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Rewilding: Science, Practice, and Politics

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rewilding, conservation, taxon substitution, reintroduction, naturalistic grazing, environmental politics

Abstract

Rewilding is being promoted as an ambitious alternative to current approaches to nature conservation. Interest is growing in popular and scientific literatures, and rewilding is the subject of significant comment and debate, outstripping scientific research and conservation practice. Projects and research are found the world over, with concentrations in Europe, North America, and on tropical islands. A common aim is to maintain, or increase, biodiversity, while reducing the impact of present and past human interventions through the restoration of species and ecological processes. The term rewilding has been applied to diverse concepts and practices. We review the historical emergence of the term and its various overlapping meanings, aims, and approaches, and illustrate this through a description of four flagship rewilding case studies. The science of rewilding has centered on three different historical baselines: the Pleistocene, the Holocene, and novel contemporary ecosystems. The choice of baseline has differing implications for conservation in a variety of contexts. Rewilding projects involve a range of practical components-such as passive management, reintroduction, and taxon substitution-some of which have attracted criticism. They also raise a series of political, social, and ethical concerns where they conflict with more established forms of environmental management. In conclusion, we summarize the different goals, approaches, tools, and contexts that account for the variations in rewilding and identify priorities for future research and practice.

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INTRODUCTION

Rewilding has been presented as an ambitious and optimistic agenda for conservation that does more than just expose and manage species extinctions (1, 2). References to rewilding and its correlate terms¹ are growing in the scientific and practitioner literatures (**Figure 1***a*); however, much of the existing literature is commentary, with little empirical research (3). In practice, rewilding is still a marginal conservation activity, taking place in a few flagship locations. The big four are the Oostvaardersplassen (OVP) (Netherlands), Yellowstone (United States), the Pleistocene Park (Russia), and Mauritius and neighboring islands. Nonetheless, rewilding is the subject of a growing popular interest and critical discussion (**Figure 1***b*) (4, 5).

Rewilding is a plastic (7) term that has been applied to a range of visions and land management practices. It has multiple meanings. These usually share a long-term aim of maintaining, or increasing, biodiversity, while reducing the impact of present and past human interventions through the restoration of species and ecological processes. Understanding and addressing the trophic cascades associated with species extinctions have emerged as central organizing agendas for rewilding research and practice (3). Rewilding activities may include instigating naturalistic grazing and fire regimes on prairies or in boreal forests, or modifying flood patterns in river systems (8–10). Rewilding may also involve passive management, natural recolonization, assisted migration, and the reintroduction of species believed to be missing from a system. These could include (de)domesticated and/or non-native analogues of missing species (taxon substitution) (11, 12).

This article reviews the historical emergence of the term rewilding and its various overlapping meanings, aims, and approaches, and establishes the key criteria that account for contemporary varieties. It first explores three different historical baselines that have been proposed for rewilding and examines their implications for conservation in a variety of contexts. It looks at some practical components of rewilding projects—such as reintroduction and taxon substitution—and the criticisms they have attracted. It examines some of the political, social, and ethical issues

¹Here, we would include reintroduction, ecological restoration, dedomestication, back-breeding, taxon substitution, deextinction, and naturalistic grazing.



Figure 1



associated with rewilding as a conservation measure-attending in particular to conflicts between rewilding and prevalent forms of environmental management.

Rewilding interventions and debates have tended to focus on either North America and Europe, or island ecosystems (3); however, important literatures and examples on Siberia, Australia, Brazil, and parts of Africa are emerging. North America and Europe have featured prominently because they have large areas of modified landscapes, including land that is underused for production or being abandoned, and more extensive conservation resources. Island ecosystems have offered sites for controlled and limited rewilding experiments in reintroducing or eradicating species.

REWILDING AND ITS VARIETY OF MEANINGS

The term rewilding first emerged from a collaboration between the conservation biologist Michael Soulé and the environmental activist David Foreman in the late 1980s that led to the creation of The Wildlands Project (TWP) (7, 13). In this North American version, rewilding focuses on securing large and well-connected core areas and releasing keystone species-most notably wolves (14, 15; see also Figure 2). This became known as the 3Cs approach (core areas, corridors, and carnivores). Soulé and his coworkers sought to position wilderness conservation and biodiversity conservation as complementary agendas. The reintroduction of wolves in Yellowstone National Park (United States) is commonly seen as the flagship practical example of this approach (see sidebar, Rewilding Through the Reintroduction of a Keystone Species: Wolves at Yellowstone).

Donlan et al. (18) expanded this initial vision in an influential (and controversial) intervention, calling for the rewilding of parts of North America through Pleistocene megafauna replacement. They proposed that the ecological structure of Pleistocene ecosystems, prior to the megafauna extinction, should be the appropriate baseline for ecosystem restoration. To restore this baseline the authors suggested the introduction of surrogates for species hunted to extinction in the Pleistocene, for example the African or Asian elephant and lion in place of the American mastodon (Mastodon americanum) and American lion (Panthera atrox).

