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Essay

# Rewilding is the new Pandora's box in conservation

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Rewilding — the proposed restoration of ecosystems through the (re-)introduction of species — is seen by many as a way to stem the loss of biodiversity and the functions and services that biodiversity provides to humanity. In addition, rewilding might lead to increased public engagement and enthusiasm for biodiversity. But what exactly is rewilding, and is it based on sound ecological understanding? Here, we show that there is a worrying lack of consensus about what rewilding is and what it isn't, which jeopardizes a clearer account of rewilding's aims, benefits and potential consequences. We also point out that scientific support for the main ecological assumptions behind rewilding, such as top-down control of ecosystems, is limited. Moreover, ecological systems are dynamic and ever-evolving, which makes it challenging to predict the consequences of introducing novel species. We also present examples of introductions or re-introductions that have failed, provoking unexpected negative consequences, and highlight that the control and extirpation of individuals of failed translocations has been shown to be extremely challenging and economically costly. Some of rewilding's loudest proponents might argue that we are advocating doing nothing instead, but we are not; we are only advocating caution and an increased understanding and awareness of what is unknown about rewilding, and what its potential outputs, especially ecological consequences, might be.

Over the past century, a variety of conservation approaches have been introduced with the hope of stemming the loss of biodiversity. Several approaches have met with some success, while others have not, for a variety of ecological, sociological and political reasons. In 1998, rewilding, was proposed as a new potential panacea for restoring not only biodiversity, but also wilderness [1]. Rewilding is receiving increased media attention in major newspapers, TED talks and the scientific literature. Also, several conservation organizations are considering rewilding as a potential solution to a suite of conservation problems, and practitioners are implementing it in the field. Proponents of rewilding have raised awareness about what they see as rewilding success stories, such as the reintroduction of the wolf to Yellowstone National Park, promising that rewilding will lead to increased biodiversity and ecosystem function, while also providing enhanced cultural enjoyment of the landscape. We agree with rewilding's proponents that those are admirable goals, but we disagree that rewilding is a panacea and urge caution in its widespread implementation.

Any emerging approach or discipline, regardless of the field, should regularly revisit its critical assumptions and identify limitations and knowledge gaps. As the drumbeat for rewilding gets faster and louder, such self-evaluations have been rare. While some suggest that rewilding is ready to take over as a major paradigm in conservation [1], the support for its main theoretical and underlying foundations may be limited. To our minds, rewilding as a conservation discipline consists of significant unknowns in the ecological and socio-economic realms, and the risk-to-reward ratio is often unknown. If nothing else, rewilding could take limited funds from other arenas of conservation. Our intent here is simply to muffle the drumbeat for rewilding by encouraging its proponents to reach a consensus on the disparate aims and means across definitions of rewilding and to (re-) consider the soundness of rewilding. Specifically, we want to clarify what rewilding is and is not. Moreover, we aim to show that many of rewilding's main ecological foundations have only limited support. This essay will not touch on practical concerns (e.g., more than 70% of reintroductions fail), ethical concerns (e.g., what happens to the organisms involved in failed introductions?), or socio-economic concerns (e.g., when tourists visit Kansas in the US to see the magnificent grazers from East Africa, what are the consequences of those lost tourist dollars in East Africa?). Instead, we focus on terminology and ecology.

## What exactly is rewilding?

The definition of rewilding has evolved and diversified since its inception (Figure 1), introducing confusion and contradictory views of its main conservation aims and tools. At least in its initial incarnations, rewilding sought to restore self-regulating ecosystems, with a strong emphasis on the role of top-down control of ecosystems by large predators. Since those early days, rewilding has evolved and mimicked to some degree the aims of restoration ecology. In much of Europe, at the turn of the century, rewilding quickly turned its focus to 'naturalized grazing' (rewilding without predators) as a means to preserve and develop particular kinds of landscapes, where grazing was perceived as a natural process that had been lost [2]. Thus, the focus of rewilding today is on species introductions or reintroductions as a way to restore ecosystem functioning through the facilitation of assumed natural processes that existed before the ecosystems were profoundly altered by human impacts [3]. The discipline encompasses a variety of views regarding, for example, how 'wild' nature should be or how much management should be applied to ecosystems [4].

