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Emerging perspectives in the restoration of biodiversity-based ecosystem services

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Given the large-scale anthropogenic alteration of natural habitats, ecological restoration is emerging as one of the most important disciplines in environmental science. Once habitats are physically restored, an important goal of restoration is to recover the ecosystem services provided by the diversity of species and their interactions (e.g., seed dispersal, pollination, pest control, and invasion resistance). However, current understanding of the ecological processes underlying this recovery is often incomplete and poorly integrated across different ecosystems. Here, we highlight recent conceptual findings in biodiversity–ecosystem functioning, food-web theory, and metacommunity theory that are relevant to restoration. We also identify knowledge gaps that will contribute to moving restoration from a site- and situation-specific discipline to a more globally applicable science.

Ecological concepts and restoration

Anthropogenic disturbance of natural habitats has led to large-scale loss of both biodiversity and ecosystem services (see Glossary). The Convention on Biological Diversity declared recently that the 'restoration of terrestrial, inland water and marine ecosystems will be needed to re-establish ecosystem functioning and the provision of valuable ecosystem services' (15% of the degraded ecosystems of the world are targeted [1]). Restoration ecologists usually identify two fundamental, non-exclusive steps in the process of recovery of biological communities [2]: the restoration of the abiotic environment and the recovery of populations. The restoration of populations and, more generally, of the ecosystem services provided by species and their interactions, is a critical step for the recovery of important services, such as seed dispersal, pollination, and pest control. In this context, there has been considerable progress in recent years in gathering data that can contribute to a firmer scientific footing ([2,3]). Yet, understanding of the ecological processes underlying successful restoration of the ecosystem services provided by biodiversity often remains incomplete, for example in many cases, the identity of the providers of that service are still unknown (sweeping statements, such as 'bees', are still common in pollination studies, for example).

Although ecological restoration already makes use of concepts from ecology (e.g., population dynamics, ecological

Glossary

Body-size spectra: the distribution of the body sizes and abundances of organisms across trophic levels [35]. Body size influences network structure and ecosystem functioning (e.g., [35]) and, thus, the distribution of body sizes in a community is an indicator of the state of the community.
Ecological engineering: design and management of ecosystems for the mutual benefit of humans and nature. The energy supplied by humans is small relative to the natural sources but sufficient to produce large effects in the resulting patterns and processes.
Ecological restoration: process of assisting the recovery of ecosystems that have been degraded, damaged, or destroyed.
Ecosystem function: changes in energy and matter over time and space through the interplay of biological activity and abiotic factors (physical and chemical). Examples include production of carbon, respiration, denitrification, and nutrient uptake.
Ecosystem service: products of ecosystem functioning that are of value to humans, such as pollination, pest control, food production, and water catchment services.
Evenness: diversity index that measures how close in number the species abundances and interactions in a community are to each other. Low evenness is associated with fragile, less stable communities because it implies that most interactions and energy flow along one or only a few pathways [61].
Functional complementarity: diversity-related measure that refers to the interaction among functionally unique species when performing ecosystem functions. Functional complementarity allows mixed communities to contribute more to the function than any individual species alone, and is associated with a direct and positive effect of biodiversity on ecosystem functioning.
Functional redundancy: refers to the presence of several species performing similar functional roles, so that these species are at least partially substitutable in terms of ecosystem functioning. Redundancy implies functional stability because the loss of species is compensated for by other species, although the addition of functionally similar species to the system adds nothing to ecosystem multifunctionality. This stabilizing mechanism is called the 'functional redundancy hypothesis' [5].
Functional uniqueness: refers to the presence of species each performing different functional roles, so that species make unique contributions to ecosystem functioning. The loss or addition of these species causes changes in ecosystem multifunctionality.
Insurance hypothesis: heuristic description of the theoretical results underlying the stabilizing effect of increasing species diversity in terms of community function [5]. It predicts more stable ecosystem functioning with higher diversity under fluctuating environments.
Interaction symmetry: measures the relative dissimilarity between the two mutual dependences in a pairwise interaction [14]. Asymmetric interactions are characteristic of persistent communities.
Network modules or compartments: link-dense regions of the ecological network where species interact more closely within than between modules [29].
Population stability: refers to the magnitude of change in population numbers within a biological community. It can be measured as the coefficient of variation of species abundances.
Restoration ecology: science upon which the practice of ecological restoration is based. Although it is not limited to the direct service of restoration practice, restoration ecology ideally provides concepts, models, and methodologies for restoration practitioners.