Similar thinking informs rewilding through taxon replacement on islands, for example the use of giant tortoises for seed dispersal on oceanic islands, including the Galapagos and Mauritius (12, 19, 20) (see sidebar, Rewilding Through Taxon Substitution: Mauritian and Galapagos



Figure 2

Key species and landscapes that feature in the four flagship rewilding projects reviewed in this article. (*a*) Grey wolf (*Canis lupus*) (Mike Cline, Wikimedia Commons, public domain). (*b*) Aldabra giant tortoise (Bjørn Christian Tørrissen, Creative Commons, Share Alike 4.0 international license). (*c*) Landscape view of the Oostvaardersplassen (EM Kintzel, I Van Stokkum, Creative Commons, Share Alike 3.0 unported license). (*d*) Large herbivores at the Oostvaardersplassen (M Gerard, Creative Commons, Share Alike 3.0 unported license). (*e*) Artistic impression of the Pleistocene Park (Mauricio Antón, Creative Commons Attribution 3.0 license. Adapted from Reference 6).

Tortoises). The introduced animal acts as an ecological analogue for kin made extinct as a result of anthropogenic impacts during the colonial period.

Janzen & Martin (25) suggest that the introduction of horses and cattle in parts of Central America may have in part restored the local ranges of trees that had large mammals as dispersal agents. As a consequence, plant distributions and grassland mixes that are moderately browsed by free-ranging livestock may be more similar to those before megafaunal extinction than to those that were present at the time of the Spanish conquest (25). Further work has examined the role of rodents as substitute seed dispersers (26). To date, there have been few interventions aimed

REWILDING THROUGH THE REINTRODUCTION OF A KEYSTONE SPECIES: WOLVES AT YELLOWSTONE

Yellowstone National Park (mainly within the US state of Wyoming) covers ~898,000 hectares of mountain habitats, grassland, and forest. Humans have lived in the region for at least 11,000 years, and although it was declared a national park in 1872 various forms of intervention continued. Most of the pre-Columbian fauna survived in the park, but wolves were eradicated in the early twentieth century. From the 1960s onward there was discussion about reintroducing the species because of concerns about the impact of the increasing populations of elk *Cervus Canadensis*, and reintroduction took place from 1995–1996. Subsequent research on growth of aspen, willow, and cottonwood in recent years suggests that wolves have initiated a restructuring of northern Yellowstone's ecosystems via improved recruitment of woody browse species (16, 17). Concurrent with the declining elk population, the bison population has been increasing on the northern range. Wolves may be allowing the bison population to increase through a decrease of interspecific competition with lower elk numbers. Increases in beaver have also been seen, likely due, at least in part, to the resurgence of willow communities since wolf introduction.

at rewilding areas that are commonly understood as wild, for example through the restoration of seed dispersal or grazing and predation functions. However, there have been calls to set up Pleistocene parks accommodating reintroduced megaherbivores to restore ecological functions in the Cerrado and the Pantanal in Brazil (27).

A second understanding of rewilding and body of literature has developed in a European context, emerging out of an interest in ecological networks and naturalistic grazing, alongside an exploration of the challenges posed to conservation by a reappraisal of paleoecological theory

REWILDING THROUGH TAXON SUBSTITUTION: MAURITIAN AND GALAPAGOS TORTOISES

Efforts to restore historic vegetation ecosystems and reduce secondary extinctions are underway using tortoises in Mauritius (21) and the Galapagos Islands (22).

Giant *Cylindraspis* tortoises, once abundant on the Mascarene islands, acted as selective agents on native flora. Extirpation in the nineteenth century colonial era led to degeneration of native grassland floral assemblages. Extant proxies with similar life-history traits—the Aldabra (*Aldabrachelys gigantea*) and Madagascan radiated (*Astrochelys radiata*) tortoises—were introduced on Round island, off Mauritius in June 2007 by the Mauritian Government and a local NGO.

The tortoises aided dispersal of large seeds of the dispersal-limited endemic palm *Latania loddigesii* (21). They suppressed prolific weeds outcompeting native plants, thereby helping restore historic grazing assemblages. On Ile aux Aigrettes, another Mascarene island, Aldabra tortoises have significantly enhanced dispersal and improved germination of the large-fruited ebony tree (*Diospyros egrettarum*) (23).

Similar endeavors in the Galapagos have involved introducing replacements for the extinct giant Pinta Tortoise (*Chelonoidis abingdonii*). Saddleback and Domed tortoises of various origins were released as potential proxies to fill in vacant niches. Saddlebacks aided in the dispersal of *Opuntia*, besides arresting woody plant encroachment and increasing local vegetation patchiness (24). Domed tortoises moved to locations with lower cacti densities, and did not contribute to *Opuntia* dispersal (22).

The extinction and rewilding biogeographies of tortoises have sparked considerable interest, with candidates proposed for a number of other island complexes including Madagascar, Seychelles, and the Caribbean (12).

(28, 29). An ecological network approach to spatial planning and conservation arose from the realization that protection of special sites alone would not secure conservation goals (30). It argues for a coherent ecological spatial configuration of core areas, corridors, restoration areas, and buffer zones to develop connected functional landscapes (31). This geography is consistent with the North American 3Cs understanding of rewilding.

In the European model, greater importance is afforded to naturalistic grazing, that is, grazing hardy animals outside of a field-based farming system. This has become popular, partly as a result of changes in farming and concerns over the impact of rural depopulation and land abandonment on biodiversity (32). An interest in grazing regimes was also triggered by Frans Vera's (8) influential theory of cyclical vegetation turnover. Vera posited that the natural vegetation of lowland Europe was not the closed forest that is central to prevalent paleoecological understandings of Europe in the middle of the Holocene. Instead, he argues for a shifting mosaic or park-like landscape where large graziers played an essential ecological role in opening up the forest canopy (8, 29, 33).

