REVIEW SUMMARY

REWILDING

Rewilding complex ecosystems

Andrea Perino*, Henrique M. Pereira*, Laetitia M. Navarro, Néstor Fernández, James M. Bullock, Silvia Ceauşu, Ainara Cortés-Avizanda, Roel van Klink, Tobias Kuemmerle, Angela Lomba, Guy Pe'er, Tobias Plieninger, José M. Rey Benayas, Christopher J. Sandom, Jens-Christian Svenning, Helen C. Wheeler

BACKGROUND: Rapid global change is creating fundamental challenges for the persistence of natural ecosystems and their biodiversity. Conservation efforts aimed at the protection of landscapes have had mixed success, and there is an increasing awareness that the long-term protection of biodiversity requires inclusion of flexible restoration along with protection. Rewilding is one such approach that has been both promoted and criticized in recent years. Proponents emphasize the potential of rewilding to tap opportunities for restoration while creating benefits for both ecosystems and societies. Critics discuss the lack of a consistent definition of rewilding and insufficient knowledge about its potential outcomes. Other criticisms arise from the mistaken notion that rewilding actions are planned without considering societal acceptability and benefits. Here, we present a framework for rewilding actions that can serve as a guideline for researchers and managers. The framework is applicable to a variety of rewilding approaches, ranging from passive to trophic rewilding, and aims to promote beneficial interactions between society and nature.

ADVANCES: The concept of rewilding has evolved from its initial emphasis on protecting large, connected areas for large carnivore conservation to a process-oriented, dynamic approach. On the basis of concepts from resilience and complexity theory of social-ecological systems, we identify trophic complexity, stochastic disturbances, and dispersal as three critical components of natural ecosystem dynamics. We propose that the restoration of these processes, and their interactions, can lead to increased self-sustainability of ecosystems and should be at the core of rewilding actions. Building on these concepts, we develop a framework to design and evaluate rewilding plans. Alongside ecological restoration goals, our framework emphasizes people's perceptions and experiences of wildness and the regulating and material contributions from restoring nature. These societal aspects are important outcomes and may be critical factors for the success of rewilding initiatives (see the figure). We further identify current societal constraints on rewilding and suggest actions to mitigate them.

OUTLOOK: The concept of rewilding challenges us to rethink the way we manage nature and to broaden our vision about how nature will respond to changes that society brings, both intentionally and unintentionally. The effects of rewilding actions will be specific to each ecosystem, and thus a deep understanding of the processes that shape ecosystems is critical to anticipate these effects and to take appropriate management actions. In addition, the decision of whether a rewilding approach is desirable should consider stakeholders' needs and expectations. To this end, structured restoration planning—based on participatory processes involving researchers, managers, and stakeholders—that includes monitoring and adaptive management can be used. With the recent designation of 2021–2030 as the "decade of ecosystem restoration" by the United Nations General Assembly, policy- and decision-makers could push rewilding topics to the forefront of discussions about how to reach post-2020 biodiversity goals. ■

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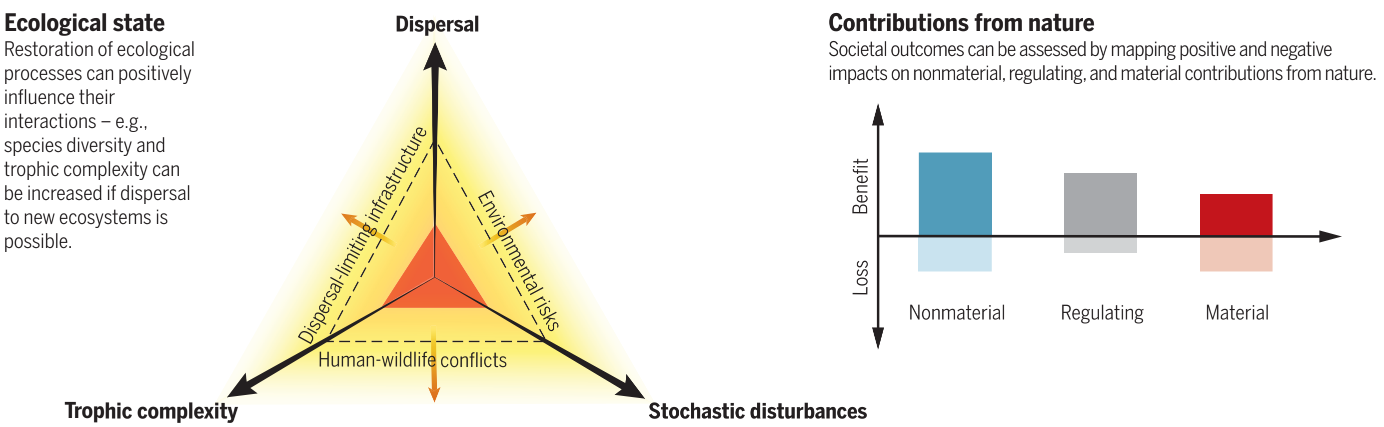

Rewilding actions and outcomes are framed by societal and ecological context. Rewilding can be assessed by representing the state of ecosystems in a three-dimensional space where each dimension corresponds to an ecological process. The difference in volume between the restored (yellow pyramid) and the degraded ecosystem (orange pyramid) is a proxy for the effects of rewilding on the self-sustainability of the ecosystem. The dashed line within the yellow pyramid represents the societal boundaries that determine to what extent ecological processes can be restored. Rewilding actions can help push societal boundaries toward the ecological potential (orange arrows) by promoting societal support and opportunities for people to experience the autonomy of ecological processes in enjoyable ways.