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succession, and alternative states), some recent conceptual advances that are highly relevant for restoration are not yet widely considered in restoration projects. Here, we highlight recent scientific findings in the fields of community assembly theory, functional ecology, food-web theory, and metacommunity theory, which, in our opinion, are of considerable relevance for the restoration of ecosystem services. By identifying knowledge gaps in restoration ecology, we also suggest future directions where these findings can provide important insights. We focus on services that have direct, immediate links to species and their interactions (e.g., pollination, seed dispersal, pest control, and invasion resistance), rather than on their indirect services (via other ecosystem services). For example, although pollination is a service that results from direct interactions between plants and animals, because of its reproductive value to plants it also has an important, indirect role in other vegetation-based services, such as water filtration, erosion control, and carbon storage and sequestration. Our goal is not to develop a theory or conceptual model for restoration. Rather, we aim to identify research that is currently not widely applied in ecological restoration, but which has considerable potential for contributing to the development of such general theory. Our perspective is a consensual one arising from three backgrounds, that of a theoretician (D.M.), a conservation practitioner (L.R.) and a field ecologist (J.M.).

What is known: recent findings relevant for restoration
The restoration of function
During the past decade, the focus of ecological research has shifted from species to functional groups [4], and this is relevant for restoration in two ways. First, not all species contribute equally to ecosystem function; rather, some species are functionally more 'important' than others. Despite species richness acting as a biological 'insurance' [5], it is these functionally important species that should be priorities in restoration programs. For example, Hegland *et al.* [6] identified key plant species in a particular plant–pollinator community with regard to pollinator restoration. Similarly, Forup *et al.* [7] found that a few widespread insect species were the main pollinators, and Montoya *et al.* [8] reported that animal-dispersed trees were robust to habitat loss as long as key seed-dispersing animals were present. These studies highlight the possibility of targeting the reinstatement of functionally important species to jump-start the restoration of ecosystem services in natural and managed communities.

Second, trait-based research shows that community diversity (e.g., species richness) is not as relevant as functional diversity when reinstating ecosystem functioning [9]. Functional diversity quantifies similarities and differences in the phenotypes or ecologies of species that range from their environmental tolerances to how they impact ecosystem functioning. For the purposes of restoration, greater functional diversity is linked to greater levels of ecosystem functioning and greater long-term stability, as multiple functional traits help buffer ecosystems against disturbances [9]. In our opinion, restoration projects should aim to reintroduce the dominant species of key functional groups first, rather than the number of species, and then restore ecological redundancy by the addition of species that vary in functional traits. This approach is very practical for plants, which usually are the first, easiest targets in most restoration projects.

Aliens: friends or foes?
A contentious topic in ecological restoration, especially considering the expansion of novel ecosystems [10], is the role of alien species in the native community [11]. Where invasive species have negative effects, or are in the early stages of invasion, removal is usually prioritized, and concepts such as limiting similarity, functional diversity, and ecological filters are relevant (see [12] for further discussion of these points). Importantly, despite invasive species being major drivers of biodiversity loss, in terms of maintaining ecosystem functions, native and non-native species can have equivalent roles if non-native species take on the role of extinct native species. Furthermore, the introduction of non-native species as ecological replacements for extinct native species can sometimes be an effective restoration action [13]. These ideas are based on food-web theory, where the structural properties of species interactions involving native and non-native species, especially those regarding the distribution and (a)symmetry of interaction strengths, provide relevant information on the stability of communities [14]. Alien species can become central nodes and alter network structure by reducing the interaction strength of the entire network, and promoting asymmetric interactions involving alien species compared with those interactions involving native species only [15]. These properties are characteristic of persistent communities. Equally, however, alien species can substantially reduce pollination [16] and seed dispersal [17]. Thus, we believe that network and functional approaches are important in understanding the exact role of alien species in the community and that they should be increasingly used to help inform the restoration of communities that host both native and non-native species.