Although contested as a model for mid-Holocene landscapes (34–36), Vera's theory has had a powerful influence on rewilding practice in Europe. European rewilding through naturalistic grazing generally focuses on re-establishing a guild of large herbivores—cattle, horses, wild boar, beavers, and bison—whose grazing and browsing would restore or create complex and species-rich ecosystems on reclaimed areas or those previously used for agriculture or forestry (37, 38). Here, rewilding can involve the creation and release of captive bred animals into the wild, sometimes linked to practices such as dedomestication, back-breeding, and de-extinction (39). In these cases, the genetics, anatomy, and behaviors of specific animals may become the topics of concern in advance of their landscape impacts (40).

The OVP reserve in the Netherlands (see sidebar, Rewilding Through Naturalistic Grazing: The Oostvaardersplassen Nature Reserve) has emerged as a practical expression of this

REWILDING THROUGH NATURALISTIC GRAZING: THE OOSTVAARDERSPLASSEN NATURE RESERVE

The Oostvaardersplassen (OVP) is a 5406 ha reserve in the Flevoland province of the Netherlands managed by the State Forest Service, *Staatsbosbeheer*. The OVP came into existence when a polder on the shores of the Markermeer was completed in 1967. Due to an economic downturn plans for the development of heavy industry on the polder were dropped and it was instead earmarked for agriculture. However, during the process of reclamation a bird-rich marsh developed and huge numbers of greylag geese arrived to molt.

Inspired by the spontaneous ecological development of the area and the observation that grazing geese were driving habitat dynamics, Frans Vera wrote an article about the potential for developing a novel ecosystem similar to those which had vanished from the Netherlands long ago. Working with colleagues he convinced the authorities to rewild the polder and create a nature reserve.

Cattle, horses and deer were introduced into the area under a policy of minimal intervention, so that natural processes might be given a central position in the management of the OVP ecosystem. These herbivores increased rapidly. By 2000 numbers of herbivores began to approach population-based carrying capacity and annual mortality rose and became more variable. Large die-offs in the winters of 2005 and 2010 caused significant public and political debate, which led the Minister to establish an International Commission on the Management of the Oostvaardersplassen (ICMO).

Reports from this commission address specific questions regarding ecology, welfare and management and together establish key principles for rewilding projects (42, 43). The OVP is the first reserve in Europe where the rebuilding of tropic levels and natural processes are central to management. It has simultaneously inspired and challenged, and has provoked scientific, public and political debate (44, 45).

REWILDING THE TUNDRA: THE PLEISTOCENE PARK IN SIBERIA

The North-East Scientific Station and Pleistocene Park are scientific organizations located in northern Siberia, 5 km from the town of Chersky (Yakutia) (68° 44′N, 161° 23′E).

The North-East Scientific Station was established in 1977 and has become one of the world's largest Arctic research stations. Pleistocene Park is a major initiative that includes an attempt to restore the mammoth steppe ecosystem, which was dominant in the Arctic in the late Pleistocene. The initiative requires replacement of the current unproductive northern ecosystems by highly productive pastures, which have both a high animal density and a high rate of biocycling. The idea is that during the Pleistocene the collective behavior of millions of competitive herbivores maintained the grasslands. In the winter, the animals ate the grasses that grew the previous summer. Their activity stimulated plant productivity by fertilizing the soil with their dung; they trampled down moss and woody species, preventing these plants from gaining a foothold.

Experiments with animal reintroductions began in 1988. Currently, Pleistocene Park consists of an enclosed area of 16,000 hectares that is home to five major herbivore species: bison, musk ox, moose, horses, and reindeer, although the bison have not done as well as the other species. The aim is to increase the herbivore density until it is sufficient to influence the vegetation and soil. As the animal density increases, so the fenced boundary will be expanded. There is an ultimate goal of acclimatizing Siberian tigers should the herbivores become sufficiently abundant (46, 47).

understanding of rewilding and is presented as a means to test Vera's hypothesis. Naturalistic grazing is also central to *Rewilding Europe*, a continental initiative aiming to rewild upland and marginal areas of Europe (41).

An interest in the ecological agencies of herbivores and the impacts their extinction has on nutrient cycling and vegetation dynamics informs Sergey Zimov's (46) Pleistocene Park rewilding experiment in the Siberian Tundra (see sidebar, Rewilding the Tundra: The Pleistocene Park in Siberia).

Proactive programs for introducing grazers and building ecological networks can be differentiated from a third understanding of rewilding, which describes a more passive, or "self-willed," ecological transition that results from the land abandonment that is currently taking place in marginal areas of Europe and North America following local agricultural depression (48). This transition has been accompanied by the recovery and return of some of the large carnivores from remnant populations, sometimes, but not always, associated with active reintroductions (49).

BENCHMARKS FOR REWILDING

Variations in rewilding practice relate in part to the choice of ecological baseline for guiding future restoration. Rewilding research seeks to learn from how ecosystems functioned in the past in the absence of, or under more limited, human interventions. Many of the ecosystems that come to be valued for conservation are as much cultural as natural landscapes (**Figure 3**), and this cultural element extends into the Pleistocene and has increased through the Holocene.

