Perspective

Challenges and directions toward a general theory of ecological recovery dynamics: A metacommunity perspective

Daniel Montoya[1,2,3,*]

[1]Basque Centre for Climate Change (BC3), Edificio Sede 1, Planta 1, Parque Científico UPV-EHU, Barrio Sarriena, Leioa, Spain
[2]IKERBASQUE, Basque Foundation for Science, Bilbao, Spain
[3]Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, UMR 5321, CNRS, 09200 Moulis, France
*Correspondence: daniel.montoya@bc3research.org
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SUMMARY

Global change degrades ecosystems worldwide. Scientific research has advanced our knowledge of the impacts of global change on ecosystems. Comparatively, however, it remains unclear how ecosystems recover after disturbances. In this perspective, I contend that ecological restoration should advance toward a general, dynamic theory that describes the recovery rates and trajectories of ecosystems along restoration. This approach should address three fundamental challenges corresponding to three components of ecological systems: complexity (how do we quantify ecological restoration?), space (what are the spatial scales of restoration?), and global change (how does global change determine restoration's reference states?). A generic model and experiment based on metacommunities is used to illustrate how these challenges can be addressed. Given the extent of ecosystem degradation and the international consensus to restore ecosystems, revealing the patterns and mechanisms underlying recovery is a fundamental and timely issue toward a general theory of ecological restoration.

INTRODUCTION

Anthropogenic global change has degraded the natural world to unprecedented levels. Climate change, landscape destruction, and fragmentation of natural habitats are major threats to biodiversity and the functioning and stability of ecosystems. To understand and mitigate the effects of global change on ecosystems is thus the environmental challenge of our age. In this context, ecological restoration has emerged as one fundamental tool to stem the biodiversity crisis and repair damaged ecosystems, and there is international consensus on the urgent need to understand ecological recovery and restore ecosystems. The standards initially established by the Convention on Biological Diversity (i.e., restore 350 million hectares across the world)[1] have repeatedly been ratified,[2–4] and 2021–2030 has been declared the United Nations (UN) Decade (2021–2030) of Ecosystem Restoration.[5] Accordingly, the recent times have witnessed an incredible advance in the number of restoration studies, and many datasets on the recovery of biodiversity and ecosystem functions have been assembled and are available today.[6–10]

Despite this progress, the outcome of restoration is variable, e.g., Suding[11] and Brudvig et al.,[12] and its success has so far been limited, failing to achieve the 2020's international biodiversity targets.[13] This is partially because most restoration studies are largely phenomenological and context-dependent, limiting our ability to develop general principles for a firmer scientific theory, as scaling from single species and populations through to biotic interactions, multispecies community dynamics, and ecosystem functioning, is challenging. From a scientific perspective, it has been argued that "restoration ecologists should concern ourselves with developing the science to improve the speed, magnitude, and efficiency of ecosystem recovery."[14] Therefore, it is essential to advance toward a general theory of ecological recovery dynamics, which will ultimately allow identification of the patterns and mechanisms of recovery, to understand what actually is recovery and how it evolves over time, and how active efforts can accelerate it. This theory should be able to describe the dynamics of ecological restoration, specifically two fundamental phenomena: the recovery rates (speed of recovery) and recovery trajectories (shape of recovery, e.g., nonlinearities, thresholds) of ecological systems along restoration, as well as the factors influencing those rates and trajectories.

Despite the development of a general theory is beyond the scope of this study, I contend that a dynamical, holistic approach will be fundamental to achieve this goal. A dynamical perspective is important to reveal the temporal changes of ecological variables along restoration. Most information on ecosystem recovery patterns is based on a few data points, usually corresponding to pre-, end-of-, and one or few post-disturbance states, e.g., Moreno-Mateos et al.,[6,8] Curran et al.,[7] Rey-Benayas et al.,[9] and Jones et al.[10] This prevents detailed analyses of how fast or slow communities recover—i.e., rates—and the shape of such recovery. Restoration would also benefit from adopting a holistic approach where multiple variables describing the structure, function, and stability of ecological systems are investigated. Although the feasibility of this approach depends

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Box 1. The restoration of the Brazilian Atlantic Forest: a metacommunity view

The Atlantic rainforest is a biodiversity hotspot with high levels of endemism,[15] of which ~12% of the original surface remains today.[16,17] In 2009, nongovernmental organizations, governments, and research institutions joined forces and created the "Atlantic Forest Restoration Pact" (AFRP),[18] which aims to restore 15 million hectares of the Brazilian Atlantic Forest by 2050.[19,20] Although initial restoration concentrated on site-, species-specific vegetation approaches, e.g., Barbosa et al.[21] and Siqueira,[22] studies now tend to consider several facets of ecological complexity. For example, Ribeiro et al.[23] showed that the diversity and complexity of species interactions between plants and seed dispersers increases with time since restoration, with positive implications for landscape-scale seed dispersal.