REVIEW

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Andrea Perino[1,2]*, Henrique M. Pereira[1,2,3]*, Laetitia M. Navarro[1,2], Néstor Fernández[1,2], James M. Bullock[4], Silvia Ceauşu[5,6], Ainara Cortés-Avizanda[3,7,8], Roel van Klink[1], Tobias Kuemmerle[9], Angela Lomba[3], Guy Pe'er[1,10], Tobias Plieninger[11,12], José M. Rey Benayas[13], Christopher J. Sandom[14], Jens-Christian Svenning[5,6], Helen C. Wheeler[15,16,17,18]

The practice of rewilding has been both promoted and criticized in recent years. Benefits include flexibility to react to environmental change and the promotion of opportunities for society to reconnect with nature. Criticisms include the lack of a clear conceptualization of rewilding, insufficient knowledge about possible outcomes, and the perception that rewilding excludes people from landscapes. Here, we present a framework for rewilding that addresses these concerns. We suggest that rewilding efforts should target trophic complexity, natural disturbances, and dispersal as interacting processes that can improve ecosystem resilience and maintain biodiversity. We propose a structured approach to rewilding projects that includes assessment of the contributions of nature to people and the social-ecological constraints on restoration.

Shifting societal and environmental conditions, including land-use change and increasing demand for resources, are accelerating biodiversity loss and ecosystem degradation (*1*–*4*). The associated loss of many important ecological processes (*5*, *6*) can decrease the complexity and resilience of ecosystems by hampering their capacity to recover from perturbations (*7*–*9*). Although responses to the biodiversity crisis—especially the establishment of protected areas—have reduced biodiversity loss in some instances (*10*–*12*), reports of ineffective protected areas (*13*) and ongoing declines of threatened species (*14*) indicate that conservation strategies must go beyond current efforts (*15*, *16*).

A growing body of literature emphasizes the need for novel, process-oriented approaches to restoring ecosystems in our rapidly changing world (*4*, *17*–*19*). Dynamic and process-oriented approaches focus on the adaptive capacity of ecosystems (*4*) and the restoration of ecosystem processes promoting biodiversity, rather than aiming to maintain or restore particular ecosystem states characterized by predefined species compositions or particular bundles of ecosystem services. Such approaches recognize ecosystems as dynamic systems (*20*) whose future development cannot always be predicted (*21*, *22*).

Rewilding is one such approach to restoration. This strategy aims to restore self-sustaining and complex ecosystems, with interlinked ecological processes that promote and support one another while minimizing or gradually reducing human interventions (*23*–*25*). Rewilding also emphasizes the emotional experience and perception of wild nature and wild ecosystems without human intervention (*26*). Although conventional restoration projects often aim to minimize human intervention, many scientists and practitioners consider some level of management as critical to replace ecosystem processes that have been lost because of human activities or to maintain important aspects of cultural landscapes (*27*). Such management often focuses on selected processes via precisely defined actions targeting concrete goals [e.g., management of Satoyama landscapes in Japan (*28*)]. Rewilding, on the contrary, recognizes and works with complexity and autonomy as ecosystem-inherent characteristics and acknowledges their dynamic, unpredictable nature (*29*).

Despite the potential for rewilding to address pressing restoration challenges, critics have pointed out several shortcomings that have as yet hampered the application of rewilding principles. Criticism includes a lack of a consistent definition of rewilding (*30*) and insufficient knowledge about the possible outcomes of rewilding endeavors (*31*). In addition, concerns have been raised about rewilding activities being planned in a manner that excludes people from landscapes rather than being designed with local support (*32*).

Here, we articulate a conceptual framework for rewilding projects that addresses the aforementioned criticisms. We start by briefly reviewing the history of the rewilding concept, from its initial emphasis on protecting large connected areas for carnivore conservation (*33*) to the diversity of rewilding concepts today (*25*). We propose a framework to design and evaluate rewilding plans that integrates the current variety of rewilding approaches. Our framework draws on ecological theory to identify three interacting ecological processes that promote the self-organization of ecosystems and, therefore, should be the focus of rewilding actions. For each of these processes, we review ecological knowledge and identify rewilding actions that can assist the restoration of self-sustaining, resilient ecosystems (Fig. 1). Notably, these actions will vary depending on the societal context. Rewilding can occur spontaneously if humans withdraw from landscapes—for example, after agricultural abandonment (*34*–*36*) or in areas that have become inhospitable as a result of armed conflict (*37*–*39*) or environmental catastrophes such as the Chernobyl disaster (*40*, *41*). In other cases, rewilding projects are driven by active choices about how societies want to experience nature (*42*) and the extent to which they can accept an autonomy of natural processes. In these cases, the feasibility of rewilding projects also depends on material, nonmaterial, and regulating contributions from nature (Fig. 2). We discuss how rewilding projects need to account for social-ecological dynamics by addressing people's preferences as well as human effects on ecosystems. Finally, we apply our framework to a set of ongoing rewilding projects and illustrate how interactions among the key processes can be promoted to increase both ecosystem resilience and societal benefits.