The cultural aspect of biodiversity is particularly obvious in northwestern Europe where a range of habitats, including, for example, highly valued grassland and heathlands, have been maintained in historic times, if not actually created, by past farming practices (51, 52). Forests often described as primeval, such as the Białowieża National Park in Poland, or Fiby Urskog in Sweden, turn out to have had a more active management history than at first appears (53, 54). Certain forest structures—and their wildlife—such as those associated with coppicing or wood pasture are



Figure 3

Conceptual view of development of cultural landscapes. Figure adapted from Reference 50.

similarly the product of historical management, even if they are to some extent analogues to more natural systems (8, 37, 55).

In North America, conservationists routinely turn to the arrival of Columbus in 1492 as a restoration benchmark, but the pre-Columbian landscape was also not a pristine wilderness and had been actively modified in various ways for thousands of years by indigenous peoples (18, 56). Many other supposed areas of wilderness, such as the Amazon basin (57, 58) or the Australian outback (59, 60), have also been modified by people for millennia.

Many ecologists therefore argue that most of the world's ecosystems functioned largely independently of modern humans only prior to the Pleistocene extinctions (\sim 50,000–7,000 ybp). Although, some argue for pushing this benchmark back further, as *Homo* has been using fire for several hundred thousand years, and this may have affected many ecosystems (61). Globally, 97 genera of large animals (>44 kg) (megafauna) went extinct during this period. These extinctions were concentrated in the Americas and Australia, but with also striking losses of large mammals in Europe (62, 63). There is still debate as to whether the extinction of the megafauna was caused by humans, through human-driven overkill extinction (64, 65), or through climate change, or a combination of both (62, 66).

Thus, rewilding research has encouraged a questioning and rethinking of the historical benchmarks or baselines that inform contemporary conservation—pushing back the historical horizon to better comprehend the ecological dynamics of a prehuman world and the ecological and evolutionary consequence of living in a defaunated world. In subsequently applying this knowledge to guide conservation in the Anthropocene, rewilding has also encouraged a reexamining of the ways in which knowledge about the past can be used to position the present and inform conservation interventions for the future. There are three significant historical benchmarks that have figured in these discussions.

A Pleistocene Benchmark for Rewilding

Pleistocene systems, particularly those of the Late Pleistocene of the Last Interglacial and Glacial (132,000 ybp to \sim 10,000 ybp), offer an ecologically varied benchmark to inform rewilding. Choosing this period requires an understanding of the consequences of the loss of the Pleistocene megafauna, which would have impacted the remaining fauna, plant communities, vegetation openness, species diversity, and fire regimes. Although there is a good understanding of which mammals went extinct during this period (62, 63), much less is known about what Janzen (67, p. 50) terms the more "insidious type of extinction, the extinction of ecological interactions."

Loss of the megafauna may have led to trophic cascades. Due to their relative invulnerability to nonhuman predation on adults, megaherbivores (>1,000 kg) are likely to have attained sufficiently high densities to play a major role in determining vegetation structure and composition. Evidence suggests the elimination of megaherbivores at the end of the Pleistocene altered vegetation structure and dynamics (37, 68, 69) and in the process eliminated habitats for smaller animals that subsequently went extinct (70). Species richness of large hypercarnivores (>20 kg) in the Pleistocene was far greater than today, which suggests that in the past, smaller prey densities were likely limited much more by predators than today (71).

Interactions with the now extinct herbivores could have left some plant species with obsolete defenses and nonfunctional adaptations for seed dispersal (72). The extinction of the Pleistocene megafauna may have had a large effect on plant species distributions by reducing distributors of large seeded fruits (25, 73). Such loss of dispersers may have reduced large-seeded fruit tree populations in the Amazon (74) and in other parts of South America (75). Megaherbivores can play a dominant role in the maintenance of grassland against the expansion of trees in savannas (37, 68, 76). In a comparison of two African savannah systems, woody cover increased ~9% over ~36 years when megafauna were excluded (77, 78). Elephants are chiefly responsible for the tree falls, and can uproot up to 1,500 trees per elephant per year (79).

In addition to changes in plants, there would have been changes in the populations and extinctions of insect species. For example, removing large temperate or tropical animals, and their dung, can disrupt the diversity and abundance of dung beetle communities (80), or force them to alternative feeding habits (81). These beetles provide many ecosystem services such as nutrient cycling, plant growth enhancement, seed dispersal, and trophic regulation (82).

The extinctions of the megafauna could also have affected large-scale nutrient cycles. Animals distribute nutrients through their bodies and feces. Larger animals may be disproportionally important in the spread of nutrients because they travel further distances and have longer food passage times than smaller animals (83, 84). Metabolic scaling theory has been used to make predictions about the megafauna nutrient-spreading capacity; the study hypothesized that the extinction of Amazonian megafauna may have led to a >98% reduction in the lateral transfer flux of the limiting nutrient phosphorus (P) in Amazonia (85, 86), although the extent of megafauna presence in Amazonian forests remains unknown. Nutrients in Siberia have been hypothesized to have become less labile following the extinction of the megafauna (47, 87). Following human hunting, marine ecosystems may have less nutrient dispersion, with one study finding that whales can transport significant quantities of nutrients from depth to surface waters. This transport may have decreased by an order of magnitude following widespread declines of whale populations (88).

More broadly, a global analysis of nutrient distribution indicates that the ability of animals to move nutrients away from concentration patches has decreased to $\sim 8\%$ of the pre-extinction value on land and $\sim 5\%$ in oceans (89). Overall, recent research supports the idea that animals perform several vital ecosystem services globally, and their absence would cause a reduction of these services (90, 91).

