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# Reversing defaunation: Restoring species in a changing world

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However, we must also address the often nonlinear impacts of continued human population growth and increasingly uneven per capita consumption, which ultimately drive all these threats (while still fostering poverty alleviation efforts). Ultimately, both reduced and more evenly distributed global resource consumption will be necessary to sustainably change ongoing trends in defaunation and, hopefully, eventually open the door to refaunation. If unchecked, Anthropocene defaunation will become not only a characteristic of the planet's sixth mass extinction, but also a driver of fundamental global transformations in ecosystem functioning.

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### SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/345/6195/401/suppl/DC1
Materials and Methods
Figs. S1 to S6
Tables S1 to S3
References (*80–167*)

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REVIEW

# Reversing defaunation: Restoring species in a changing world

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**The rate of biodiversity loss is not slowing despite global commitments, and the depletion of animal species can reduce the stability of ecological communities. Despite this continued loss, some substantial progress in reversing defaunation is being achieved through the intentional movement of animals to restore populations. We review the full spectrum of conservation translocations, from reinforcement and reintroduction to controversial conservation introductions that seek to restore populations outside their indigenous range or to introduce ecological replacements for extinct forms. We place the popular, but misunderstood, concept of rewilding within this framework and consider the future role of new technical developments such as de-extinction.**

Recent analyses have shown that the rate of biodiversity loss has not slowed despite global commitments made through the 2002 Convention on Biological Diversity (*1*). Projected future extinction rates for terrestrial species might exceed current rates of extinction (*2*). A key component of biodiversity loss is defaunation, the loss or depletion of animal species from ecological communities (*3*, *4*). Such losses can reduce the stability of ecological communities (*5*), with cascading effects (*3*).

In situ conservation measures—including the creation and management of protected areas, increasing connectivity between wildlife populations, and reduction of the impacts of predation and hunting—can achieve some success where the amount of habitat remaining is sufficient for viable populations (*6*). Increasingly, however, more intensive forms of threatened species management are required to address local extinctions and impending threats to critical areas of habitat. Progress in reversing defaunation is emerging from conservation translocations—the intentional movement of animals to restore populations (*7*) (Fig. 1).

### Population restoration: Reintroduction and reinforcement

The intentional movement and release of animals has occurred for millennia, but the use of translocations to address conservation objectives is barely 100 years old (*8*). In recent decades, there has been an increase in the number of species that are the focus of conservation translocations to restore and enhance populations; for vertebrates alone, at least 124 species were translocated during 1900–1992, and this had risen to 199 species by 1998 and to 424 species by 2005 (*9*). Two types of translocation for population restoration are recognized: (i) reinforcements, involving the release of an organism into an existing population of conspecifics to enhance population viability, and (ii) reintroductions, where the intent is to reestablish a population in an area after local extinction (*7*) (Fig. 1). The critical feature of these translocations is the release of animals into their indigenous range, the known or inferred distribution derived from historical records or other evidence (*7*).

Previous work has shown that conservation translocation projects, as with other types of conservation management, show a marked taxonomic bias toward birds (33% of projects, whereas birds make up 18% of species represented in nature) and mammals (41% of projects versus 8% of species), particularly the larger, more charismatic species, almost irrespective of the degree of threat or vulnerability (*10*). Recent data on reinforcements show that this bias toward birds and mammals is continuing (*11*). For conservation translocations in general, relatively few invertebrate, reptile, amphibian, or fish species are represented relative to their prevalence in nature (Fig. 2). The global distribution of species' translocations suggests a geographic bias also, with most activity in developed regions (Fig. 2).

The ultimate objective of any reintroduction is the establishment of a self-sustaining population and, using this definition, reviews of reintroduction outcomes have indicated generally low success rates (*12*), as low as 23% (*13*). Concern over high failure rates prompted analyses of the factors associated with translocation success. In 1989, the first comprehensive review looked at the reintroduction and reinforcement of 93 species of native birds and mammals (*12*). This data set was updated, and 181 mammal and bird programs were reanalyzed in 1998 (*14*). Both studies identified habitat quality at the release site, release into the core of a species range, and total numbers released as determinants of success (*12*, *14*). An independent analysis of a broader taxonomic range of animal translocations over 20 years highlighted the greater likelihood of success associated with the release of wild versus captive animals and confirmed the importance of larger founder group sizes (*13*).