Most of the variation in how the term 'rewilding' is used depends on the degree of human intervention in improving the functions and services provided by ecosystems that are 'rewilded' (Figure 1). Rewilding strategies range from emulating the past by direct and intense human intervention, called 'Pleistocene rewilding' [5], to attempting to foster the future co-existence of natural and anthropogenic systems with minimum human intervention, dubbed 'passive rewilding' [6,7]. Advocates of Pleistocene rewilding propose introducing functionally equivalent extant species as substitutes for extinct taxa. Translocation rewilding [3] shares the roots of Pleistocene rewilding but focuses mainly on re-introducing species that occurred more recently than the Pleistocene. At the other extreme of the human intervention gradient is passive rewilding, which requires little human intervention in order to allow ecological succession to reach

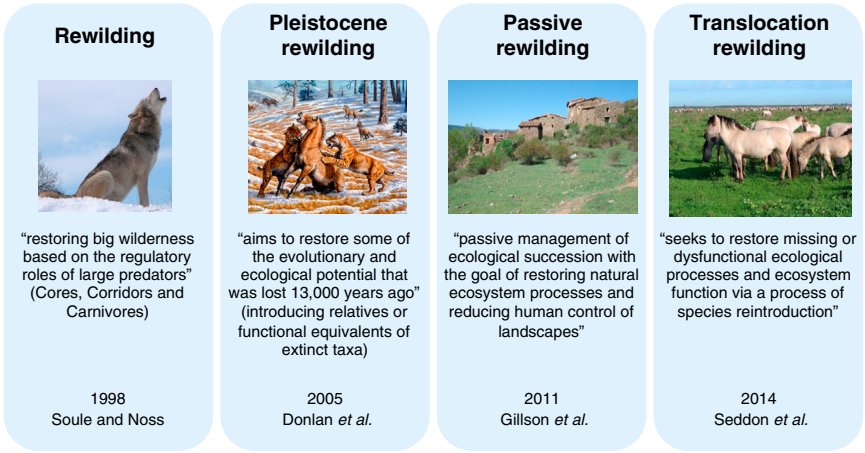


**Figure 1. Rewilding: old wine in new bottles?**
Key definitions of rewilding in the last 20 years shows that rewilding has developed towards species reintroductions as the main operative tool and toward embracing the mission of restoration ecology. Image credits (left to right): Retron, Wikimedia Commons, Mauricio Antón, Teodoro Lasanta, GerardM, Wikimedia Commons.

a sustainable state within a landscape matrix of cities, infrastructure and croplands by exploiting opportunities provided by long-term socio-economic trends, such as the release of lands for wilderness owing to rural abandonment. Our view is that practitioners, proponents and journalists too often play too loose with rewilding terminology. We advocate reaching a consensus among definitions within the panchreston of rewilding to define what rewilding is and what it is not in order to promote a clearer account of rewilding's conservation aims, benefits, and potential consequences.

## Top-down control, novel species and threats to biological diversity

Rewilding differs from simple reintroduction in that it is mostly concerned with reintroducing species that have a high potential to exert an influence across several trophic levels, under the assumption that such species will have disproportionally large and beneficial effects on communities and ecosystems. Generally speaking, the idea is to introduce a top predator (such as wolves) or a dominant herbivore (such as bison that once roamed the Great Plains of the US or similar landscapes in Europe) in the hope that these reintroductions will restore key ecological processes via top-down control (control of populations on a lower trophic level by activities at a higher trophic level, e.g. when predators control a prey population), return an ecosystem to a previous state or re-initiate key ecosystem functions.

Which assumptions underlie restoration of a key ecosystem process? One fundamental assumption is that ecologists understand the complexities of interaction webs well enough to predict the effects of any introduced species on the other species in the community. We are learning more about how top predators and dominant herbivores affect community structure and ecosystem function [8]. For example, increases in population sizes of sea otters led to increases in production of kelp forests, because otters prey on urchins, the dominant herbivore of kelp [9]. But of course there is variation among experiments and systems that arises for a whole host of context-dependent reasons. Meta-analyses often provide the false notion that we know the effects of top predators or dominant herbivores on communities and ecosystems, but that is clearly not the case. For instance, recent meta-analyses report that the effects of terrestrial herbivores on plant community biomass and community structure vary among ecosystem types and depend strongly on environmental context [10,11]. Effects of predators on their prey and on plant communities also vary from system to system. And, oddly enough, the apparent impacts of predators also vary from meta-analysis to meta-analysis, with some finding evidence of strong cascading effects, while others find only weak cascading effects [11–13]. As a result, it is hard to predict accurately what the impacts of introducing a predator or dominant herbivore will be on a community or ecosystem.

