populations, which in turn affected bird foraging patterns that cascaded back to the trees. When the main factor limiting tree growth switched from water availability to herbivory, the avian predators gained the potential to reduce herbivory. Such conditionality is consistent with numerous studies showing how fundamental relationships might switch over time, space, or with addition

of another interacting community member (e.g., reviewed by Bailey & Whitham 2007). This dynamic complexity might preclude the predictability of ecosystem response to the addition or loss of top predators at a given place or time (Bridgeland et al. 2010; Mäntylä et al. 2011). This also poses challenges in terms of understanding potential triggers of species invasions in the context of trophic rewilding. Rewilding might present increased opportunities for non-native species to become established, out-compete native species, and reduce species diversity. The reintroduction of dingoes (*Canis dingo*) has been proposed to help restore degraded rangelands in Australia (Newsome et al. 2015). This proposal is based on results of studies suggesting that dingoes can suppress prey populations (especially medium- and large-sized herbivores) and invasive predators such as red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) that prey on threatened native species. However, dingoes are themselves mesopredators and there is a high risk of increased predation on threatened native predators (Allen & Fleming 2012). On the other hand, eliminating feral cats could release other mammalian predator invaders, such as rats (*Rattus* spp.), from predation pressure, with resulting cascading effects on the ecosystem.

Even very well-documented rewilding experiences, such as that of the wolf in Yellowstone, may not have been able to flag unforeseen outcomes with the same species in other systems. Exemplarily, in the Adirondack ecosystem in New York State, USA, coyotes (*Canis latrans*) are thought to be causing a trophic cascade by limiting populations of herbivorous small mammals in recently burned areas, and this in turn could benefit deer mice (*Peromyscus maniculatus*), while indirectly influencing vegetative composition (Ricketts 2016). Predation by coyotes has been identified as the greatest cause of mortality for red and swift foxes (*V. velox*) in Kansas and Colorado (Sovada et al. 1998; Kitchen et al. 1999) where they tend to persist when coyote numbers are low. Therefore, coyotes might be filling the wolf's ecological niche today; this means that the reintroduction of wolves in this system could have unknown

effects such as increasing populations of foxes, further affecting the trophic system in the Adirondack ecosystem (Ricketts 2016).

Other unanticipated outcomes of trophic rewilding might be driven by predator-prey interactions, and there are many examples illustrating these. For example, in the Addo Elephant National Park (South Africa), ungulate prey species at risk of predation are more likely to be active diurnally when co-existing with nocturnally active predators, thereby reducing the activity overlap with these predators (Tambling et al. 2015). In the absence of predators, such as following their extirpation, the responses related to predator avoidance can be lost or diluted, which suggests that if predators are reintroduced, prey will likely lack the full spectrum of adaptive behaviours to predation, potentially resulting in dramatic effects for prey communities (Tambling et al. 2015).

It is widely known that the fear large carnivores inspire in mesocarnivores can have powerful cascading effects affecting ecosystem structure and function (Prugh et al. 2009; Ritchie & Johnson 2009; Ripple et al. 2014; Suraci et al. 2016). However, Clinchy and collaborators (2016) have suggested that mesocarnivores are much more fearful of humans than of large carnivores. Indeed, the numerical suppression of mesocarnivores by humans far exceeds that by large carnivores (Darimont et al. 2015), which suggests that fear of humans could affect mesocarnivore demography and behaviour (Dorresteijn et al. 2015; Oriol-Cotterill et al. 2015; Smith et al. 2015), with implications for rewilding initiatives. For example, in human-dominated landscapes, such as in Europe, the recovery (Chapron et al. 2014) or reintroduction (Manning et al. 2009; Svenning et al. 2016) of large carnivores is unlikely to "restore" fear to mesocarnivores "released" from behavioural suppression (Prugh et al. 2009; Ritchie & Johnson 2009), but will instead add to the elevated fear that mesocarnivores are evidently experiencing of humans (Clinchy et al. 2016).