Reintroduced populations go through a period of relatively small population size where the risks of inbreeding and loss of genetic variation is high; the challenge, therefore, is to minimize loss of genetic variation by creating large effective population sizes (*15*). The key determinants of the genetic diversity retained in a reintroduction will be the total number of founders and the proportion contributing genetically to the next generations (*16*). Thus, even when a large population results, there might be considerable loss of genetic diversity during the early stages of population establishment (*17*), and the number of founders necessary for preservation of genetic diversity might be substantially greater than that required for population establishment and growth (*18*). Low initial population sizes might also make reintroduced populations vulnerable to Allee effects, which might have contributed to past reintroduction failures, although this link has not been shown (*19*). Reinforcement of existing populations can increase population size, prevent Allee effects, and increase genetic diversity, but also carries a risk of loss of local adaptation and the introduction of pathogens, particularly from captive breeding programs (*11*).

Simple classification of any reintroduction as success or failure to result in a self-sustaining population is of limited use because the time scale for success evaluation is important, and there are examples of successful projects failing at a later stage (*13*). The International Union for Conservation of Nature (IUCN) guidelines advocate that projects make clear definitions of success in relation to three phases of any reintroduction: establishment, growth, and regulation, with future population persistence assessed through population viability analysis (*7*). Assessment of success or of the causes of failure can be made only through adequate postrelease monitoring (*20*). Monitoring is needed also to facilitate meta-analyses (*13*), to track genetic diversity (*16*), and to evaluate the performance of reintroduced populations and the possible impacts on recipient ecosystems (*21*).

### Conservation introductions

Perhaps the greatest challenge facing practitioners of species or ecosystem restoration is the definition of a target state (*22*). Attempts to return a system to some historical condition make somewhat arbitrary decisions about how far back in time to go. Historical restoration reference states vary according to the history of human occupation, with pre-European settlement conditions often held up as the baseline (*23*). However, a desire to return to some past state makes some assumptions, including the implication that near-pristine conditions existed in pre-European times and that historical restoration targets will be sustainable with changing climate (*22*). It is now recognized that past species distributions do not indicate current suitability and that current species' distribution does not guarantee future suitability (*24*). Climate change, in tandem with human-facilitated species invasions and land transformation, contribute to the creation of novel ecosystems: systems that differ in composition and function from past systems (*25*).

If we acknowledge that restoration and maintenance of species within their indigenous ranges will remain a foundation of conservation efforts, the realization that a return to a completely natural world is not achievable frees us to think about more radical types of conservation translocation. Conservation introductions involve the movement and release of an organism outside its indigenous range (*7*). Two types of conservation introduction are recognized by the IUCN: assisted colonization and ecological replacement (Fig. 1).

### Assisted colonization

In 1985, Peters and Darling (*26*) suggested that climate change might alter habitat suitability for species confined within protected areas, effectively stranding them in increasingly unsuitable sites. They proposed the translocation of individuals into new reserves encompassing habitat that was or would become appropriate. Possibly because of the low profile of global climate change, the unreliability of early predictive models of climate, and the radical nature of the proposal, the idea of proactive translocation initially gained little traction (*27*). However, there is growing acknowledgment that conservation managers could take action to address climate-induced changes in species' habitats where individuals of affected species are unable to naturally colonize new areas as habitat suitability shifts (*28*–*30*). Understandably, given the devastating ecological impact wrought by invasive species, assisted colonization has been greeted with extreme skepticism, which has promoted a vigorous debate in the literature (*31*, *32*). The 2013 IUCN guidelines define assisted colonization in broad terms as the intentional movement of an organism outside its indigenous range to avoid extinction of populations due to current or future threats (*7*). Under this definition, far from being a radical new translocation approach, assisted colonization is already being applied as a conservation tool in Australasia to protect, on predator-free islands, populations of species, such as the kakapo

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(*Strigops habroptilus*), threatened by predation from exotic mammalian predators in mainland habitat (*24*). The creation of a disease-free population of Tasmanian devils (*Sarcophilus harrisii*) outside the species' indigenous range in Tasmania (*33*) also fits this definition.