A Holocene Benchmark for Rewilding

A second set of rewilding benchmarks focus on the ecological conditions from the Holocene. The early Holocene (\sim 10,000 ybp) has been suggested as an alternative conservation benchmark for Europe (35). Pre-Columbian conditions have been suggested for North America, and equivalent benchmarks for Australia focus on the ecological conditions before European colonization in the late eighteenth century (92). There is good evidence for the ecological conditions in Europe and North America during these periods (8, 51), and the characteristic large carnivores and

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herbivores largely still survive, at least in some areas. Alternatively, there are potentially close analogue species that could be used, which would help bypass the problem of how to substitute for the missing megafauna.

In some cases, replicating Holocene reference conditions involves only the restoration of a single keystone species. The wolf *Canis lupus* in Yellowstone (16), the Bolson tortoise *Gopherus flavomarginatus* formerly found in the Chihuahuan desert (18), or giant tortoises on Indian Ocean islands as analogues to tortoise species that went extinct during the colonial period (12); buffalo *Bison bison* on American prairies (93); or the European beaver *Castor fiber* in the United Kingdom and other parts of Europe (94) are examples. Conceptually, the removal of introduced species that have changed the Holocene processes could also be considered rewilding, for example the many cases of the removal of rats from islands where they had severely damaged seabird colonies (95), or attempts to eradicate cats and foxes in parts of Australia through fencing and pest control (96).

In other cases, rewilding has sought to reinstate naturalistic dynamics associated with the Holocene. It has, for example, involved attempts to shift to extensive, rather field-based grazing (97) or using fencing to manage grazing (98); stopping management of woodland to allow more natural gap dynamics to operate (99); less intervention in the case of major fires (9); or less control of riverine dynamics (10). Interactions between restored species and restored dynamic processes may often occur, for example between fire and grazing in prairie systems (100). Passive rewilding is also occurring through the natural reforestation of abandoned farmland in many mountain regions of Europe or the return of successional processes on old military or derelict industrial areas (101, 102), including, for example, the area around Chernobyl (103, 104).

Rewilding in Novel Ecosystems

A third, nonanalogue approach to benchmarking seeks to calibrate rewilding for the novel ecosystems that characterize the most human-modified parts and systems on the planet. For example, there have also been suggestions for completely novel forms of rewilding involving the introduction of African elephants into the Australian outback to tackle species invasive in Australia but native to the elephants' home range (105). In Australia, there has also been a reconsideration of the status and role of camels (106) and dingoes (107) as potential controls on invasive plant and mammal species. On a much smaller scale are recent interventions to rewild urban spaces—such as Vancouver and London—through the design of green infrastructure such as living roofs and the restoration of postindustrial or brownfield land (108). Although the direct ecological impacts of these interventions are modest, their public accessibility and thus political potential are perhaps significant.

REWILDING IN PRACTICE

These benchmarks for the wild are premised on an understanding of humans as entangled with and exerting a significant influence on—the nonhuman world. In interpreting the past, rewilding argues that humanity has caused dramatic changes to the structure and functioning of the natural world. Nevertheless, scientists suggest that it should still be possible to establish how ecosystem dynamics would broadly operate in periods before the anthropogenic defaunation of megafauna. This can be achieved through documenting how defaunation impacts ecosystem process and structure and by comparing systems with intact (or partially intact) assemblies with those without (109).

Rewilding thus takes place in the inhabited and thus political landscapes and ecologies of the Anthropocene (110, 111). The ideal rewilding scenario is often presented as one where all the key missing elements, both biotic and abiotic, are restored (100); however, this might not be feasible for a variety of ecological, practical, social, and political reasons. There is then a trade-off

between practicality and the rewilding ideal. If not all elements can be restored then there may be a need for varying degree of ongoing intervention, for example herbivore culling in the absence of appropriate large carnivores (112). Thus, although rewilding may sometimes be presented as an attempt to recreate past ecosystems from the early Holocene or Pleistocene, in practice all such projects will be moving toward some new future-natural state (113, 114).

Changes would also have taken place by now, such that the baseline conditions used as a basis for rewilding might not have survived even in the absence of humans. For example, during past interglacials, vegetation and soils in central Europe appear to have developed through a phase of deciduous and mixed tree cover, resulting from soil leaching and podzol development by expansion of heath or moorland development, or conifer-dominated landscapes (115). What vegetation stage would we be at now? Would some of the megafauna on islands such as the United Kingdom have died out or become smaller in the absence of human impacts (116)?

Changes may also have occurred in the abundance or distribution of other species, which may have implications for reintroducing lost species. For example, since the extinction of the wolf in the northeastern United States, the range of coyote *Canis latrans* has expanded, and it may now be occupying at least part of the niche formerly filled by wolves (117). In Italy, the genetic status of the wolves that are recolonizing may be compromised by interbreeding with domestic dogs (118; although see 119).

Species respond individualistically to conservation action, and rewilding may benefit some but not all of the missing assemblages. For example, within the United Kingdom otter *Lutra lutra*, pine marten *Martes martes*, and wild cat *Felis sylvestris* had all become rare with restricted ranges by the late 1970s. Otter has now recovered much of its former range as a result of restrictions on the use of persistent pesticides and improvements in water quality (and may now be contributing to the decline of invasive mink *Neovison vison*) (120); pine marten is slowly spreading back with increased forest cover, and reintroductions to its former range are being considered (121); but wild cat populations, despite similar protection, remain highly vulnerable, partly because of hybridization with domestic cats (122).