2.2 Large herbivores

Large herbivores play key roles in ecosystems, either through direct impacts on vegetation and/or indirect effects on food web structure and ecosystem functioning. Therefore, the decline of large herbivores can lead to loss of ecological interactions and key ecosystem services (Ripple et al. 2015; Bakker et al. 2016). Modern exclosure experiments and palaeoecological records provide evidence of this (Bakker et al. 2016). The megafaunal extinction at the end of the Pleistocene can be viewed as a natural experiment that highlights the ecological roles played by large herbivores at a global scale (Ripple et al. 2015; Bakker et al. 2016). However, the ecological state shifts caused by herbivore depletion were not the same everywhere (Barnosky et al. 2016). The extent of ecological change after megafaunal loss largely depended on the removal of a number of different effective ecosystem engineers among the lost megafauna, and on soil properties or other abiotic constraints that influence vegetation changes (Barnosky et al. 2016). Thus, given the fact that a number of species and processes are involved, it is important to thoroughly understand the ecological role of each before making predictions on the cascade effects expected in an ecosystem (Barnosky et al. 2016).

Given the known impacts of the introduction and reintroduction of large herbivores on the functioning of an ecosystem, herbivores have been at the centre of many trophic rewilding initiatives. Restoring a diverse and abundant wild large-herbivore guild is presumed to help maintain a mosaic of vegetation that will effectively promote landscapes of higher biodiversity (Sandom et al. 2014). A noteworthy example of rewilding with large herbivores is Pleistocene Park in Siberia (Zimov 2005), where bison and other large herbivores were introduced to restore the grazing-dependent mammoth steppe vegetation. Palatable high-productivity grasses, herbs and willow shrubs, originally dominated these steppes and grazing by high densities of large herbivores is believed to suppress woody growth and accelerate nutrient cycling in

these cold ecosystems (Zimov et al. 2012). Thus, as a result of the megafaunal collapse during the Holocene, the mammoth steppe was replaced by a water-logged landscape dominated by moss and shrub tundra (Zimov et al. 1995). Results from experimental enclosures in Pleistocene Park demonstrate that a shift occurs from shrub-dominated to grass-dominated vegetation when high densities of large herbivores are included (Zimov et al. 2012), showing that this process can be used to maintain and recreate lost ecosystems (Zimov et al. 1995). However, predators and a strong hunting pressure are needed to keep the overall number of herbivores relatively low, so that their impact on vegetation and soils is not excessive (Zimov 2005).

Another rewilding initiative, Oostvaardersplassen in the Netherlands is the oldest large-scale rewilding area in Europe. The area was designated for industry and agricultural use but converted to a nature reserve in the 1970s (Vera 2009). To keep the area more open and prevent the area becoming a woodland, park managers introduced primitive cattle and horse breeds in the 1980s, as a replacement for their extinct wild ancestors. In Oostvaardersplassen herbivore populations are limited only by resource availability, as there is no human management, nor any effective wild predator control. Given the relatively high productivity of the area, herbivores attain high densities, which can have negative impacts on biodiversity and ecosystem function (Ims et al. 2007). For instance, the high densities of herbivores in Oostvaardersplassen limit seedling establishment and prevent the regeneration of wood-pastures (Smit et al. 2015; Fig. 1). In these cases, the existence of grazing refuges, in the form of areas inaccessible to herbivores or as herbivore numbers temporarily decline are essential to create windows of opportunity for woody species to establish themselves (Cornelissen et al. 2014). Thus, rewilding initiatives with large herbivores aimed at restoring wood-pasture landscapes in productive areas need to create grazing refuges that allow the regeneration of woody species (Smit et al. 2015).

As shown in the examples above, proposals to conserve grazed ecosystems often focus on introducing herbivores as surrogates of locally extinct herbivores that were deemed important for the maintenance of these ecosystems. However, where a species has gone globally extinct, the restoration of its ecological functions might be achieved only through ecological replacement, that is, the introduction of an exotic, functionally similar species (Seddon et al. 2014). An example of these ecological replacements is the introduction of non-native giant tortoises as replacements for extinct tortoise species in oceanic islands (Hansen et al. 2010). In the case of Aldabran giant (*Aldabrachelys gigantea*) and Madagascan radiated (*Astrochelys radiata*) tortoises, taxonomically and functionally similar to the extinct Mauritian giant tortoises (*Cylindraspis* spp.), their successful establishment improved dispersal and recruitment of endemic tree species in Round Island, Mauritius (Griffiths et al. 2011) and supressed invasive plants (Griffiths et al. 2013). Yet, in some cases plant communities are so severely degraded that the introduction of these ecological replacements alone is insufficient to restore the ecosystem (Griffiths et al. 2013), and large-scale habitat restoration might be additionally required (Gibbs et al. 2014). Taxonomic relatedness and functional equivalence to the native herbivore are important criteria when selecting potential ecological replacements, yet the difficulties in predicting their effects on recipient ecosystems is a main barrier for their widespread use in conservation. However, the introduction of livestock as a surrogate of extinct wild herbivores circumvents the problem of taxonomic relatedness since domestic breeds are derived from wild herbivore ancestors and are therefore taxonomically and, theoretically, functionally similar to wild herbivores. Hence, it has been proposed that grassland conservation could be achieved through grazing of domestic herbivores or native species such as bison (Towne et al. 2005). But, when livestock species are introduced into a co-evolved assemblage of native wild herbivores, they might compete with and even exclude native wild herbivores (Mishra et al. 2002, Madhusudan 2004).