The 2013 IUCN guidelines place great emphasis on feasibility and risk analysis as essential components of any conservation translocation. Given the uncertainties involved in moving species outside their range, assisted colonization is inherently more risky than "traditional" translocations such as reintroductions. New approaches for understanding and managing risk under uncertainty are being applied to conservation introduction planning, including quantitative risk analysis (*34*), active adaptive management (*35*), and structured decision-making (*36*). Where protection from threats in the indigenous range is unfeasible and where appropriate habitat can be identified elsewhere, application of carefully planned assisted colonizations might become more acceptable (*37*).

A critical aspect in planning for assisted colonization is selection of suitable release sites that match the biotic and abiotic needs of the focal species (*7*) under future climate scenarios. Climate-envelope models have been used to determine species' future habitat suitability to guide some of the first experimental assisted colonizations of two butterfly species to sites ~35 and ~65 km beyond their indigenous range in northern England (*38*). But static bioclimatic envelope models might not adequately account for species' ability to disperse or for changing demographic processes as habitat quality shifts. More complex integrative climate suitability models will be required (*39*), although these too can never be perfect predictors of complex environments. Improved approaches to predict future habitat suitability explicitly integrate species distribution data with population dynamics or physiology. For example, stochastic population modeling combined with habitat suitability models predict how the vital rates of hihi (*Notiomystis cincta*), a New Zealand endemic passerine, could be influenced by climate change, with at least two populations potentially at risk of extinction (*40*). Ecoenergetic and hydrological models were integrated to evaluate the long-term suitability of habitat for the Western swamp tortoise (*Psuedemydura umbrina*) and extended to identify new regions that would meet the tortoise's thermodynamic requirements under a range of warmer and drier climates predicted by 2030 (*41*). Future developments around assisted colonization planning will include the