Cost-efficient monitoring
Ecological restoration is bedeviled by a lack of funding, which raises the issue of how to measure properties of the restored communities on a tight budget. For species interactions, some relatively quick and cost-efficient ways to monitor communities have been proposed recently. These include sampling during peak seasons [6], focusing on network-stability properties that change little with sampling effort [18], and, for pollination networks, sampling using transects instead of timed observations [19]. Restoration ecologists can also make use of *in silico* experiments that are already implemented in statistical environments (e.g., R software) to evaluate the stability of restored communities. These experiments enables researchers to compare the probable stability of the proposed, restored communities in terms of, for example, robustness to extinction (Figure 1). Regarding functional diversity, phylogenetic data could be used as a proxy for trait similarity for functional traits that are not straightforward to determine [20]. We believe that the inclusion of these and other cost-efficient measures to monitor restoration would significantly increase knowledge of the restoration process at little additional cost.
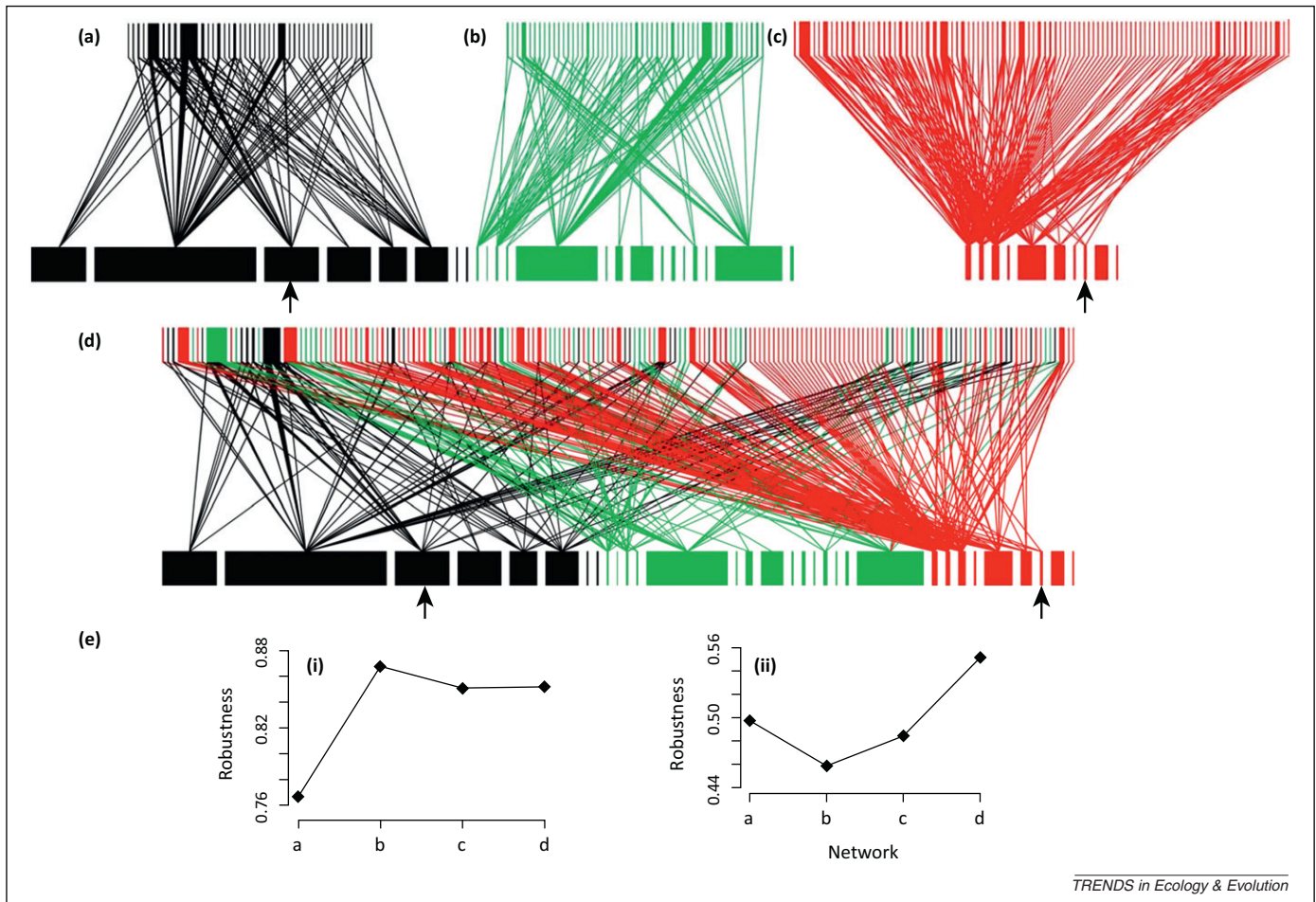
Figure 1. Landscape-scale restoration of species networks. Habitat networks from **(a)** heathland [7], **(b)** woodland [16], and **(c)** wetland (Memmott, unpublished data) shown separately and **(d)** collectively as a landscape-level web that incorporates the three habitats. The bottom row of boxes denotes plant species, the top row flower-visiting insects, with the size of the line linking the two boxes indicating the frequency of the interaction. The color given to the insect in the landscape network is that from which the insect was only found, or in which it was the most abundant. Although the three networks were joined for the purpose of illustration, these habitats are found adjacent naturally. Only one plant was found in more than one habitat (*Rubus agg.*, its location is indicated by an arrow) but overlap in pollinators between the habitats was substantial, with 19% of species being found in one or more habitats; these species tended to be the most abundant and, overall, 43% of individuals came from species found in more than one habitat. This suggests that habitats are permeable for species and interactions and supports multiple habitat restoration. Robustness analysis: we conducted robustness analyses for the three local webs and the landscape web to search for differences in the restoration of single versus multiple habitats. Robustness analysis looks at how species removal in one trophic level induces secondary extinctions in other trophic levels. We simulated two scenarios where species were sequentially extirpated either from high (pollinators) or low (plants) trophic levels. We show the normalized results for the random loss of species of pollinators **(i)** and plants **(ii)** in terms of the area under the curve (AUC) [64]. Differences in robustness between (i) and (ii) are caused by differences in species richness between trophic levels (i.e., there are more pollinators than plants). Although single and landscape networks are similarly robust to the loss of pollinators, pollinator robustness to plant removal is higher in landscape webs, probably because pollinators have larger choice of flowers to feed from at the landscape level. These results suggest that landscape-scale restoration provides added benefits in terms of robustness and ecosystem service provision.