In any case, how communities respond to the introduction or reintroduction of large herbivores will be determined by the extent to which the recipient ecosystem has been modified. Environmental changes and human activities that have taken place since the extirpation of the herbivore might have produced new communities and novel ecological equilibria (Smith 2005). Reintroductions of extirpated species have complex effects on plant communities, and can give rise to mixed management outcomes. For example, although the successful reintroduction of the recently extirpated Tule elk (*Cervus elaphus nannodes*) in California effectively reduced the abundance of a highly invasive exotic grass, at the same time the abundance and richness of other non-native taxa increased in the community (Johnson & Cushman 2007). Similarly, the management of some introduced species is complicated if their impacts threaten native communities. For example, reindeer (*Rangifer tarandus*) introduced to South Georgia by Norwegian whalers in the early 1900s (Leader-Williams et al. 1989) have caused major changes to the vegetation, including favouring the expansion of various exotic plants (Leader-Williams et al. 1987). Part of the explanation for this result is that the South Georgia species-poor vascular flora is not adapted to grazing by vertebrates. However, by feeding on native tussock grassland, reindeer control the expansion of non-native brown rats that use tussock grassland as shelter (Leader-Williams et al. 1989).

Finally, it is important to keep in mind that an underlying assumption of trophic rewilding with large herbivores is that species that share a recent evolutionary history will interact in the same way today and in the future (Caro 2007). This is less likely under rapid on-going environmental changes. For example, the effects of megafauna on vegetation during the Pleistocene may have been exacerbated by the lower CO_2 atmospheric concentrations, that may have further inhibited woody vegetation growth and made it more susceptible to browsing pressure (Malhi et al. 2016). In contrast, with

increased levels of atmospheric CO_2, vegetation today may be more able to withstand browsing pressure.

3. Passive rewilding

The absence of sustained human intervention is central to passive rewilding (chapter 6). In other words, passive rewilding is based on a "leave it to nature" philosophy, although any justification for this approach is more philosophical than scientific (Schnitzler 2014). But, what happens if, for example, large areas of former agricultural land are simply left alone? Over the past decades, land abandonment has occurred in developed countries in Europe and North America (Shengfa & Xiubin 2017), and its effects on biodiversity have been widely studied. In general, impacts of land abandonment on ecosystem composition and functioning are heterogeneous and depend on a variety of factors (Plieninger et al. 2014). This means that both benefits and detrimental impacts of land abandonment on ecosystems have been documented (Queiroz et al. 2014; Lasanta et al. 2015). The highest proportion of studies reporting negative impacts of land abandonment are found in Europe and Asia (Queiroz et al. 2014). Detrimental impacts are particularly evident in semi-natural habitats that have been traditionally maintained by anthropogenic activities, such as grazing or mowing, and that harbour a remarkably rich biodiversity in terms of both animal and plant species (Carboni et al. 2015). Such ecosystems could be threatened by passive rewilding attempts if the risks of getting unwanted interactions because of land abandonment are ignored.

Detrimental effects of land abandonment on biodiversity have been documented at multiple levels (Fig. 2). At the species level, these include the decline in species abundance and the modification of species distribution. Multiple studies on different taxa clearly illustrate this point. For instance, the abandonment of traditional activities such as extensive grazing or farming threatens plant species typical of semi-natural