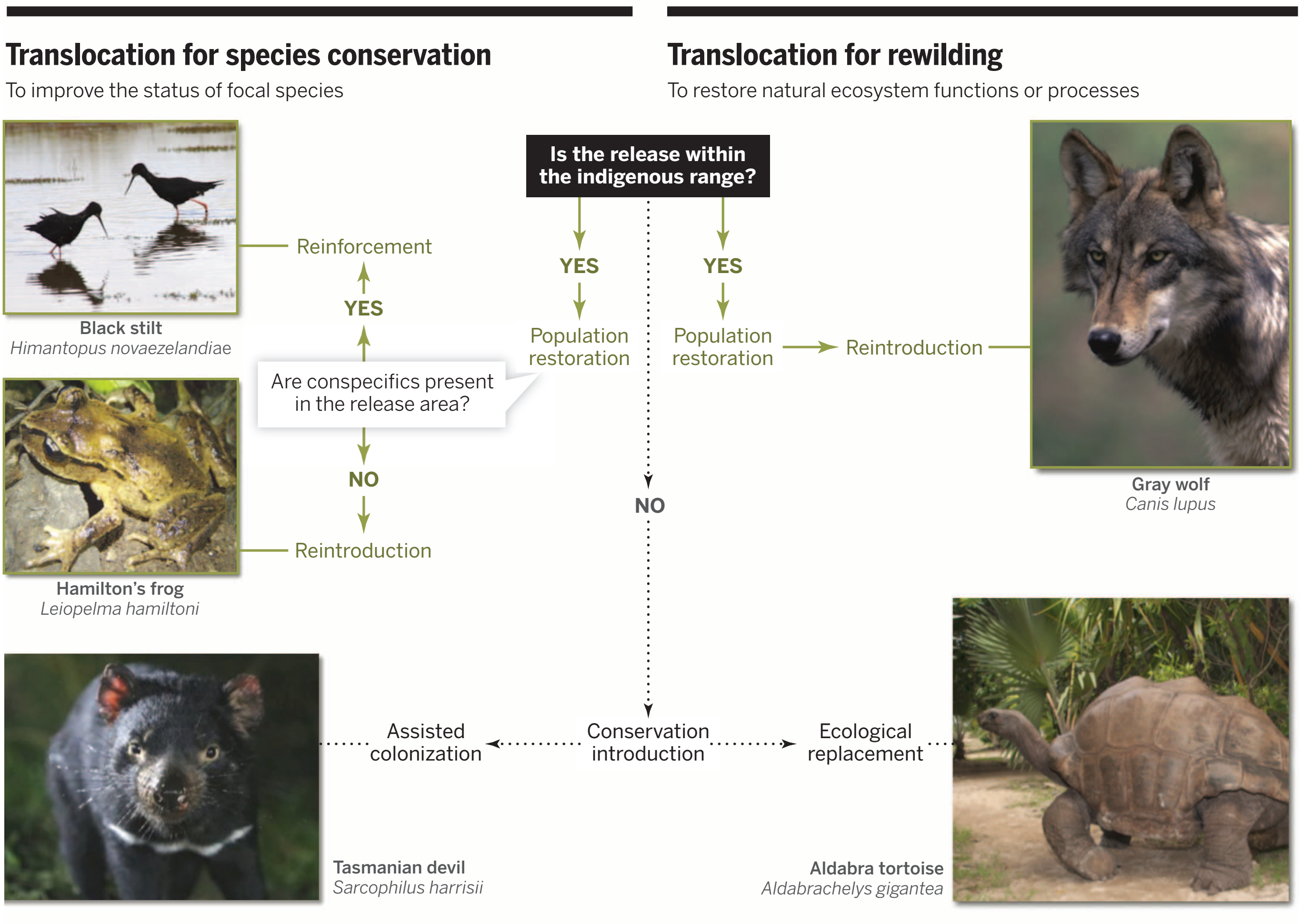


**Fig. 1. The conservation translocation spectrum [based on (*7*)].** Translocations with the primary objective of improving the status of the focal species are a species conservation tool, and releases can take place inside or outside the indigenous range. Releases inside the indigenous range may be for reinforcements, as illustrated by the black stilt (*68*), or reintroductions, for example, of amphibians, such as Hamilton's frog (*69*). Releases outside the indigenous range for species conservation are assisted colonizations, e.g., Tasmanian devil (*33*). Translocations with the primary objective of restoring ecosystem functions are a component of rewilding and may include reintroductions, e.g., gray wolf (*46*). Rewilding releases outside the indigenous range might be justified if an ecological function has been lost due to extinction, e.g., dispersal of large-seeded plants by giant tortoises (*70*). Releases may have both objectives, but these should be explicitly stated as each will require specific targets and outcome monitoring. [Photo credits: black stilt (P. Guilford), Hamilton's frog (P. Bishop), Tasmanian devil (G. King), gray wolf (B. Quayle), Aldabra giant tortoise (M. Whittaker)]

application of fully integrated models that combine climatic suitability, habitat availability, population dynamics, and mechanistic movement models of dispersal (*39*, *42*). These may involve a single species or two or more interacting species.

## Ecological replacements

Biodiversity can increase ecosystem stability by buffering the effects of environmental change, resisting species invasions, and preventing secondary extinctions after species losses (*43*). Species extinctions reduce interaction network diversity (*44*) and can lead to cascading effects, including the loss of other species and their biotic interactions (*45*). Where only local extinction occurs, critical ecosystem functions might be reinstated through reintroductions; for example, the reintroduction of wolves into Yellowstone National Park in 1995–1996 restored direct effects on their prey and a range of indirect effects (*46*). The global extinction of a species, however, means that restoration of functions might be achieved only through introduction of functionally similar exotic species.

The 2013 IUCN guidelines define ecological replacement as a form of conservation introduction involving the release of an appropriate substitute species to reestablish an ecological function lost through extinction. Although the rationale for ecological replacement is different from that of assisted colonization, the two terms have often been used interchangeably in the literature [e.g., (*47*)]. Although, in some situations, an assisted colonization to prevent extinction of the focal species could serve in parallel to restore an ecosystem function outside the indigenous range (*47*), in many cases, the most appropriate ecological replacements might not be endangered species. Recognition of ecological replacement as a valid conservation tool represents a departure from the single-species focus that once characterized conservation translocations and conforms more closely to the current global conservation emphasis on restoring natural processes rather than addressing only extinction risk (*48*).