Restoration of species for rewilding is usually focused on what are believed to be keystone species, and this selection is frequently geared toward selected groups of charismatic flagship animals (123). Even so, not all the missing elements may be restorable for a variety of ecological and social reasons, in which case either more intervention may be needed—for example large herbivores are culled because it has not been possible to reinstate the relevant carnivore trophic layer—or the landscape composition and function will move off in an unintended direction.

Limitations on site size and quality may restrict which species can be included in particular rewilding projects; for example, successful reintroduction of the black-footed ferret (*Mustela nigripes*) in North America appears to be linked to the size of the prairie dog prey base (124). Continued intervention may be needed in low-quality landscapes; for example, survival of the Californian condor (*Gymnogyps californianus*) is compromised by ingestion of lead fragments and other pollutants, and supplementary feeding with clean carcasses is still considered necessary, even though this creates other problems (125).

Risks and Uncertainties

Conservationists and others have expressed concerns about the risks and uncertainties associated with a whole-scale embrace of rewilding (126, 127). The experimental nature of rewilding means it is largely unproven, and the future natural landscapes created may not maintain as much biodiversity (or other benefits) as more targeted approaches. There are inevitably more rewilding projects being talked about than are actually underway. Those that have been undertaken are

still in their infancy, and their landscapes are still evolving. There have also been different interpretations of the outcomes of these interventions, for example on the significance of the wolf effect in Yellowstone National Park (17, 128).

Risks that have been identified with programs involving species introduction or reintroduction are, for example, depletion of the donor populations, risks of bringing in disease, or low genetic variability among the introduced individuals (129–131). Sourcing species to restore ecosystem function may however pose less of a challenge than for reintroducing species of conservation concern, because the former are not necessarily threatened themselves.

There may be unexpected interactions or effects, even where a species is brought back into a system in which it was formerly a part. If herbivores are reintroduced without their historic predators, then major changes in vegetation composition and structure may follow, not all of which may be viewed as positive (132, 133); if top predators are reintroduced after a long absence, prey species may take time to learn to react to them and there will be implications for mesopredators (134–136). These risks can be reduced through well-designed projects, use of pilot or smallscale schemes to test ideas and staged actions (2, 137), and adherence to International Union for Conservation of Nature (IUCN) guidelines on translocation (138).

The risks and uncertainties may be increased when the original species is not available and taxon substitution is involved. Taxon substitution can give positive results (20), but even subtle differences in behavior might have long-term ecological impacts. Cattle on American prairies do not graze in quite the same way as bison (139). Similarly, we cannot know how similar the behavior of the Heck cattle introduced at OVP really is to that of the lost aurochs (140). Even higher levels of uncertainty would be involved if attempts were made to bring back extinct species.

Hughes et al. (141) illustrate (**Figure 4**) how for British conditions the extent of rewilding and the open-endedness of the project—is limited by ecological factors at small site sizes; as the projects become bigger, however, it is more likely that social or economic factors will be critical because of competition with other land uses and public influence. The uncertain, open-ended nature of rewilding projects presents issues for those seeking to monitor their success. Sutherland (142) argues that rewilding therefore requires a greater openness in science and management, including a willingness to accept uncertainties and ecological surprises. **Figure 5** illustrates this approach. For example, if European conservation is detached from premodern



Figure 4

The relationships between the size of the area considered for rewilding and the degree to which an open approach can be deployed for habitat creation projects. In sector A their use is limited by the site size. In sector B economic and social factors put limits on their application. Two examples are illustrated in italics. Figure adapted from Reference 141.



A schematic illustration of the rewilding process.

agricultural baselines, then multiple future ecologies are possible. This open-endedness has political implications, as there are often multiple groups of actors with a stake in which future is accepted, including animal welfarists, farmers, hunters, tourists, and local residents (143, 144). Negotiating this politics requires techniques for public engagement and deliberation (113).

THE POLITICS AND ETHICS OF REWILDING

A range of economic, social, and political benefits have been proposed for rewilding, but the emergence of rewilding has also been characterized by a range of political tensions and controversies within and beyond conservation biology. There are likely to be significant differences in the costs and benefits accruing from rewilding interventions to different social groups. These differences relate largely to the tensions between rewilding and prevalent modes of environmental governance, which are encoded in legislation, subsidy regimes, territories, and broader social norms.

Economic and Social Benefits of Rewilding

Advocates identify several social and economic benefits of rewilding, some of which are shared with more interventionist forms of conservation. Rewilding has been proposed as a cheaper mode of conservation. For example, in parts of Europe naturalistic grazing could replace low-intensity agriculture, which currently receives significant subsidy from the Common Agricultural Policy (145). Rewilding could also be a cheaper means for delivering ecosystem services such as flood defense or carbon sequestration (48, 146). Rewilding ecosystems might also be more resilient to environmental change (147). There is the potential for rewilding to invigorate rural economies in many parts of the world, creating livelihoods through employment in forms of nature-based

tourism and the provision of associated goods and services (2, 41). However, many of these claims have yet to be properly assessed and constitute an important area for future research.

Rewilding has also been promoted as a means of reconnecting people and nature, addressing the so-called nature deficit disorder (148) or conditions of so-called ecological boredom that are described by some to characterize modern, urban life in industrialized societies (5). Programs to engage various sectors of the public with the wild are understood to deliver a range of mental and physical health benefits (149). Rewilding can produce landscapes that are more valued by people (150, 151). However, people can value rewilded landscapes less where there has been significant loss of traditional culture (152, 153). More broadly, rewilding visions promote social and political benefits across a range of scales, from engaging people with local and national wildlife, to continental visions for the future unification of Europe through the shared purpose of wildlife conservation (39, 41, 154).