The role of ecological engineers

Assembly theory has long acknowledged that biological communities are contingent to the historical sequence of colonization–extinction dynamics, and that restoration can be viewed as an attempt to recover a natural range of community structure and dynamics that result in certain levels of ecosystem function. Recent studies show that immigration history affects community structure at multiple scales and taxonomic groups, which in turn affects ecosystem functioning [21,22]. For example, in a microcosm experiment, Jian *et al.* [22] found that assembly history of a community can affect its susceptibility to invasion. This has profound implications in ecological restoration, where the restoration process can be 'engineered' to some extent by controlling the sequence of species arrival, which is a fairly straightforward process in the case of revegetation work.

Phylogenetic information is also relevant for the restoration of species and interactions. For example, looking at interactions between nurse plants and facilitated plants, Verdú *et al.* [23] concluded that restoration practices based on the use of nurse plants can be maximized by increasing life-form disparity and phylogenetic distances between the neighbor and the facilitated plant. These results show how phylogenetic relatedness among species can be used as an informative tool in restoration practice.

Finally, Devoto *et al.* [24] explored how reintroduction sequence affects ecosystem service provision in mutualist communities. These authors modeled two scenarios based on the order in which plant species are reintroduced: functional complementarity, which is important for restoring pollination of the whole community, and functional redundancy, which is most important when restoring the pollination of particular plant species (e.g., a crop). Although

replicated large-scale experiments that vary the order of species arrival should be implemented to generalize conclusions, these results suggest that different restoration aims require different assembly histories, and that different sequences of species seeding, planting, and removal, will be critical when designing restoration programs.