There has been interest in the replacement of ecological functions once performed by extinct

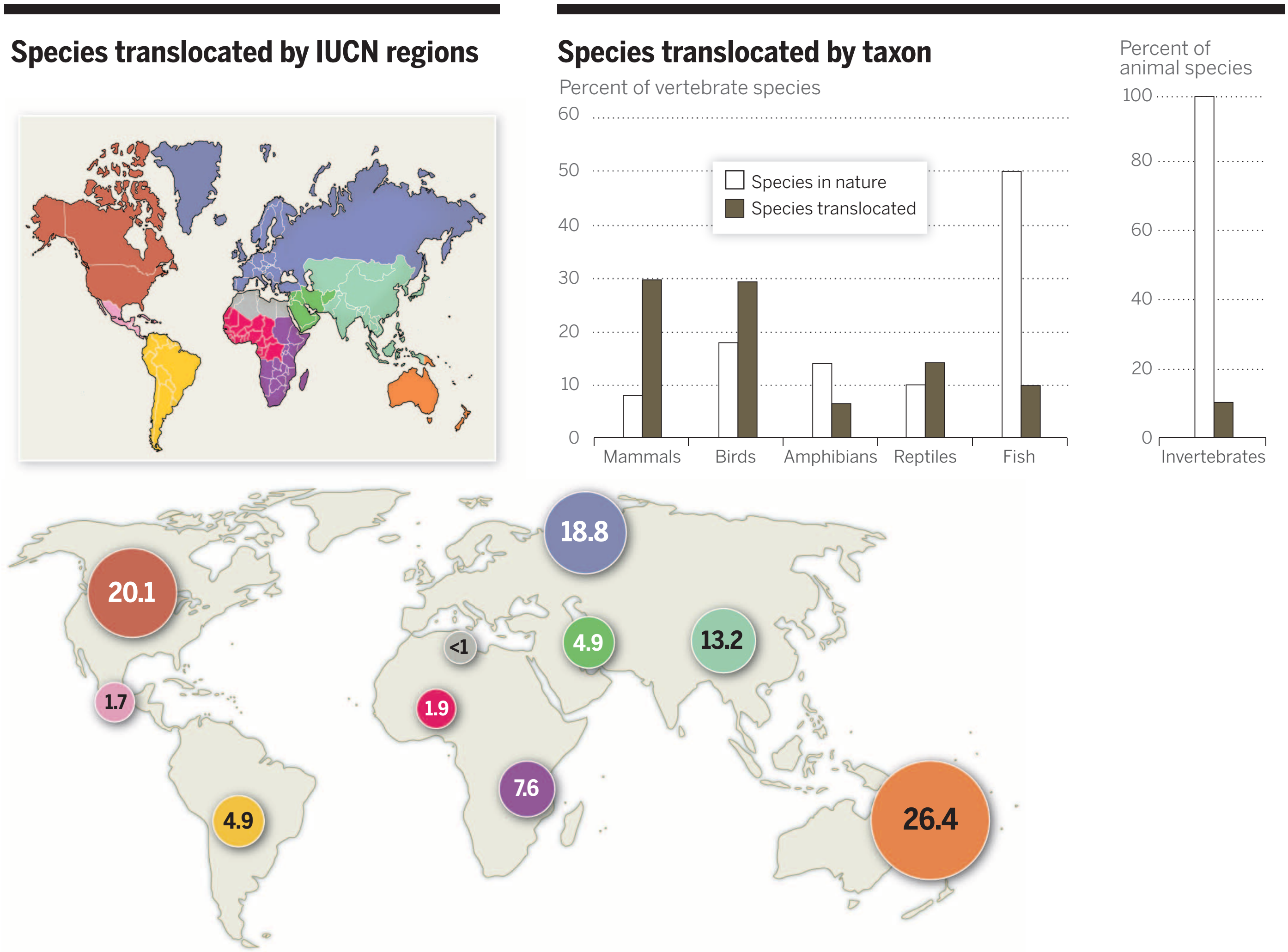


**Fig. 2. Global and taxonomic range of conservation translocations.** The proportions of 303 species that have been translocated for conservation purposes, by IUCN region (main map—the larger the circle the greater the proportion of species), and by taxon (inset bar chart: shaded bars are proportions of species translocated out of the total of 303; unshaded bars are proportions of species in nature. Because invertebrate species are estimated to be >99% of all animal species in nature, for clarity, the relative proportion of invertebrates in nature and the proportion of invertebrate species that have been translocated out of the total of 303 animal species are presented on the right; the proportions relative to vertebrate species only are on the left. [Data from (*10*).] The color inset map shows the 10 IUCN regions; west to east, these are North America and Caribbean, Meso-America, South America, North Africa, Central and West Africa, East and Southern Africa, West Asia and the Middle East, Europe and the Mediterranean, Asia, and Oceania (source iucn.org). Data on the 303 species was derived from downloadable project summaries available at iucnsscrsg.org. Base map source: commons.wikimedia.org