A brief history of the rewilding concept

Rewilding, as it was originally conceived 20 years ago (*33*), referred to "the scientific argument for restoring big wilderness based on the regulatory roles of large predators" (*33*) that could act as keystone species and maintain the resilience and diversity of terrestrial ecosystems through top-down control (*33*, *43*). The protection and restoration of "large, strictly protected core reserves,

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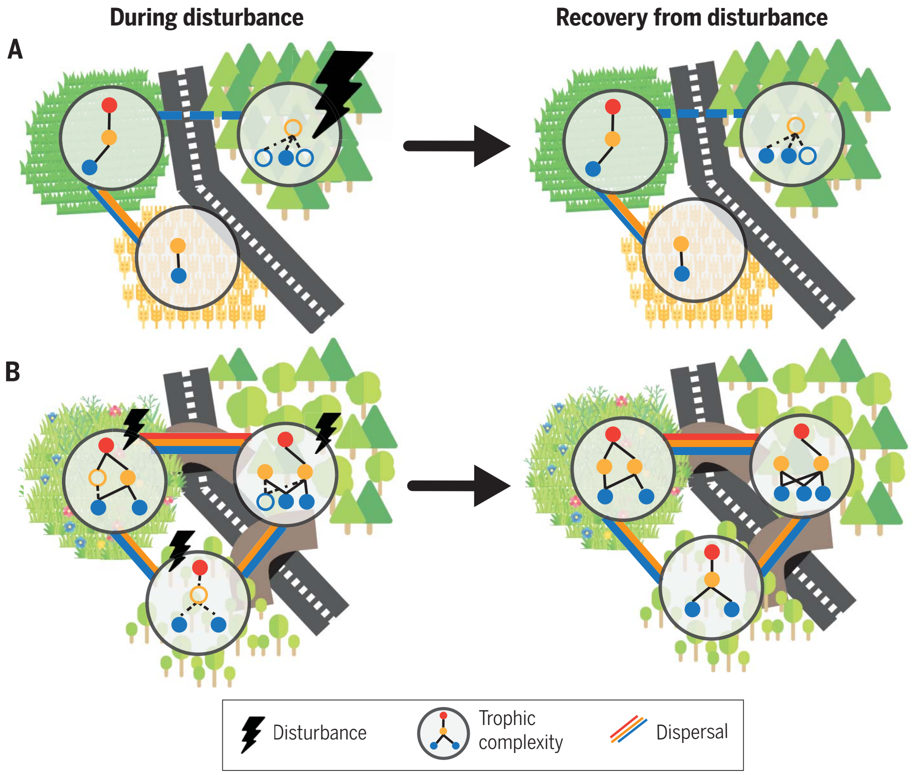

Fig. 1. Promoting interactions among ecosystem processes enhances resilience of rewilding areas. (**A**) Intensively managed areas are often characterized by decreased trophic complexity. Dispersal barriers between ecosystems impede the movement of individuals, particularly at higher trophic levels. Natural disturbances are often suppressed or altered in magnitude and frequency, potentially leading to even larger disturbance events. Impoverished trophic networks, dispersal barriers, and deterministic disturbances can hamper recovery of depressed populations (open nodes in the trophic webs) after major disturbance events. (**B**) Rewilded areas have restored complex trophic webs, with functional roles for top predators (red nodes), herbivores (yellow nodes), and primary producers (blue nodes). Improved connectivity among habitats allows for dispersal of species at all trophic levels. Frequent disturbance events occur in the landscape. Dispersal among habitats aids recovery of ecosystems after disturbance events by allowing recolonization and population recovery of affected species. Large vertebrates in complex ecosystems often act as dispersal agents for plants and can introduce stochasticity into a system, e.g., through predation or grazing.

connectivity and keystone species" (33) were the central characteristics of this first definition of rewilding. Although the conservation of large carnivores and their habitats is still an important aspect of rewilding (25, 44), the concept has evolved from this original idea to include a range of diverse approaches (25). Trophic rewilding, perhaps the closest to the original concept, advocates the reintroduction of missing keystone species, such as large carnivores and large herbivores. Trophic rewilding often promotes the use of functional replacements—i.e., the introduction of non-native species as ecological proxies for species that became extinct centuries or millennia ago (25, 32, 44). A particular type of trophic rewilding is Pleistocene rewilding, which aims to restore ecosystems that include and are shaped by populations of megafauna extirpated since the Late Pleistocene, taking a long-term evolutionary perspective on biodiversity and ecosystems (44). In contrast, ecological (or passive) rewilding emphasizes the passive management of ecological succession in abandoned landscapes. Passive rewilding actions include the creation of no-hunting areas, low-intervention forestry management, setting aside agricultural land, the removal of dispersal barriers, and the restoration of natural flood regimes (22, 25, 34).

The ecosystem features that rewilding aims to restore are characteristic of, but not restricted to, wilderness areas (45, 46). Instead we refer to wildness, which is the autonomy of natural processes (46, 47) that can occur in a variety of settings and across spatial scales. The restoration of wildness, rather than wilderness, is thus the key goal of rewilding efforts. Broadening the original definition of rewilding and articulating the restoration of wildness rather than wilderness as its central goal makes rewilding applicable across spatial scales and adaptable to a wide range of societal and landscape contexts, from urban green spaces to abandoned agricultural landscapes (29).

A theoretical framework for rewilding

In many ecosystems, complexity and resilience are maintained by trophic complexity, natural disturbances, and dispersal (48, 49) (Fig. 1). Human activities often lead to degradation in one or more of these ecological processes. Rewilding aims to restore these three ecological processes to foster complex and self-organizing ecosystems that require minimum human management in the long term (50). If missing or degraded ecosystem processes are not expected to recover (on policy-relevant time scales) without assistance, rewilding may encompass initial interventions, sometimes followed by continuous minimal management. In the following paragraphs, we explain each of the processes in detail, elaborate on how interactions among them can promote biodiversity and ecosystem resilience, and illustrate how rewilding can be used to restore and promote such interactions.

Trophic complexity

Species at higher trophic levels are often highly connected and functionally important to ecosystems (Fig. 1) (51). Large-bodied herbivores exert strong influences on the diversity and abundance of other taxa such as birds, small mammals, insects (52, 53), and plants (54, 55). These effects occur through direct pathways, such as the provisioning of dung and carrion (56) or the facilitation of dispersal (54, 55), but also through the modification of the physical environment, for instance, by grazing and trampling or the building of dams by beavers (53, 57). Large carnivores can, through predation, affect population sizes and behavior of herbivores and create spatiotemporal heterogeneity in these processes. In the absence of top-down control by carnivores, high densities of large herbivores can have detrimental effects on the abundance and diversity of other species groups (52, 53).