habitats. A paradigmatic case is set in Sweden and Norway, where the future distribution of the endemic *Primula scandinavica* is projected to decrease with continued relinquishment of grazing (Wehn & Johansen 2015; Speed & Austrheim 2017). The abandonment of traditional human activities has also had negative impacts on many animal species. For example, land abandonment and pine reforestation have led to landscape homogeneity in the Collserola Natural Park (NE Spain) that might have caused the extinction of six open-habitat gastropod species in the area (Torres et al. 2014). Similarly, the abandonment of low intensity grazing is associated with the decline in the abundance of several ground spider species in Greece (Zakkak et al. 2014), and the threat to the conservation of endangered, endemic butterfly species in Spain (Munguira et al. 2017). Moreover, land abandonment has caused clear detrimental impacts to vertebrates that primarily use open habitats. For example, studies on avifauna mainly report negative abandonment-related impacts (Queiroz et al. 2014), revealing the decline of many farmland bird species across several European regions (e.g., Zakkak et al. 2015a; Mischenko & Sukhanova 2016; Regos et al. 2016) and Asia (e.g., Katayama et al. 2015). Also, land abandonment leads to the reduction in abundance of several mammal species. For example, the loss of farmland landscape diversity as a consequence of agricultural intensification and crop abandonment is thought to be the prime factor responsible for the long-term decline of European hare (*Lepus europaeus*) populations across most of its range (Edwards et al. 2000). Similarly, in Greece, the abandonment of agricultural fields has contributed to the decline of lizard species that typically inhabit open agricultural landscapes or prefer open grassy habitats (Zakkak et al. 2015b).

A large body of knowledge suggests that the abandonment of traditional human activities, as expected in passive rewilding attempts, can result in the appearance of negative, unwanted ecological interactions (Fig. 2). The encroachment of forests as a consequence of agricultural abandonment has resulted in a remarkable increase in

ungulate numbers in Europe and North America (e.g., Acevedo et al. 2011), which has affected negatively other species of herbivores through competition. For example, the increasing number of wild boar (*Sus scrofa*) in Spain could have a negative effect on European rabbit (*Oryctolagus cuniculus*) populations (Cabezas-Díaz et al. 2011; Carpio et al. 2014), and as a consequence negatively affect the numerous Iberian rabbit predators (Lozano et al. 2007). Likewise, grazing abandonment has favoured the invasion of the tall grass *Brachypodium genuense* in the central Apennines (Italy), reducing by competitive exclusion the availability of palatable plants for the Apennine chamois (*Rupicapra pyrenaica ornata*), whose numbers have dramatically declined in the area (Corazza et al. 2016). In addition, allowing ecosystems to evolve away from human control, as proposed by passive rewilding advocates (Corlett 2016), can compromise the constraining of harmful invasive species. In this sense, the lack of management in abandoned lands in Nepal facilitates the spread of invasive plant species, hindering the growth of native vegetation (Jaquet et al. 2015). Furthermore, the abandonment of traditional practices can foster the establishment and spread of invasive species. Abandoned farmsteads support the persistence and spread of formerly cultivated alien plants (Pándi et al. 2014).

As environmental conditions change with time after abandonment, new communities establish, and a shift in species composition occurs (Fig. 2). In Japan, the succession of grasslands to secondary forests after land abandonment leads to the dominance of tall grasses and woody species that suppress the growth of many threatened grassland plants, which in addition decreases grassland herbivorous insects (Uchida & Ushimaru 2014). Similarly, in European mountains the abandonment of productive pastures or the decrease in herbage use typically encourages the invasion of coarse tall grasses mostly with competitive stress-tolerant strategies, and leading to the competitive exclusion of subordinate and accidental plant species (Corazza et al. 2016). Also, the loss of grasslands and semi-open formations due to land abandonment changes the

composition of animal communities (Fig. 2). In the southern Balkans, land abandonment caused a shift in the butterfly community from Mediterranean endemics towards species with European or Eurosiberian distribution (Slancarova et al. 2016). Analogous shifts in the community structure of belowground invertebrate species after abandonment have also been documented (e.g., in Alpine soils; Steinwandter et al. 2017). Similar patterns have been demonstrated for vertebrate communities. In many European areas where land has been abandoned, forest-dwelling bird species increase at the expense of farmland birds (Zakkak et al. 2015a).

Overall, the abandonment of traditional human practices considered in passive rewilding projects can reduce species diversity and richness (Fig. 2). In this sense, land abandonment usually leads to vegetation homogenization and a reduction in landscape heterogeneity (Rey-Benayas et al. 2007). Vegetation homogenization triggered by secondary succession after abandonment increases fire frequency (Moreira & Russo, 2007). Fire on abandoned land often leads to a further decline in biodiversity, as it enhances the growth of fire-adapted species (Rey-Benayas et al. 2007). Examples of vegetation homogenization and plant diversity loss as a result of abandonment have been often reported across many regions in Europe (e.g., Persson 1984; Campagnaro et al. 2017) and Asia (Uchida et al. 2016; Suzuki et al. 2016). But land abandonment can also threaten animal diversity and species richness (Fig. 2). In semi-grasslands of Japan, the diversity of both threatened and common butterflies is significantly higher in traditional land-use sites than in those where land has been abandoned (Uchida et al. 2016). Similar findings have been reported in Europe (Loos et al. 2014; Buvobá et al. 2015). The diversity of other invertebrates could be also threatened by the land abandonment supported by advocates of passive rewilding. In the Italian Alps, the number of orthopteran species decreases with increasing time since abandonment (Marini et al. 2009), and ground spider species diversity also declines after abandonment in Greek ecosystems (Zakkak et al. 2014). Passive rewilding might also