megafauna, because they would have had large ecosystem impacts in relation to their abundance (*49*, *50*). The megafaunal concept must, however, be viewed as context-dependent, because in island ecosystems, the largest native frugivore may be an order of magnitude lighter than those in continental systems, yet loss of large island frugivores can result in more sizable cascading effects owing to the lower functional redundancy on islands (*51*). The most important application of ecological replacements to date has been in the restoration of herbivory and seed dispersal functions in island ecosystems. Extinction of large frugivores can disrupt seed dispersal, interrupt recruitment, and reduce genetic variation of large-seeded fleshy-fruited plants (*52*); it can also drive rapid evolutionary reduction in seed size, affecting seed survival (*45*). There is evidence of the ecosystem-engineering role of giant tortoises, as tortoises are important dispersers of large-seeded plants, and their grazing and trampling is critical for creating and maintaining some vegetation communities (*53*). To restore grazing functions and the seed dispersal of native large-seeded plants, exotic Aldabra giant tortoises (*Aldabrachelys gigantea*) have been introduced to Mauritian offshore islands to replace the extinct Mauritian *Cylindraspis* species (*54*, *55*) (Fig. 3). Not only has seed dispersal resumed, but passage through the tortoise gut also improves seed germination success (*55*). Further projects are planned or under way to use ecologically similar species of giant tortoise to reinstate processes lost with the extinction of endemic giant tortoises in the islands of Madagascar, the Galapagos, the Mascarenes, the Seychelles, and the Caribbean (*56*).

The future challenge is the identification of suitable replacements to perform the desired ecosystem functions within a given system. The longer the time since the extinction of the original form, the greater the uncertainty about the best substitute. The best replacements might not be closely related taxa. If and when risk and uncertainty are adequately evaluated, radical substitutions could be considered, such as the use of tortoises as replacements for moa-nalo, a group of extinct gooselike ducks, in Hawaii (*57*). The focus must be more on reinstatement of functions and processes to restore degraded ecosystems (*58*) and to enhance ecosystem resilience, rather than on restoration to some arbitrary historical state. For any conservation introduction, the risk of unintended effects must be evaluated and weighed against the expected benefits (*7*). The greatest progress will come from carefully designed experimental substitutions using species that can be readily monitored and managed (*58*) and easily removed should the manifestation of unwanted effects reach some predetermined threshold.

## Rewilding

In 1998, the concept of "rewilding" was proposed as a "fourth current in the modern conservation movement" that would complement the protection of representative biotic elements (*59*). The original concept of rewilding was built around the keystone role played by wide-ranging, large animals—particularly carnivores—able to maintain ecosystem structure, resilience, and diversity through top-down trophic interactions (*46*, *59*). Rewilding would entail restoration of "big wilderness" through the creation and management of large, strict, core protected areas, enhanced connectivity between core reserves, and critically, the restoration of keystone species (*59*). The term rewilding is going through a surge in popularity in the media, but its original meaning is often misinterpreted or lost. Rewilding has been widely and variously misused to mean: (i) the reintroduction of any recently extirpated species; (ii) the rehabilitation of ecosystems through reintroductions; (iii) the return of an ecosystem to a prehuman state; or (iv) the release of non-native, rather than native, species. The increased