Humans cause changes in species composition and alter species interactions through hunting, harvesting, or planting selected species in agriculture and forestry (Fig. 1A). Large vertebrates are particularly susceptible to human-driven defaunation, owing to their body size, long reproductive cycles, and high metabolic demands, leading to the need for large foraging ranges (58–62). Thus, even where large vertebrates are still present in human-dominated landscapes, they might not be able to exert the top-down control they have in wild ecosystems, owing to their reduced densities (63, 64). Selective defaunation of top predators and large herbivores can result in trophic cascading effects and greater susceptibility of ecosystems to collapse (51, 65).

Rewilding can enhance trophic complexity through a variety of actions that depend on the characteristics of the ecosystem. Passive rewilding measures can, for example, include the creation of no-hunting areas. Where spontaneous recolonization is unlikely, the restoration of trophic complexity may also be achieved by translocating species. Introductions of ecological replacements can be an option if species have gone extinct globally (44). However, such replacements can entail unforeseeable uncertainties and ecological risks and should be assessed with caution (25). Rewilding can also be supported by

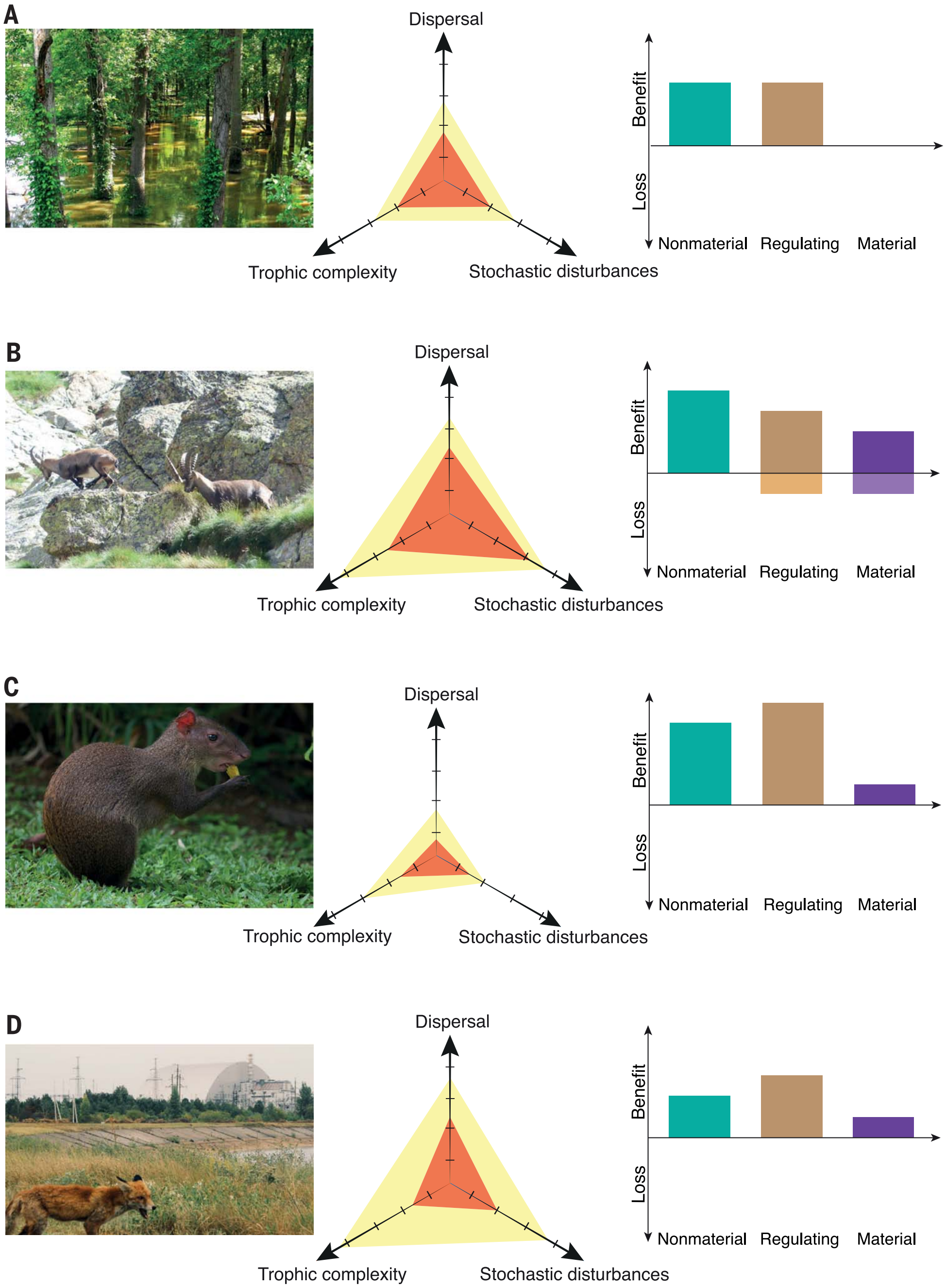

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Fig. 2. Restored ecological processes and their influence on contributions from nature. The ecological state of each case study is represented in a three-dimensional space with one axis for each ecological process of our framework (trophic complexity, dispersal, and stochastic disturbances). The initial ecological state is represented by the orange pyramids, whereas the yellow pyramids represent the ecological state after rewilding actions. The bar plots indicate the number of contributions to people (*42*) that are positively or negatively affected by rewilding actions. (**A**) Rewetting of a river branch in the Leipziger Auwald (Germany) led to increases in flood-tolerant species and an overall increase in species richness in several taxa. Management actions increased the provision of nonmaterial services (e.g., opportunities for learning and inspiration) and regulating services (e.g., habitat creation and maintenance). Impacts on material services are negligible, as the project neither affects large agricultural areas nor substantially improves nature-based income opportunities. (**B**) Nonmanagement, a hunting-ban, and reintroductions improved trophic complexity and stochastic disturbance in the Swiss National Park. Management actions promoted economic prosperity (positive material contributions) and agricultural abandonment (negative material contributions). The park provides nonmaterial and regulating contributions (e.g., opportunities for nature experiences, habitat creation and maintenance). (**C**) Reintroductions of mammals to Tijuca National Park (Brazil) improved ecological interactions. The park's urban location limits the restoration potential of all three processes. Management actions may increase material contributions (i.e., income generation through ecotourism). Nonmaterial contributions (e.g., supporting identities or maintenance of options) can potentially emerge from community-based projects. (**D**) Land abandonment, protection, and reintroductions led to the recovery of the large mammal community in the Chernobyl exclusion zone (Belarus). Positive regulating, nonmaterial, and material contributions include habitat creation and maintenance, as well as opportunities for learning, inspiration, and wildlife tourism.

activities to promote coexistence between people and wildlife—e.g., through compensation schemes for crop or livestock damage (66, 67).

Stochastic disturbances

Natural disturbances often occur in a stochastic manner at different locations, magnitudes, and frequencies, enhancing spatial and temporal heterogeneity in ecosystems (48). These perturbations can trigger reorganization and reconfiguration of ecosystems (68) and may lead to increased ecosystem complexity. They promote coexistence, as there is often a trade-off in species' competitive abilities and resilience to events such as fires, floods, or pest outbreaks (68). Species that are able to survive disturbances act as biological legacies that promote recovery and reorganization (e.g., seed banks or small mammals surviving a fire) (48).