To make predictions of the effects of reintroduced herbivores or predators on ecosystems less challenging, one could make several other assumptions. One could assume that Pleistocene rewilding and translocation rewilding are able to reconstruct the selection pressures that existed in the Pleistocene when translocating individuals of a species into a similar environment. One might also assume that species that share a recent evolutionary history somewhere in their overlapping ranges will interact in the same way today and in the future, because they have not evolved (or there is no phenotypic plasticity) [14]. Alternatively, one could assume that systems are not dynamic, that things today are just as they were 10,000 years ago, or that interactions among species do not vary temporally. Indeed, some versions of rewilding rely heavily on Pleistocene (or other pre-historic) baselines to justify the assumption of strong top-down control of ecosystems by large animals. But there are substantial differences between the Pleistocene and today (Figure 2). Extant carnivore and herbivore communities lack the largest animals of the Pleistocene, such as the American lion (*Panthera leo atrox*), Irish elk (*Megaloceros giganteus*), and giant beaver (*Castoroides ohioensis*). Whether smaller extant species can control ecosystems in a top-down fashion as did their larger counterparts in the Pleistocene is at best an open question, and at worst unlikely [15].

Most proponents of rewilding in the scientific community are not naive enough to assume such things, but if we do not acknowledge them up front, such key assumptions are at risk of being forgotten if or when rewilding is implemented by NGOs and practitioners. Rewilding is indeed being applied, or at least advocated, in a significant number of ecosystems across Europe (e.g., www.rewildingeurope.com) and North America. Any attempt

 

at rewilding will likely introduce a novel species [16], where the extent of novelty can dramatically alter the impact on the rest of the community or ecosystem. We can think of examples of novel predators (e.g., the brown tree snake (*Boiga irregularis*) on Guam [17], the Nile perch (*Lates niloticus*) in Lake Victoria [18], the Burmese python (*Python bivittatus*) in south Florida [19]) and large herbivores (e.g., Canadian beaver (*Castor Canadensis*) in Tierra del Fuego [20] or reindeer (*Rangifer tarandus*) on South Georgia [21]) altering resident communities and ecosystems. Admittedly, those that were deliberately introduced (such as the Nile perch, beaver and reindeer) were not carefully considered or well thought out prior to introduction, and of course no proponent of rewilding would suggest introducing species such as these. But when Tule Elk were rewilded in California, complex and unpredictable changes occurred in the native and invasive plant communities [22].

Proponents of rewilding insist that any attempt at rewilding will be preceded by careful study of the potential consequences of the introduction. However, "carefully considered" and "well thought out" introductions of herbivores and predators can produce major unintended consequences. Indeed, advocates of rewilding should not assume ecologists and conservation biologists know more than we do about how dynamic, ever-evolving, idiosyncratic ecological systems once functioned, and they surely should not assume that we can predict the consequences of adding novel species. Likewise, when we predict resulting ecosystem impacts of rewilding, in reality we know little about the effects of natural or introduced diseases and pathogens when animals are introduced and how outbreaks can afflict introduced and native faunas. For example, after the species went extinct ca. 10,000 years ago, seven Eurasian bison were introduced in 2012 to a Danish forest without proper medical and deworming treatment. After the introduction three individuals died of liver parasites in 2015. Other surveys showed that the introduced bison had a rich worm fauna — a well-known health issue for bison — resembling that of the Bialowieza forest of Poland, the origin of the translocated animals [23].