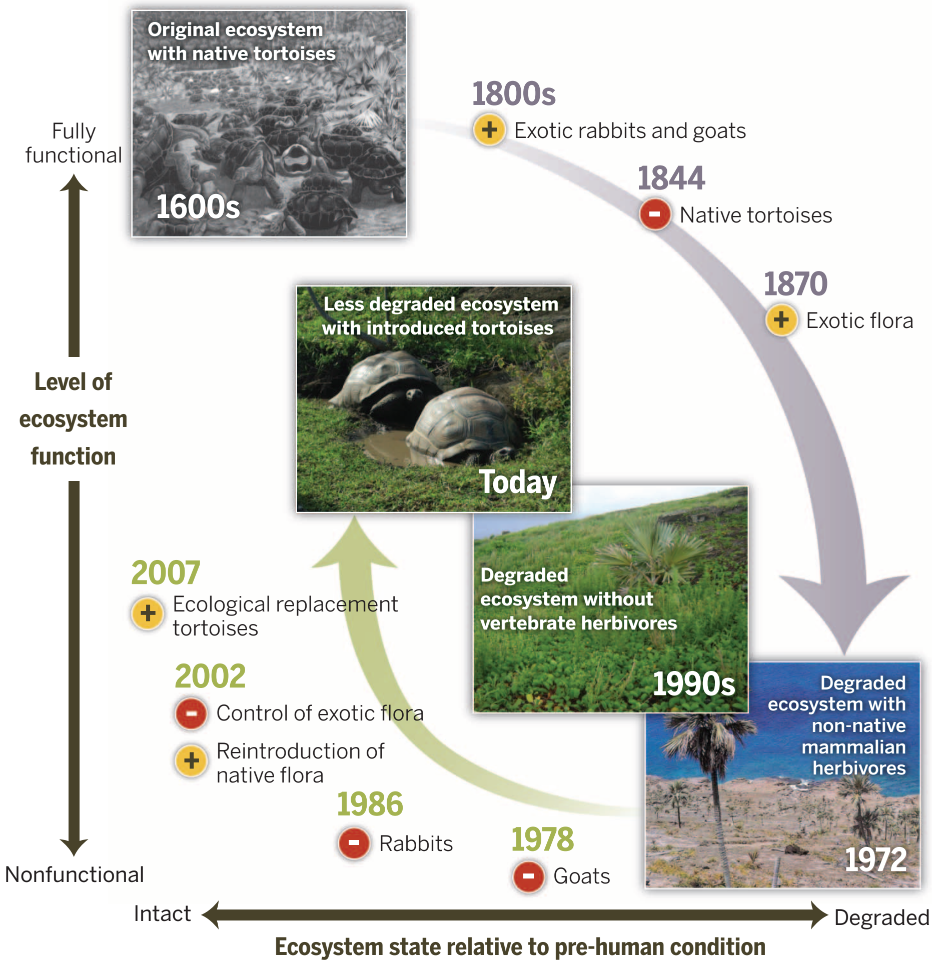


**Fig. 3. Rebuilding ecosystems by removing invasive species and introducing ecological replacements.** The extinction (–) of keystone ecosystem engineers, such as the Mauritian giant tortoises (*Cylindraspis* species), and the addition (+) of non-native mammalian herbivores and invasive plants degraded (gray arrow) Round Island's ecosystem. The restoration phase (green arrow) first entailed the eradication of goats and rabbits. Without vertebrate herbivory, exotic vegetation flourished, suppressing native plants adapted to tortoises' grazing pressure. Restoration efforts then focused on weeding invasive flora and rebuilding the native plant community, although weeding was costly and limited in spatial area. A long-term, more cost-effective solution sought to restore the grazing and seed dispersal functions once performed by the giant tortoises. In 2007, a small population of Aldabra giant tortoises was introduced as part of a reversible experiment to restore and increase ecosystem resilience (68). Tortoises are preferentially grazing the fast-growing exotic plants and avoiding much of the native vegetation believed to have evolved to withstand the high density of Mauritian giant tortoises. [Image credits: Giant tortoise 1600s (J. P. Hulme), giant tortoises today (Z. Ahamud), 1990s (C. Griffiths), 1972 (C. Jouanin)]

use and misuse of the term rewilding has been perhaps due to controversy around the proposed introduction of megafauna to North America to replace species lost 13,000 years ago (*60*). Pleistocene rewilding is at its core true to the original concept of rewilding, as it recognizes the important ecosystem-shaping role of large vertebrates, but made a major departure by arguing for the ecological replacement of long-extinct species. The radical nature of the Pleistocene rewilding concept spawned other, similarly controversial suggestions—such as the introduction of elephants to Australia to control invasive plants (*61*)—but also usefully reenergized the debate on ecological replacements as a valid conservation tool.