In human-dominated landscapes, natural disturbances are often suppressed (e.g., fire suppression or flood regulation) or altered in their magnitude and frequency (Fig. 1A), which may lead to even larger and potentially devastating disturbance events (e.g., large wildfires rather than smaller and more frequent ones). Instead, stochastic disturbances are replaced by predictable and constant disturbances [e.g., use of fertilizers and irrigation to maintain constant inputs to ecosystems, or annual soil mobilization to weed out competing species (48)]. Because these deterministic disturbances often act in the same place over a long period of time without a chance for the affected ecosystem to recover and reorganize (68), sensitive species may be lost (1). Moreover, human efforts to repair damage after natural disturbance events can remove biological legacies (48, 68) and lead to additional perturbations that hinder natural regeneration and reorganization processes (69). For example, salvage logging to remove dead trees after wind throw or pest outbreaks often eliminates important resources and habitats for saproxylic beetles or cavity-nesting species (70).

Rewilding actions aim to release ecosystems from continued and controlled anthropogenic disturbances to allow for natural variability and sources of stochasticity (71) (Fig. 1B). Mowing of grassland can be reduced or replaced by natural grazing. Dams can be removed or their management modified to restore natural flood regimes (72). Logging can be replaced by allowing natural fire and pest regimes.

Dispersal

Populations depend on dispersal among habitats to avoid overcrowding (73), intraspecific competition, and loss of genetic diversity (74). The exchange of individuals from different populations can increase gene flow, mitigate inbreeding, and hence lead to more viable populations (75). Habitat degradation or anthropogenic dispersal barriers reduce habitat connectivity and dispersal ability (Fig. 1A).

A rewilding approach includes the improvement of connectivity within and among ecosystems to promote dispersal. Whereas connectivity efforts often focus on corridors alone, a multiscale approach should seek to identify and link opportunities ranging from local features, such as hedgerows to support birds or insects (76), to large-scale corridors, which allow recolonization by large mammals over long distances. Connectivity can also be improved by removing or increasing the permeability of dispersal barriers (Fig. 1B) such as roads, dams, or fences. The permeability of unsuitable habitat, particularly homogeneous agricultural areas, can be improved by the introduction of natural landscape elements (77).

Integrating across ecological processes

The three ecological processes can influence and promote one another (Fig. 1). Disturbances can, for example, promote habitat heterogeneity and increase resource availability for less competitive species and may therefore lead to an increase in species diversity (78). High levels of dispersal among habitats aid recovery of ecosystems after (major) disturbance events by allowing recolonization and recovery of affected populations (Fig. 1B). Large vertebrates present in complex ecosystems often act as dispersal agents for plants (54, 55) and can introduce stochasticity into a system, e.g., through predation or grazing (79). Therefore, the restoration of one of these processes may positively influence the functionality levels of the two other processes (Fig. 1B). Interactions among the processes can increase ecosystem resilience by jointly promoting, for example, functional redundancy or recolonization.

Rewilding efforts can be assessed by representing ecosystems in their degraded and restored states in a three-dimensional, pyramid-shaped space where each axis corresponds to an ecological process and the faces represent the interaction between processes (Fig. 2). During the restoration of a process, the respective vertices of the pyramid move farther from the origin and the volume of the pyramid increases. The difference in volume between the restored and degraded ecosystem is thus a proxy for the effect of rewilding on the resilience of the ecosystem. Because the processes interact, restoring only one dimension but leaving the other two unaddressed typically corresponds to a smaller improvement than that facilitated by restoring the three dimensions simultaneously (e.g., the change in the volume of the pyramid is very small when one of the axes is fully restored but the other two axes remain highly degraded).