Political Challenges

In contrast, an established strand of the social science literature on conservation examines how forms of colonial and neo-colonial wilderness conservation (that precede the recent enthusiasms for rewilding) evicted and denigrated indigenous land users in different parts of the world. Cronon's (155) "The Trouble with Wilderness" prompted extensive debate (156, 157), and postcolonial environmental historians have argued that the divisions between nature and society on which a wilderness model is based are largely absent in some parts of the world (158, 159). Jørgensen (7) identifies the persistence of this troublesome model of wilderness conservation in some strands of the rewilding argument.

Opposition to rewilding is particularly likely where projects are perceived as being imposed from "outside," with little consideration for local interests. For example, Mackenzie (160) argues that rewilding has received an adverse reception in parts of Scotland as it has become associated with forced displacement with historic resonances of the Highland Clearances of the nineteenth century. In the United States, Hintz (161) argued that a TWP rewilding project that sought to reintroduce the grizzly bear into the Bitterroot ecosystem in Idaho failed, at least in part because its proponents denigrated the working relationships that various marginal local people had with the land, alienating and excluding them from political discussion. Similar criticisms have been made of rewilding initiatives in South America (162). Schwartz explores how the efforts of an alliance of domestic and Western European NGOs to introduce wild horses onto recently abandoned farmland in Latvia met with resistance from local and national political movements. Opponents and that this rewilding threatened agrarian cultural landscapes central to both rural livelihoods and national identity (154).

The flagship taxa of rewilding tend to be megaherbivores and carnivores, species that generate considerable public appeal and revenues for conservation. A focus on these animals can impact local livelihoods. For example, conservationists have argued that the transfer of African and Asian proxies to America or Europe could diminish tourist-related conservation revenue in developing countries, thereby undermining in situ conservation efforts (126). Megafaunal transfer can aggravate conservation conflicts in Asia and Africa, where landscapes for large mammals have often been produced through colonial modes of governance (163). Furthermore, the keystone species for rewilding—such as wolves or elephants—can generate significant and debilitating human-wildlife conflict, the burden of which tends to fall on marginal people (164, 165).

In contexts where there is no recent history of cohabitation with megafauna, it is difficult to know in advance what state and public responses to problematic megafauna might be. For example, concerns over economic impacts underpin continuous efforts to down-list the wolf from the Endangered Species Act in the United States (166). Opposition from farmers may prevent reintroducing the wolf in Scotland (167) and may lead to lynx *Lynx lynx* being seen as the more likely first option for carnivore reintroduction in the United Kingdom (168).

Conservation Institutions and Legislation

Rewilding science and practice can also come into conflict with contemporary conservation institutions and legislation. Priority in conservation is generally given to protecting cultural landscapes dependent on some form of past human intervention—most noticeably in some European landscapes (e.g., coppices, hay meadows) (8) but also in Australian and North American landscapes shaped by aboriginal fire practices (100, 169). Contemporary conservation legislation and institutions embody a compositionalist world view derived from ecological biogeography and community ecology (170). This views ecosystems as interacting hierarchies of individuals, populations, and communities. It affords systematic and target-driven policy based on the conservation of species, targets, and habitats (specified according to benchmark species compositions). Rewilding by its nature implies a more dynamic and functionalist approach with less predictable or desirable outcomes for some species, possibly even those of high conservation concern, which were favored by past human interventions and may not do so well under rewilding. This can create conflict.

For instance, European Union member states are required under the Habitats and Birds Directive to designed sites identified on the basis of specific target species and representative examples of particular habitat types (171). Conservation bodies are legally required to manage their land so that the designated values of a nature area are maintained in a favorable condition. The reintroduction of large herbivores could change the composition of habitats and make their condition unfavorable (145).

In the wider countryside, European conservation is delivered through agri-environment schemes (EEC Regulation 2078/92) (172). These tend to promote continued extensive farming on marginal lands that might be suited for rewilding. They can distort land prices and lock land managers into unproductive, uneconomic, and ecologically destructive practices (145). Recipients of such funding must manage their land and livestock as domestic animals rather than wildlife. However, subsidies for heritage breeds, tree planting, and deer culling provide a vital source of income for other rewilding projects.

In South America, Galetti (27) has suggested that the removal of livestock from the Emas National Park in Brazil to comply with prevalent conservation legislation has resulted in "unnaturally" frequent fires and an increase in invasive plant species. Without rewilding concepts, he argues that the Cerrado, the Pantanal, and other flagship National Parks in Africa will always be difficult to manage, as they lack purpose and are full of vague niches. In Australia, rewilding concepts are finding expression in proposals to tackle invasive species that conflict with existing conservation legislation. Flannery (173) has proposed that the reintroduction of apex predators such as dingoes and Tasmanian devils may suppress populations of red foxes and feral cats. A 5,500-km dingoproof fence currently divides the agricultural southeast of Australia from the dingo-populated north. Newsome et al. (107) propose opening this fence to allow dingoes into southern national parks. As with Galetti, they argue for creating experimental reserves to better understand the ecosystem dynamics produced by rewilding and to provide proofs of concept for policy.