Landscape-scale restoration
A landscape perspective in restoration is increasingly embedded in restoration practice (e.g., [25,26]). Recent findings in food-web and metacommunity theory show that network modules or compartments are associated with different habitats [27,28]. These modules are connected to each other by relatively few 'hub' species and it is these species that are structurally important for the robustness of the community overall (Olesen *et al.* [29] reported that only 15% of the species in their pollination networks were structurally important). These observations have significant implications for landscape-scale projects where several habitats are targeted for restoration. In such projects, which are increasing in popularity, the re-establishment of structurally important species that link different community modules is a fundamental step toward restoring robust, resilient communities at the landscape scale.

What needs to be known in restoration science?
Simple straightforward assays of restoration outcome
Restoration ecologists aim at a long-term restoration outcome that needs no more maintenance than similar undamaged habitats. Although restoration studies increasingly assess diversity, vegetation structure, and function (yet rarely together [30]), what are ideally needed are simple, straightforward assays that provide information on the efficacy of ecosystem functions and thereby provide a benchmark of restoration progress. Because defining specific endpoints is rarely possible, assessment of restoration outcomes should be based on the rates of change of quantifiable properties that describe the community in terms of structure and function, rather than in static assessments of species composition. Although this perspective is being increasingly considered in restoration (e.g., [31]), many ecological indicators are still not taken into account when assessing restoration outcomes. For instance, the presence and abundance of functionally important species (see above), and of high trophic-level species (e.g., predators act as energy channel couplers and can promote community stability [32]) provide effective and relatively easy proxy variables to quantify functional restoration. Additional measures of community structure associated with stability and function, such as evenness [33], population stability, and body-size spectra, are rarely assessed in restoration. Body-size spectra, which are now widely used to assess the state of marine ecosystems (e.g., [34]), are affected by habitat degradation and restoration [35], and so monitoring the rate of change in the size–structure patterns of a community could be a valuable and relatively straightforward way to assess restoration in aquatic and terrestrial ecosystems. In our opinion, the incorporation of measures that link community structure to function and stability will be a major step forward in the assessment of restoration outcomes.

Ecosystem multifunctionality
Despite many ecosystems providing multiple services (e.g., a farm hosts pollination, pest control, and water-catchment services), most research considers ecosystem functions and services individually (e.g., [36]). However, in reality, species contribute to multiple services and overlap in their provision [37]. High overlap in service or function provision implies that only a few species need to be reintroduced because functional redundancy is high, whereas low overlap implies that each species is more 'unique' and, therefore, more species need to be reintroduced to restore function. We believe that understanding the degree of functional overlap among species in the provision of ecosystem services will be highly informative when designing and monitoring the restoration of fully functional communities.

Monitoring beyond the 'easy' groups
Many community ecology studies are limited by their inability to quantify organisms other than plants and animals (e.g., microorganisms) and incorporate them into food webs. New molecular techniques to identify all species in a community, from mammals to bacteria, are becoming widely available and relatively inexpensive. For example, metagenomics allows for the identification of common and rare microorganisms, and metatranscriptomics provides a direct window to the functioning of the community by quantifying the functional genes of interest [38]. Monitoring the restoration of the 'big' community is now a realistic proposition [39,40]. Microbial communities are crucial for the functioning of ecosystems [41], enhance biodiversity levels (e.g., plants), and interact intimately with the larger organisms (e.g., gut faunas) that supply important ecosystem services [42]. Consequently, considering the restoration of bacteria, fungi, and viruses alongside that of plants, invertebrates, and vertebrates will provide a more complete, holistic picture of the recovery of the biodiversity-based ecosystem functions and services.