Where does this leave rewilding as a concept? The most valuable redefinition of rewilding replaces the "keystone species restoration" component with "species reintroduction to restore ecosystem functioning" (*50*). More broadly though, the restoration of ecosystem function could also involve the introduction of ecological replacements (*50*). This harmonizes rewilding with the current conservation translocation framework (Fig. 1). There is a distinction between translocation for species conservation—where the primary objective is to improve the status of the focal species through reinforcement, reintroduction, or assisted colonization—and translocation for rewilding—where the objective is to restore natural ecosystem functions or processes. Translocation for rewilding could entail population restoration through reintroduction, where releases occur in the indigenous range with the primary aim of restoring some ecological function. A rewilding translocation could also take the form of a conservation introduction through ecological replacement using suitable substitute species.

In its original form, rewilding was seen as a way to restore wilderness, the implication being that there would be large areas of land where human influence was minimal and ongoing management interventions unnecessary. The restoration of keystone species would facilitate the recovery of other "habitat-creating" species and the recovery of natural disturbance regimes (*59*). Oostvaardersplassen (OVP) is a 6000-ha state-owned polder 40 km north of Amsterdam, Netherlands. In the 1980s, the ecologist Frans Vera began to recreate an ecosystem shaped by grazing of large ungulates (*62*), unregulated by large predators. Red deer (*Cervus elaphus*) were released, along with back-bred Konik horses (*Equus ferus caballus*), and the domestic descendants of the Auroch, Heck cattle, as replacements for extinct Auroch (*Bos primigenius*) and Tarpan (*Equs przewalski gmelini*). Rather than seeking the preservation or restoration of indigenous biodiversity, OVP is one manifestation of a European vision of rewilding, as the restoration of ecological processes to create untamed landscapes reminiscent of ecological conditions at the end of the Pleistocene (*63*). The challenge is uncertainty over the emergent properties and climax equilibrium vegetation of the area, but the emphasis is on minimizing human interventions.

However, restoration that aspires to exclude human influence and activity has been challenged as being unobtainable or unsustainable. The positive average annual population growth rates for the larger carnivores, the golden jackal (*Canis aureus*), gray wolf (*Canis lupus*), Eurasian lynx (*Lynx lynx*), Iberian lynx (*Lynx pardinus*), and wolverine (*Gulo gulo*), in Europe between 1961 and 2005 (*64*), for example, has shifted emphasis away from preventing extinctions and prompted thinking toward future planning under a new model of coexistence between predators and humans over large spatial scales (*65*). This reshaping of rewilding acknowledges that humans are an integral part of, not apart from, nature and recasts the retrospective goals of restoring "wilderness" as future-oriented visions of creating "wildness" in which ecological processes, such as predator-prey interactions, are managed within landscapes shared by humans and wildlife (*65*).

## Future prospects and implications

With official IUCN recognition of a spectrum of conservation translocation tools, the emphasis has now shifted to how best to apply these approaches to maximize conservation benefit while minimizing the risk of unintended consequences. Particularly for the inherently more uncertain conservation introductions, the focus needs to be on development and application of rigorous methods to match species to habitats while evaluating risk. The IUCN guidelines (*7*) provide a framework for dealing with the complexities of conservation translocations and are sufficiently comprehensive to be able to accommodate new developments. The prospect of species de-extinction, the resurrection of extinct species using selective breeding or the clonal technologies of synthetic biology potentially broadens the range of species and associated processes we might seek to restore. De-extinction of multiple species will occur at some future time, but one question that must be addressed is which species? Because the goals of de-extinction relate to ecological enrichment, selection of de-extinction candidates should be guided by the feasibility and risks of their release into suitable habitat (*66*).

Daniel Pauly (*67*) called attention to "shifting baselines" in fisheries—a concept extended to encompass the gradual attrition in people's expectations of what the natural world around them should look like, whereby each generation grows up within a slightly more impoverished natural biodiversity. Defaunation is a major contributing factor to this extinction of experience. Translocations for the restoration of populations of threatened species, for reestablishment of ecological functions and processes, and for the re-creation of wildness provide a foundation for resetting public aspirations for biodiversity. Conservation translocation projects provide a powerful means to reconnect people with their natural heritage, to engage them as conservation partners, and to make them stewards of the wild animals and habitats around them.

Part of this reconnection with nature will entail a new appreciation of the concept of wild, moving away from increasingly unobtainable concepts of self-sustaining wildlife populations within pristine landscapes untouched by human influence. We are moving instead toward understanding the value of restoring and sustaining species and their habitats, possibly in novel configurations, with ongoing management, and with the needs of humans both acknowledged and integrated.

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