Animal Welfare

Many countries with rewilding projects have legislative instruments governing the keeping of animals for farming or other purposes. In Europe, the 1976 European Convention for the protection of animals kept for farming purposes specifies animal welfare standards that require animals to be kept free from hunger, thirst, discomfort, pain, injury, and disease (174). At issue here is the distinction between animals that are kept and those that are not kept (113). This is determined by the species type and size of the site, the degree of wildness, and the self-sufficiency of the animals.

In the Netherlands, the Dutch court has ruled that cattle and horses at the OVP have become wild enough to be no longer considered livestock (i.e., they are dedomesticated) and can be left to die of starvation in the winter (113). However, the negative public response to this policy generated political pressure for a compromise. This involves identifying animals that will not survive and performing a proactive cull "with the eye of a wolf" (112), evaluating in advance of the winter which animals will and will not survive. Klaver et al. (112) welcome this policy, arguing that it shows a "respect for future wildness" by understanding dedomestication as a replacement of relations of domination with those of trust. Kymlicka & Donaldson (175) contest this argument due to the animals' lack of an exit option from the enclosed reserve.

Animal welfare legislation can also influence projects involving predator reintroductions. Relatively small sites that are fenced may be considered safari parks under relevant zoo regulations and made subject to animal welfare legislation. One example is the Alladale Wilderness Reserve in Scotland that is working toward the creation of a large fenced wilderness reserve encompassing hundreds of square kilometers, much as exists in Africa today (176). This vision has been constrained by existing regulations, which classify the reserve as a zoo and required introduced elk (*Alces alces*) to be kept in an enclosure and to separate predators and prey (177). This example indicates the need to tailor legislation on animal captivity to acknowledge differences in the scale of any enclosure. Finally, concerns over animal welfare also condition the public acceptability of controlling introduced species, for example the opposition to control of wild horses in some American states, and to some forms of eradication of deer in New Zealand and buffalo, horses, and camel in Australia (106, 178).

CONCLUSIONS

The term rewilding does not have a single simple definition. Instead, it has proved useful as a way of describing an approach to conservation that seeks to maintain or even increase biodiversity and reduce or reverse past and present human impacts by restoring more functional ecosystems. Beyond this shared ethos, rewilding describes a range of different goals, contexts, approaches, and tools.

Rewilding concepts and projects can first be differentiated by the roles afforded to human agency. Although all forms of rewilding share an acknowledgment of the deleterious consequences of past human activities, they differ as to the place of people in current and future wilds. For some, human absence can be taken as the index of wildness—an understanding akin to concepts of wilderness. For others, wildness in the Anthropocene requires ecological engineering—here certain human activities (e.g., species reintroduction) are part of rewilding that will play an import role in restoring ecological processes. Some human interventions will be required where these cannot be restored.

Broadly speaking, three different benchmarks inform rewilding projects: Pleistocene premegafaunal extinction, early Holocene (Europe)/precolonial (Americas, Australia, and tropical island ecologies), and novel ecosystems. In light of these ideals, judgments are then required as to which missing elements (species or processes) can reasonably be restored. These judgments inform the selection of tools for practical intervention. During the restoration period, the level of human intervention may need to increase temporarily, but the ultimate aim is often to minimize human intervention.

Most rewilding projects are relatively recent and so are likely to change, perhaps dramatically, in the next few decades. Although the eventual outcomes of rewilding processes are uncertain and different from the original expectations, the changes involved and benefits that arise should be monitored. This will allow the relative success of rewilding compared to other forms of land management to be assessed.

Advocates of rewilding must recognize that value is attached to cultural landscapes and that rewilding can conflict with prevalent and powerful institutions and cultural norms. Rewilding will not be appropriate everywhere and should be a complement to other forms of conservation management. There is the potential for serious conflict if attempts are made to impose rewilding against the will of public groups, even if there are no legal reasons why this should not be done. It is therefore critical to involve local and national interest groups in discussions on its future application.

In a world that is changing on many fronts, the Anthropocene opens up a possibility of reinterpreting what is natural, emphasizing ecological function over preserving species composition. Applied wisely, rewilding can be part of an ambitious, optimistic agenda that does more than just expose and manage species extinctions and habitat loss. It can be an exciting way of creating landscapes that are rich in wildlife and will develop their own new cultural associations.

SUMMARY POINTS

- 1. Rewilding is gaining in popular and scientific interest as a new approach to conservation.
- 2. Rewilding is a plastic term with several different meanings.
- These share a long-term aim of maintaining, or increasing, biodiversity, while reducing the impact of present and past human interventions through the restoration of species and ecological processes.
- Three different historical benchmarks inform rewilding research and practice: the Pleistocene, the early Holocene, and the novel ecosystems of the Anthropocene.
- 5. Rewilding has focused on addressing trophic cascades through the (re)introduction of keystone species, including large herbivores and predators.
- 6. Rewilding comes in passive and active forms, with rewilding happening by virtue of human abandonment as well as deliberate conservation interventions.
- 7. Rewilding has the potential of generating economic and social benefits.
- 8. Rewilding has proved controversial where it conflicts with prevalent forms of environmental management, including orthodox approaches to conservation.

FUTURE DIRECTIONS

- More scientific research is required, including managed experiments and studies of areas of inadvertent change.
- Greater objective assessment should be undertaken of the economic benefits of rewilding and their political distribution.
- Methods should be developed for engaging publics in deliberating rewilding decision making.
- 4. Rewilding should be examined in the context of global food and energy provisioning.

DISCLOSURE STATEMENT

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