cause negative consequences for vertebrate diversity. Moreira & Russo (2007) modelled the global impact of abandonment on 554 species of terrestrial vertebrates occurring in Europe and found that, for all groups except amphibians, open habitats or farmland sustained higher species richness. This is consistent with the findings obtained at local or regional scales; e.g., avian species richness and diversity decreased with the secondary succession after land abandonment in south-eastern Europe (Zakkak et al. 2015a). The loss of human-made structures (walls, ponds, farmland buildings, etc.) associated with abandonment can also have detrimental impacts on animal species richness. The abandonment of mountainous zones in the Iberian Peninsula has led to the loss of many ponds in Mediterranean dry forests, and such ponds harbour higher bat species richness than nearby areas, including some species of conservation concern like horseshoe bats (*Rhinolophus* spp.) or *Myotis* spp (Lisón & Calvo 2014).

Although many studies have demonstrated positive outcomes of land abandonment (chapter 6), the truth is that negative impacts on biodiversity are also frequent, which are well illustrated in the numerous examples provided in this chapter. Land abandonment can cause also unwanted abiotic consequences, such as soil erosion and desertification, and a reduction in water availability (Rey-Benayas et al. 2007). Overall, this indicates that passive rewilding attempts should not ignore the social and ecological complexity of the areas that are to be restored. Otherwise, the conservation of semi-natural habitats of high nature value will be compromised.

4. Implications of evolutionary pathways when designing rewilding schemes

The structure and functioning of biological communities can be understood only in the light of their evolutionary history, which documents the past processes that have led to their current configuration. Therefore, in order to be successful, rewilding initiatives should explicitly adopt an evolutionary perspective and take into consideration the

timeframe associated with specific biotic interactions. The general expectation is that newly established interactions (on an evolutionary timescale) will lead to unpredictable (and often undesired) outcomes (Saul & Jeschke 2015).

For instance, an important aspect to take into account in rewilding programs is the maintenance or the possible disruption of existing biotic interactions, such as predator-prey or host-parasite relationships – or even both simultaneously, such as in predator-prey-parasite triangles (e.g., Barbosa et al. 2012). Host-parasite interactions can have profound consequences on a variety of aspects, including population structure, social traits, physiology, macroecology and evolution (Guilhaumon et al. 2012; Quingley et al. 2012; Greenwood et al. 2016). Predator-prey relationships also play a major role in the functioning of ecosystems. All these interactions can be highly species-specific – i.e., several parasites and predators depend on a single species of host or prey, respectively. The maintenance of biotic interactions can even be affected by the spatial genetic structure (i.e. the geographic distribution of different genetic lineages) of the species involved (Real et al. 2009), which should be carefully taken into account when planning rewilding initiatives. On the other hand, Late Quaternary extinctions, namely of megafauna, radically transformed the habitat structure of many landscapes and the functioning of ecosystems through trophic cascade effects (Mahli et al. 2016). Many plant communities have thereon evolved in the absence of large herbivores, and now lack particular adaptations to persist under their grazing pressure (Johnson 2009). Thus, the conservation of several plant species can be compromised by the reintroduction of large herbivores within rewilding projects, which can negatively affect vegetation structure and composition (see above).

All these complex interactions need to be taken into account when designing rewilding schemes. The coevolutionary history of the taxa involved is a critical piece of information when aiming at predicting possible outcomes of new interactions at the community level. The incorporation of an evolutionary perspective on rewilding

approaches is limited by our incomplete knowledge of the Tree of Life (especially in terminal branches) and, more importantly, of fully resolved networks of species interactions in natural communities, which are the two major pillars on which any attempt to infer the evolutionary history of biotic interactions should be based. The study of the fossil record can provide key insights on the history of species interactions, but it is inherently incomplete. All these levels of uncertainty are finally translated to the practical stage (implementing rewilding programs), leaving much room for speculation and discussion.