Landscape scale and meta-communities
Metapopulation dynamics has provided a spatial component to conservation ecology and provides an extremely useful framework for studying fragmented populations of single species [43]. Ecosystem functions and services are usually the product of species interactions, and the emerging field of metacommunity dynamics [44] (the study of extinction and dispersal at the community level) could provide a similar framework for the restoration of biodiversity and ecosystem services in fragmented landscapes. For example, if non-linear relationships exist between habitat size and the restoration of community properties (e.g., because of seed dispersal constraints [8,45]), restoring at local scales might not translate into restoration at the landscape scale simply because the threshold at the landscape scale has not been reached. Restoring single habitats might also be inappropriate given the differences from local to landscape scales in the spatial distribution between consumers and resources [46], and the dependence of some species on a mosaic of different habitats that provide different resources (e.g., a bird might need nesting and feeding habitats).

Understanding the relations between (i) restoration trajectories and recovery rates (see [47] for further discussion on this topic) and (ii) restoration trajectories and the spatial scale of restoration, is fundamental (Box 1). Metacommunity studies show that mobile organisms, such as pollinators, predators, and seed dispersers, actively move among patches, functionally connect habitats in space and time [48,49], and contribute enormously to important ecosystem services [50]. These species can be generalists in habitat range and interaction patterns and, thus, can be particularly important for ecosystem recovery at landscape scales, as well as for the stability of the metacommunity [27,51]. In single habitats, larger is nearly always better; however, is a large patch of single habitat more robust than several smaller patches of adjacent, different habitats? For the restoration of habitat specialists, the answer is probably yes, whereas for the restoration of ecosystem function, the answer is not as clear. Indeed win:win situations might exist whereby restoring two adjacent habitats provides added benefits to both in terms of robustness or ecosystem service provision (Figure 1). We believe that understanding the permeability of different habitats to species and interactions, along with the extent of overlapping in the provision of ecosystem functions among the species in different habitats, is essential if the restoration is to be sustainable.

Long-term, large-scale experiments
Long-term, large-scale experiments are becoming the norm in areas such as invasion ecology [52] and community ecology [53]. Scientific projects are usually funded at short temporal scales, such as 3–5 years, even shorter in the case of restoration projects (typically funded for 1 year), and frequently cannot account for the temporal variation in species interactions (e.g., ontogenetic changes and seasonal variation in resource availability) and colonization–extinction dynamics. For example, Doherty *et al.* [54] reported temporal changes in diversity–function relationships in a 12-year salt-marsh restoration experiment that would have not been detected if the experiment had spanned only a few years. Given that evaluating restoration over short time periods might not provide a good indication of functional communities over the long term, restoration experiments and habitat management programs are starting to include long-term targets (e.g., [54–56]). However, although the lack of long-term experiments is starting to be addressed, large

Box 1. Restoration trajectories and the spatial scale of restoration

Given that most restoration projects are not able to restore 100% of original habitats, a critical question is how much area needs to be restored to restore certain community properties and to get some minimum level of robustness and ecosystem service in the restored biological community. Below, we highlight two main questions that need to be addressed by future theoretical models and field experiments.

Restoration trajectory: the pathway of recovery?
Although studies on habitat loss and fragmentation are abundant and have identified some patterns in habitat loss–biodiversity relationships (e.g., extinction thresholds), little is known about the shape of these relations along the restoration process. The few studies exploring this are either focused on single species or are not replicated, making generalizations difficult [62,63]. Furthermore, habitat loss–biodiversity relations will depend on species life-history traits, such as body size, range size, dispersal ability, and interaction patterns (Figure I). Understanding recovery trajectories is important to be able to anticipate restoration results and to identify critical thresholds or tipping points in the restoration process that might shed light on the relationships between area and effective restoration.

Spatial scale of restoration: is it better to restore one or several habitats?
For a given area, it is important to know whether including small fragments of different habitats is more effective than restoring a big fragment comprising one single habitat. The low spatial overlap of different ecosystem services and the multihabitat use of several species suggest that including different habitats is more effective (Figure II), but more models and field experiments are needed on the appropriateness of single versus multiple habitat restoration.
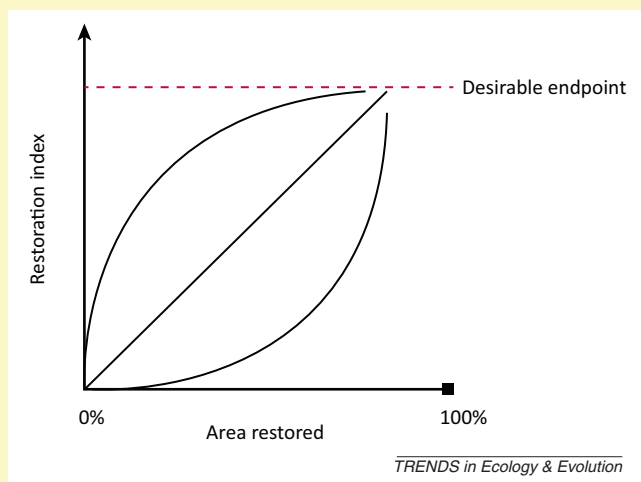