**Figure 2. Pleistocene rewilding.**
The illustration by Mauricio Anton shows a landscape of southern France during the late Pleistocene. During this period a diverse biota of plants and animals, such as woolly mammoths, musk ox, bison and wild horses populated European landscapes. Pleistocene rewilding proposes to recreate these landscapes and resurrect the ecosystem functions that were lost following the extinction of large mammals and the impoverishment of ecological communities. Proponents of Pleistocene rewilding aim to reintroduce species that are long gone from our ecosystems or species that were never present but that might serve similar functions in ecosystems. However, this de-extinction of past ecosystem functions may bring future ecological surprises and unexpected negative results for native faunas and floras. Artwork: Mauricio Antón.

One could argue that if a rewilding attempt goes awry, then we could much more easily control a large predator or herbivore than a small insect. Indeed, this is true, but success would be far from guaranteed. The beaver species introduced to Tierra del Fuego has now spread to mainland South America, and is established despite a bilateral agreement between Argentina and Chile to extirpate it from the mainland [24]. Even where extirpation of an established mammal population is probably feasible, it often leads to opposition from animal rights groups or hunters. Thus, the Eastern gray squirrel (*Sciurus carolinensis*), spreading from an escape in Italy, was targeted for eradication by an Italian government agency, but the project was halted by a successful lawsuit by an animal rights group and the species has spread northward, nearing France [25].

Most of the issues we have raised concern Pleistocene rewilding and translocation rewilding, and to a lesser extent passive rewilding (e.g., by setting domesticated animals free as various breeds of cows and horses), given the reduced emphasis of the latter on reintroductions of species and its weaker connection to top-down control of ecosystems. However, passive rewilding faces challenges of its own and can lead to unforeseen consequences. For example, passive rewilding in mountain ecosystems can increase fire risk and reduce water availability. After 70 years of abandonment of many rural landscapes in Mediterranean European mountains, forests have increased and replaced croplands and shrubs in the lowlands and displaced alpine pastures in the highlands. This passive rewilding has resulted in an overall increase of water consumption by trees and consequently lower levels of stored water in reservoirs, severely reducing water availability to humans in these arid regions [26]. Again, we argue that the downstream effects of rewilding, whether Pleistocene, translocation or passive, can be surprising yet consequential.

**Table 1. Far-reaching consequences of rewilding.**

| Realm | Knowledge gaps and potential consequences | Recommendation |
|---|---|---|
| **Biological diversity** | Unexpected cascading effects and the uncertain re-wiring of ecological communities after rewilding under global change | More experimental research on species community changes after translocation across a variety of taxa and environments |
| | Local extirpations of native and protected species after re-introductions | Focus conservation efforts on protecting biological diversity and reduce main threats to ecosystem persistence (i.e., invasive species, overhunting, land use and climate changes) |
| **Biocontrol/ invasions** | The feasibility of controlling the spread of failed translocations | Develop plans to control as an integral part of on-going and upcoming rewilding projects |
| | Spread of pest, including parasites from re-introduced individuals, across native ecosystems | Avoid translocations into highly protected areas and fragile ecosystems. Minimize translocation of species into ecosystems where they were rare or never occurred |
| | | Assess before re-introduction the potential impacts on host–parasite relationships and host survival in a new targeted ecosystem for rewilding |
| **Economy** | Lack of cost–benefit analysis | Develop specific assessments of cost-benefit for current and future rewilding projects |
| | Reduction of conservation effectiveness in relation to the amount of funding invested | Develop comparative cost-benefit analysis across conservation approaches |
| **Societal conflicts** | Context-dependency of societal perceptions of wilderness and re-introductions | Assess societal perceptions and acceptance of rewilding across a variety of social-economic and environmental contexts |
| | Conflicts in the coexistence of wild animals and humans | Take advantage of on-going socio-economic trends (i.e, abandonment of rural regions) to minimize conflicts |
| **Ecosystem services** | The role of multi-functionality in ecosystems for providing key ecosystem services | Strengthen data-driven research on the relationships between biodiversity, ecosystem functions and services |
| | Negative feedbacks in key services (i.e, water availability for human consumption) due to their complex responses to changes in ecosystem functions | Prioritize conservation approaches (i.e, protecting biological diversity instead of functions) based on the amount of scientific knowledge by which they are supported and their degree of past successful implementation |

Conserving and enhancing ecosystem functions and services via rewilding opens five realms of unknown consequences across socio-economic and natural realms. Biological diversity: cascading effects and the uncertain re-wiring of ecological communities after rewilding. Biocontrol/ invasions: impacts and management of re-introduced species and spread of pests across native ecosystems. Ecosystem service losses: negative feedbacks in key services due to their complex responses to changes in ecosystem functions. Conflict with society: managing coexistence of wild animals and humans. Economy: lack of cost-benefit analysis.