Rewilding as a societal choice

Ecosystems cannot be assessed separately from human societies (80). All areas that are candidates for rewilding are influenced by people and/or have a history of use. Consequently, any rewilding project can affect local livelihoods and well-being. Societal changes can influence ecosystems in positive or negative ways and vice versa, and the trajectories of ecosystems are often defined by human decisions that focus on the delivery of certain resources and ecosystem services (67, 81). Considering and managing for interactions between ecosystems and people while assessing and communicating the benefits of rewilding for society (Fig. 2) can incentivize actions that benefit both ecosystems and society (67), thereby increasing the acceptance and success of rewilding endeavors.

The restoration of the three ecosystem processes can positively affect people's lives in various ways. Rewilding plays an important role for nonmaterial contributions of nature and relational values of biodiversity (82). A growing body of literature concludes that exposure to green or natural spaces can reduce stress levels, increase positive emotions and cognitive function, encourage physical activity, and facilitate social cohesion in humans (83–86). In particular, wilderness experiences provide an opportunity for ecotherapy to promote psychological resilience in children and adolescents (87) and personal transformation and self-fulfillment in adults (88). Moreover, the satisfaction that people may gain from knowing that a species or ecosystem is thriving (89, 90) can reach societies in great geographical distance to an actual rewilding site. The presence of charismatic or symbolic species or landscapes can inspire spiritual, artistic, and technological development (42). Far-ranging and migrating species traveling on dispersal pathways may motivate nature-based activities such as bird-watching (42). Witnessing natural processes associated with childhood experiences, such as the migration of swallows or cranes, can promote a sense of place and rootedness and may be the basis for narratives, rituals, and celebrations that shape cultural identity (42).

Economic benefits of rewilding may arise from opportunities for nature-based economies and alternative sources of income based on nonmaterial contributions from nature [e.g., recreational activities (42, 91, 92)]. Furthermore, natural disturbance events can trigger innovation and change in social-ecological systems (93). Rewilding promotes other regulating services and nature-based solutions such as regulation of climate, air quality, pollination, and dispersal of seeds (42, 94). Improved dispersal potential and trophic complexity may prevent the depletion of material contributions from nature (42), such as economically relevant natural resources (e.g., wildlife game), not only in the areas undergoing rewilding but also in surrounding areas.

However, rewilding can also have undesired consequences for people. Natural disturbances such as fires or floods may threaten humans and human infrastructure (95). Human–wildlife conflicts—for example, crops damaged by large herbivores or livestock killed by large predators (96)—are becoming more frequent and more severe where these animals are reintroduced or their populations recover (97). Additionally, concerns about the loss of traditional, cultural landscapes, including their unique natural and cultural heritage, are growing in Europe and other regions (91, 98, 99). Particular unease has been expressed regarding impacts on farmland biodiversity and on cultural ecosystem services—for instance, aesthetic values (100), sense of place (101), and a general "erasure" of human history and involvement with the land and its flora and fauna (32).

In sum, the relationship of people with wildness in nature is and has always been characterized by sets of paradoxes (102). These range from contradictory views of wildness in nature ascribed to prehistoric peoples as a "constant threat to [human] life and livelihood" versus the "primary source of life and livelihood" to contemporary, contradictory perceptions as "a potentially dangerous, alienating and challenging place" versus "a potentially peaceful refuge to relax and conveniently enjoy" (102). This range of emotions emphasizes that well-planned rewilding projects that mitigate possible conflicts have the potential to maximize positive experiences and beneficial contributions from nature.

Applying the framework

A structured and participatory approach to rewilding is important to ensure that all stakeholders have a clear understanding of the goals, management options, desirable outcomes, and associated risks (103). The first step of a rewilding project should be an analysis of the ecological status of the focus area, by identifying missing and/or degraded components. Paleoecological data—for example, on past vegetation change, megafauna presence, or fire dynamics—as well as information on land-use histories should be considered in such analyses (4).

In the second step, managers should assess the ecological viability of different management options and potential synergies among those. Together with key stakeholders (conservationists, farmers, hunters, and the general public), managers should identify social-ecological constraints (such as infrastructure hindering dispersal, emerging human–wildlife conflicts, or risks associated with the restoration of natural disturbances) and evaluate benefits and disadvantages associated with the rewilding intervention.

The third step is the implementation of rewilding actions via an adaptive management approach. This includes monitoring of the different interventions, ideally using a before-after-control-impact (BACI) approach (104) that considers both ecological and societal outcomes. Results of this monitoring may lead to adjustments in ongoing rewilding interventions or raise the need for further management actions and decisions. The implementation phase should be accompanied by a communication strategy that involves affected communities in decisions, as well as outreach activities that inform the wider public about the outcomes of rewilding. These should ideally be offered via an array of opportunities for nature experiences (guided tours through the rewilding area, nature education tools, and opportunities for leisure activities). Additionally, managers may seek to develop opportunities for sustainable business opportunities to increase the acceptance of rewilding among stakeholders.

Our stepwise approach can also be applied for passive rewilding projects. In such cases, there is no deliberate decision to initiate a project, but instead managers can take advantage of ongoing social-ecological dynamics (e.g., farmland abandonment). If such an opportunity is identified, the first step will involve an assessment of the ongoing passive rewilding dynamics, associated risks and benefits, and potential impediments to those dynamics. The second step will focus on identifying options to support those dynamics and mitigate threats. This step will often involve the consolidation of ongoing nonintervention (e.g., establishment of no-hunting arrangements or protected areas) or the mitigation of emerging conflicts. As in active rewilding projects, the third step involves adaptive management, monitoring, and outreach activities.

We now describe the stepwise application of our framework with four rewilding case studies, spanning a range of scales, ecosystem types, and degrees of intervention (Fig. 2). As will become apparent, the development of a rewilding project is rarely a linear process. Owing to the adaptive nature of our approach, some of the steps will be carried out repeatedly and/or in parallel.