Figure I. Graphical relations between area restored and restoration outcome. Possible relations include: linear, concave (highly mobile organisms, large range sizes, large body sizes, and habitat generalists), and convex (for small organisms with low dispersal, and habitat specialists).
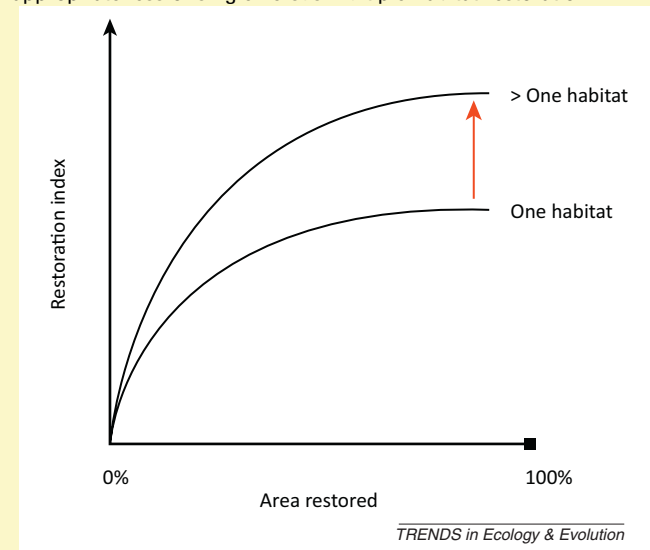

Figure II. Differences between single and multiple habitat restoration (an asymptotic curve is assumed). The restoration index in the y axis refers to the restored levels of biodiversity and ecosystem function.

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spatial-scale experiments, in the form of controlled field experiments replicated over large areas and in different regions (e.g., BIODEPTH, [57]), are still absent in restoration ecology. We believe that field experiments could be used to assess the functional consequences of assembly history, that is, testing which sequences of species addition and/or removal achieve restoration of functional, resilient communities. For restoration ecology to move from a site- and situation-specific discipline to a more globally applicable science, long-term, large-scale field experiments are badly needed.

Concluding remarks

Restoration leads to an increase in ecosystem service provision relative to degraded ecosystems [58], is usually cheaper than other 'engineering' solutions, such as artificial hand pollination [59], and provides additional services [60]. To achieve the restoration of biodiversity and ecosystem services, restoration actions need to be tightly coupled with 'state-of-the-art' scientific progress. Whereas theories of population dynamics, succession, or alternative states, are well embedded in restoration projects, other ecological concepts from biodiversity–ecosystem functioning, food-web theory, and metacommunity theory, are less commonly considered. These theories provide conceptual and quantitative knowledge on aspects of biological communities that can contribute enormously to the restoration of biodiversity-based ecosystem services.

Despite recent advances in ecological research, knowledge gaps remain regarding the recovery of the ecosystem services of biodiversity that merit further theoretical and empirical exploration. Future progress requires models that focus on restoring functional, resilient (meta)communities along with the services they provide (e.g., trait-based approaches in spatially explicit multitrophic models), as well as long-term, large-scale experiments. Although long-term monitoring of restoration projects is starting to be addressed, landscape-scale experiments replicated over large spatial scales that evaluate different restoration scenarios and recovery trajectories are lacking. These models and field experiments would be extraordinarily valuable for identifying the factors that lead (and do not lead) to successful restoration of species, interactions, and ecosystem services, and, more generally, for moving restoration ecology from a site- and situation-specific discipline to a more globally applicable science.

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