In Europe, where people and nature have interacted for millennia, it is estimated that about 50% of wildlife species now depend on agricultural habitats (Kristensen 2003), and thus the attempts to conserve most of these species contrast with the enhanced dichotomy between nature and human culture implied by rewilding (Linnell et al. 2015). This debate about the need to conserve ecological interactions that have evolved over long periods of time is not new. Some authors have argued that species that were introduced out of their native ranges in the distant past have effectively become part of the ecosystem they invaded, taking up the ecological roles of species that have either become totally or at least functionally extinct. Consequently, they question the need to remove these non-native species from invaded ecosystems, on the basis that long-term key ecological interactions need to be preserved (e.g., Lee and Bell 2008). A better integration of phylogenetic and ecological studies of species interaction networks will be needed to make progress on this exciting but as yet open debate.

5. Conclusions

This chapter shows a number of examples of potential unwanted outcomes of rewilding initiatives, largely explained by the complexity of natural systems, by the extent to which the ecosystem target of rewilding has been modified, or because our understanding of the relevant ecosystem dynamics is limited (Baker et al. 2016).

However, it is important to account for these uncertainties, as they will likely increase with future environmental changes. In this context, several modelling tools (like ensemble ecosystem modelling; Baker et al. 2016) and natural experimental settings (e.g., Mech et al. 2017) can provide additional insights on how to resolve some of the unknowns surrounding ecosystem responses to trophic rewilding in a structured and quantitative way. Overall, it is essential that rewilding initiatives do not ignore that species composition and ecological interactions of any given ecosystem reflect the history of how it was assembled.

6. Literature

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FIGURE 1. Oostvaardersplassen is the oldest large-scale rewilding area in Europe. Primitive breeds of cattle and horses were introduced as a replacement for their extinct wild ancestors to this area formerly designated for agricultural use, to prevent formation of closed woodlands. However, the lack of effective wild predator control or human management and the high productivity of the area allowed herbivores to reach high densities, which prevents seedling establishment and the regeneration of woodland-pastures. The existence of grazing refuges is essential to create windows of opportunity for woody species to establish, and rewilding initiatives aimed at restoring wood-pasture landscapes in productive areas need to manage herbivore densities to create grazing refuges that allow the regeneration of woody species.
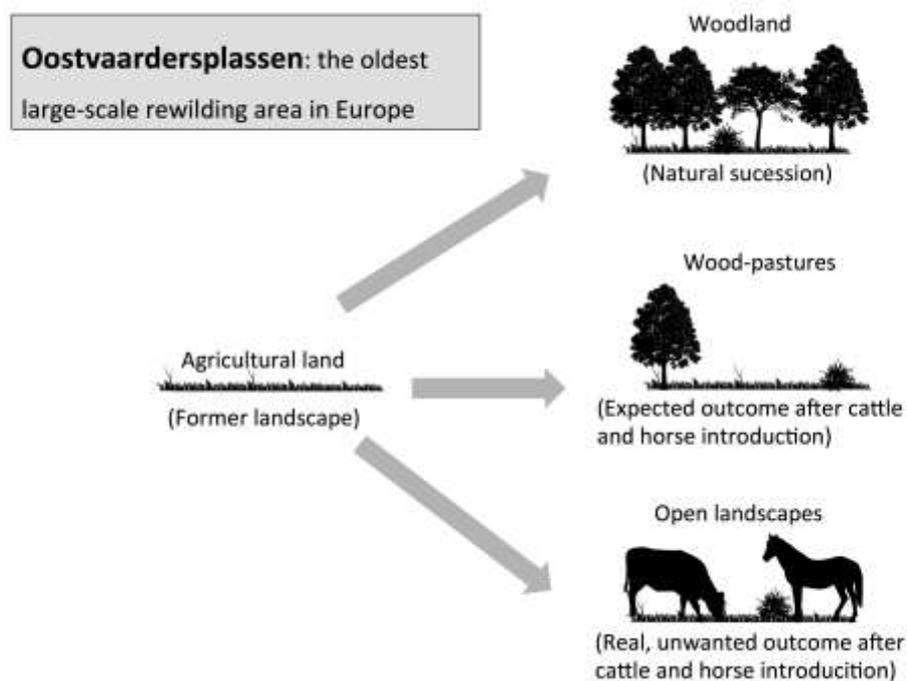
FIGURE 2. A) Levels at which negative effects of land abandonment have been documented. B) Examples of groups of animals that, according to the information provided in this chapter, have been negatively impacted by land abandonment on some occasions (see text for more details).