Restoration of the natural flood regime in the Leipziger Auwald city forest, Germany

The Leipziger Auwald is an alluvial forest surrounding and crossing the city of Leipzig in Germany. Since the middle of the 19th century, flood suppression and changes in forest management have led to a well-documented shift in tree community composition with increasing dominance of sycamore (*Acer pseudoplatanus*), Norway maple (*Acer platanoides*), and common ash (*Fraxinus excelsior*), mainly at the expense of hornbeam (*Carpinus betulus*) and oak (*Quercus robur*) (105). In this state, connectivity between the Auwald's waterbodies is severely diminished, so active management is necessary to restore the flood regime (Fig. 2A).

After identifying flood disturbance as a major missing component of this ecosystem, city managers initiated yearly experimental flooding of a pilot area in the early 1990s (106). Results of concomitant monitoring confirmed the effectiveness and suitability of this management action. Flooding led to an increase of flood-tolerant species, such as oak and hornbeam, and a decrease or local extinction of some plant species that are intolerant to flooding but had become dominant after flooding had been suppressed (e.g., sycamore and Norway maple) (106). At the same time, (re)colonization by moisture-tolerant slug species and several ground beetle species associated with alluvial forest systems was observed (106). The findings of this long-term experiment thus inform the project's implementation phase, in which the natural flood regime is restored in several drained branches of the Luppe River (Lebendige Luppe project) (72) (Fig. 2A).

The implementation phase is accompanied by an extensive outreach strategy that offers several opportunities for the public to engage with the ecosystem in the Auwald. Examples include multimedia teaching material to support environmental education and tools (e.g., magnifying glasses, landing nets, and maps) for interactive experiments that allow children to learn about the ecology and topography of the alluvial forest and explore its flora and fauna. A local conservation nongovernmental organization (NGO) organizes excursions to inform residents about ongoing management activities, and regular public discussion forums offer the opportunity to engage actively in the project. Two concomitant research programs assess the ecological outcomes of the project and monitor and evaluate the acceptance and perception of natural processes in the Auwald, respectively (107).

Nonintervention policy in the Swiss National Park

Established in 1914, the Swiss National Park is the oldest national park in Europe and the largest protected area in Switzerland (108). In 1909, the park's founders—botanists and naturalists concerned with the widespread development of tourism infrastructure threatening the area's unique flora and fauna—identified the region around the Pass dal Fuorn as a suitable target area, owing to its remoteness and species richness (108).

Making space for natural processes and conducting research on their development are central missions of the park's management (108). The establishment of the park and management decisions were advised by cartographers and naturalists with extensive knowledge of the area and its ecosystems (109). The protection status of the area was secured by a lease agreement negotiated with the local municipalities and financed through the foundation of the Swiss Federation of Nature Conservation.

Since its establishment, the National Park has been subject to a strict nonmanagement approach and has been fully protected from human activities such as hunting, agriculture, and forestry. Trophic complexity was promoted through targeted reintroductions of ibex (*Capra ibex*) in 1920, 1923, and 1926 and bearded vultures (*Gypaetus barbatus*) from 1991 to 2007 (110). Natural disturbances are not managed, and dispersal potential is high for most species (Fig. 2B). Ecosystem development has been monitored continuously, and many of the monitoring schemes have been in place for decades (109). Conflicts with local communities were mitigated via selected active management measures. For example, public discontent over sapling damage caused by red deer (*Cervus elaphus*) was alleviated by organizing hunting events outside the borders of the park (109). The nonmanagement approach has resulted in the recovery of large populations of red deer, chamois (*Rupicapra rupicapra*), ibex, and roe deer (*Capreolus capreolus*), species that were nearly extinct or very rare in Switzerland when the park was established (111). The increased red deer population density has resulted in higher plant species richness in subalpine grassland (112). Additionally, wolves (*Canis lupus*) and brown bears (*Ursus arctos*) have recently been sighted, suggesting the imminent recolonization of the area by large predators. Socioeconomic studies show that the park attracts ~150,000 visitors per year, contributing substantially to the economic prosperity of the region (109, 113, 114).

Restoring ecological interactions in the Tijuca National Park, Rio de Janeiro city, Brazil

The Atlantic Forest of Brazil is a globally important biodiversity hotspot. However, most of the protected areas containing Atlantic Forest remnants have been defaunated (115). One of these remnants is the Tijuca National Park in Rio de Janeiro. During the 17th and 18th centuries, deforestation for agricultural purposes and hunting pressure led to severe losses of native fauna. Because the forest is completely surrounded by urban infrastructure, the affected animal species could not fully recover after the area was reforested in the 19th century (116), and dispersal of mammal species to other ecosystems is still inhibited.

The REFAUNA Project was established in 2012 to restore the mammal community via gradual reintroductions of species that have disappeared from the Atlantic Forest (116). Tijuca was considered suitable for first reintroductions because its relatively small size and urban location would allow for easy monitoring and control of the released animals (116). Researchers identified two native, locally extinct candidate species, the red-rumped agouti (*Dasyprocta leporina*) and the howler monkey (*Alouatta guariba*), both of which were expected to promote ecological interactions. Agoutis are important dispersers of large seeded plants (117) and increase seed survival by transporting them to locations with lower densities of conspecific tree species. Howler monkeys influence dung beetle abundance, and the decomposition of howler dung by the beetles can enhance nutrient cycling and soil fertilization (118).