## Far-reaching consequences of rewilding

We are not the first to point out that rewilding faces significant challenges. In fact, several proponents readily acknowledge some of the challenges [27,28], including the theoretical and ecological underpinnings of rewilding and the lack of cost-benefit analyses of rewilding plans. Moreover, the management outputs that rewilding aims to achieve lack quantitative evidence and the focus of rewilding on functions rather than on biological diversity is questionable. The relationship between biodiversity and the multiple functions ecosystems provide has rarely been assessed globally in natural ecosystems, and the few existing studies [29] show, for example, that the conservation of plant biodiversity is crucial to buffer negative effects of climate change. We suggest that focusing on protecting biological diversity instead of protecting or enhancing functions is a safer approach given the current state of ecological knowledge. Advocates of rewilding should carefully consider its potential for far-reaching consequences and engage in and support basic research that provides scenarios for future states of ecosystems after rewilding (Table 1). We are not suggesting that conservation biologists give up or sit by passively and let ecosystems degrade as species are lost or novel species arrive. Instead, we advocate proactive and aggressive restoration projects, well-planned eradication programs (e.g., eradication of goats in the Galapagos) and a better understanding of the effects of species reintroduction on biodiversity, functions and services of ecosystems in the context of intense land use and ongoing climate change. Finally, we advocate robust cost-benefit analysis, where the costs and benefits are both

 

socio-economic and ecological, before any attempt at rewilding. Resources are limited, so prioritizing resources in terms of labor and direct monetary cost for one approach always comes at a cost to other approaches to maintain and preserve biodiversity.

Pandora opened the box and released evils but also found Elpis, the spirit of hope. The threats facing biodiversity as we enter the sixth great mass extinction on the backs of the evils of overhunting, the spread of invasive species, continued habitat destruction, and ongoing climate change are numerous and will require hard work, vigilance, and creativity on the part of scientists, conservation practitioners and policy makers. Our hope is that the hard work is grounded in detailed ecological theory and offers clear conservation benefits to all of biodiversity and not just the opportunity to see large, wild beasts roaming the landscape.

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## Quick guide

# Tickling

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***Why do we laugh?*** Laughter is a symptom of a positive emotion experienced, for example, during play, and is important in both children and adults. We have known for decades that play — which is not confined to humans; see articles in 25th anniversary special issue of *Current Biology* on the Biology of Fun (volume *25*, issue 1) — contributes to children's social, emotional, and cognitive success (for example, Singer *et al.* 2006). Recent evolutionary theory suggests that positive emotions, such as those associated with laughter, have a number of benefits to the individual, such as fostering creativity and flexibility in thinking, increasing longevity, reducing the effects of health risks, and engendering increased likelihood of positive emotions in the future. Here we consider a particular kind of laughter-evoking play: tickling (Figure 1).

***What is a tickle?*** A tickle is a type of touch that makes you laugh, isn't it? Actually, the word tickle refers to two classes of cutaneous sensation (Seldon, 2004): *knismesis*, a light spidery sensation that evokes a shiver or a twitch; and *gargalesis*, "the exquisitely intense, often pleasurable sensation in response to hard, rhythmic probing" (Leavens, 2009). Lightly scratching a cat under its chin apparently evokes the knismesic-type of tickling pleasure, which in human adults can range from pleasurable (a lover blowing into your ear, for example) to startling (when you realise a spider is crawling across your skin, for example). It is the gargalesis-type of tickling, however, that elicits unrestrained laughter.

***Do other animals tickle?*** Many animals appear to share with our children the exquisite yet paradoxical delight in response to tickling, including rats (Panksepp and Burgdorff, 2003), cats, sharks, and notably, the great apes (Davila Ross *et al*., 2009). Cats will sometimes solicit tickling from their owners — rubbing their chins on one's hand, for example. But only great apes have been reported to regularly tickle others; indeed, one of