Concomitant monitoring revealed that the presence of agoutis and howler monkeys enhanced ecological interactions in the park. Agoutis broadened their diet and improved the dispersal and germination success of several large-seeded plants. By interacting with the dung beetle community, howler monkeys promoted the dispersal of large seeds, with likely positive effects on forest regeneration (116) (Fig. 2C). Although Tijuca is Brazil's most popular national park (119), there is little emotional connection between the park and people living in adjacent communities (120). To improve the linkage between the park and local communities, the park administration has installed a park council through which representatives of governmental institutions, NGOs, and the private sector aim to reach satisfactory management decisions for all stakeholders (121). A community-based, cooperative project has trained locals as tourist guides and offers tours through the park and a neighboring favela. Additionally, the cooperative runs a restaurant that offers local cuisine prepared with products growing in the forest and community gardens (122, 123).

Ecosystem and wildlife recovery in the Chernobyl exclusion zone, Belarus

The meltdown of the nuclear reactor in Chernobyl on 26 April 1986 resulted in massive contamination, especially in the immediate surrounding area (124–126). The evacuation of the entire local population within a 30-km exclusion zone around the reactor and the most strongly contaminated areas outside this zone resulted in the abandonment of ~1400 km^2 of agricultural land (40, 41). The breakdown of the Soviet Union, with widespread outmigration and an additional 36% of all farmland abandoned in Belarus and Ukraine, further lowered human pressure in the region surrounding the Chernobyl site (41).

Two years after the meltdown, the Belarusian part of the exclusion zone and adjacent areas were turned into the strictly protected 1300 km^2 Polesie State Radioecological Reserve. In 1993, the reserve was extended by 850 km^2, making it the largest nature reserve in Belarus (127). Management of the exclusion zone on both sides of the border has since followed a paradigm of minimal to no intervention. Targeted reintroductions of European bison (*Bison bonasus*) in the Polesie State Radioecological Reserve and of Przewalski's horses (*Equus ferus przewalskii*) in the Ukrainian exclusion zone to restore trophic interactions in the Chernobyl area were exceptions to this passive approach. Recognizing the growing ecological and conservation value of the Chernobyl area, the Ukrainian government established the 2300-km^2 Chornobyl Radiation and Ecological Biosphere Reserve—an almost 5000 km^2 contiguous rewilding area in the heart of Eastern Europe—in 2016 (128). Management activities in the biosphere reserve aim to recover biodiversity and ecosystem resilience and include monitoring of the ecological, medical, and radiation status of the area, as well as educational activities (128).

The region now harbors the entire portfolio of extant European large carnivores [wolf, lynx (*Lynx lynx*), and brown bear], large herbivores [European bison, wild horse, moose (*Alces alces*), red deer, roe deer, and wild boar (*Sus scrofa*)], a rich mesopredator community [e.g., European badger (*Meles meles*), raccoon dog (*Nyctereutes procyonoides*), and red fox (*Vulpes vulpes*)], and key ecosystem engineers, such as the Eurasian beaver (*Castor fiber*). The Chernobyl exclusion zone is the only area where these species interact in sizable numbers in a large wilderness complex and can thus be considered one of the most iconic natural experiments on rewilding in recent history.

The way forward

Rewilding directly aims to restore ecological functions instead of particular biodiversity compositional states. Therefore, the effects of rewilding may be indirect and unexpected. Consequently, the development of sound rewilding plans requires a deep understanding of the interacting ecosystem processes that lead to resilience and the socioeconomic context in which rewilding occurs. Interdisciplinary training of scientists and practitioners is necessary to develop such understanding. Moreover, objective, evidence-based assessments of rewilding initiatives are needed to make rewilding projects fully accountable to funders, the public, and the research community. A recently proposed method to assess the progress of rewilding projects through a combination of expert opinion and monitoring data (129) is a step toward this goal.

Unfortunately, current landscape management and conservation policies do not provide sufficient opportunities for rewilding to be implemented on a broader scale. For instance, the European Union's common agricultural policy incentivizes agricultural activities in low-production areas, impeding opportunities for rewilding (130). Restoration policies often focus on the safeguarding of current or historical conditions (130) and the protection of certain species and habitats (24, 130, 131). Therefore, the successful contribution of rewilding to national and international biodiversity goals depends on policy changes that shift the conservation focus toward restoring the ecological processes identified in our framework (131).

Discussions on post-2020 biodiversity strategies by the signatory countries of the Convention on Biological Diversity are currently being initiated, and the United Nations General Assembly has recently declared 2021–2030 the "decade of ecosystem restoration" (132). We believe that rewilding provides one of the possible pathways toward the vision in which "By 2050 biodiversity is valued, conserved, restored and wisely used, maintaining ecosystem services, sustaining a healthy planet and delivering benefits essential for all people" (133). Perhaps innovative policy changes that favor rewilding can add to the current momentum for novel approaches to restoration (19, 134). For instance, Aichi Biodiversity Target 15, which aims to restore 15% of degraded ecosystems by 2020, could be revised to recognize rewilding as a major approach to ecological restoration. An ambitious positive target of increasing wildness across the globe by 2030 could be a truly inspiring goal, infusing energy and public support into global biodiversity policies.

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Rewilding complex ecosystems

Andrea Perino, Henrique M. Pereira, Laetitia M. Navarro, Néstor Fernández, James M. Bullock, Silvia Ceau?u, Ainara Cortés-Avizanda, Roel van Klink, Tobias Kuemmerle, Angela Lomba, Guy Pe'er, Tobias Plieninger, José M. Rey Benayas, Christopher J. Sandom, Jens-Christian Svenning and Helen C. Wheeler

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Facilitating "wildness"

Humans have encroached upon a majority of Earth's lands. The current extinction crisis is a testament to human impacts on wilderness. If there is any hope of retaining a biodiverse planetary system, we must begin to learn how to coexist with, and leave space for, other species. The practice of ''rewilding'' has emerged as a method for returning wild lands, and wildness, to landscapes we have altered. Perino *et al.* review this concept and present a framework for implementing it broadly and in a way that considers ongoing human interaction.

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