The Atlantic forest is highly fragmented: the remaining forest landscape constitutes a complex mosaic formed mainly by small fragments (<50 hectares) and clusters of close neighboring fragments (<200 m apart). Thus, a metacommunity perspective provides valuable insights into their conservation and the landscape-scale restoration of the rainforest, e.g., understanding the abundance and distribution of multiple species in space and time; the degree to which species are dispersal-limited; and the diversity and composition of species, their interactions, and functional groups, across spatial scales. For example, a study of a bird-seed dispersal metacommunity in 16 remnant forest fragments reveals that the cumulative frequency of different functional groups increases with fragment size, and that only a subset of the interactions (i.e., those involving small-seeded, fast-growing plant species and generalist, small-bodied bird species) dominates the metacommunity.[24] This metacommunity view shows that fragment size, distribution, and connectivity are key elements to restore diverse, functional, and stable forest ecosystems, and suggests how to select sites to be restored, e.g., the close proximity of forest fragments (distances <100 m) greatly affects the speed and trajectory of forest recovery, as well as the reestablishment of critical interactions and ecosystem functions (e.g., dispersal, pollination, herbivory[25]). Metacommunity models can predict the number, size, and connectivity of forest fragments to recover a desired level of biodiversity, function, or stability. Besides, empirical studies are based on snapshots or have a low temporal resolution due to infrequent monitoring. Models and experiments can overcome this limitation by generating highly resolved time-series; these data are useful to actively decide what, how, and when we can intervene to accelerate restoration and recover stable and functional forests. Metacommunity models can also explore the effects of global change on AFRP actions. The concepts of habitat size, number, distribution, and connectivity also apply when restoring forest sites within a fragmented landscape. On the other hand, metacommunity models and experiments can identify species and functional groups most affected by climate change, which helps design interventions to mitigate its effects and achieve successful restoration.

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on the aim of restoration, its scale, and the availability of resources, the underlying rationale is that global change impacts different community aspects at the same time, and therefore studies that encompass these elements simultaneously – rather than single species or populations – are urgently needed to understand how communities restore.

In this perspective, I discuss challenges for restoration scientists along three main components of ecological systems: (1) the challenge of complexity (how do we quantify restoration of ecological systems?), (2) the challenge of space (what are the spatial scales of ecological restoration?), and (3) the challenge of global change (how does global change determine the reference state of restoration?). Because metacommunity approaches are useful for their ability to incorporate ecological complexity at different spatial scales (see Box 1 for a practical example), I use a generic model and an experiment based on metacommunities to illustrate how these challenges can be addressed. Collectively, the approach presented in this perspective complements well-established concepts of restoration science (Box 2) with a (meta)community ecology view, and contributes toward furthering our understanding on ecological recovery dynamics.

CHALLENGES OF RESTORATION ECOLOGY

The success of ecological restoration depends on social, economic, and scientific factors. Here, I present three scientific challenges to develop a dynamic, holistic approach that allows restoration ecology to become a more rigorous, pre-

dictive science. These challenges correspond to three main components of ecological systems – complexity, space, and global change. Although the temporal component is implicitly assumed (the very notion of restoration implies "moving" from one state to another), it is the focus of recent research[6–10] and will not be addressed in this perspective.

The complexity challenge: How do we assess restoration?

Ecological restoration seeks to restore diverse, functional, and stable systems. This corresponds to three facets of ecosystem complexity: its structure (e.g., nonrandom ecological interactions), functioning (the provision of functions and services), and stability (dynamics or flexibility/variability of ecological properties). This perspective focuses on the importance of these three facets for restoration, and how to quantify them. Efforts to restore the evolutionary potential of ecosystems have been discussed elsewhere[36] and will not be included here.

Species interactions

Species interactions are fundamental to understand ecological recovery for several reasons. First, communities change to disturbances without changes in species richness,[37,38] i.e., the loss of species and interactions are decoupled. In addition, interactions are lost faster than species and affect the provision of functions and services at faster rates than species extinctions.[38,39] Therefore, interactions are a better, or at least complementary, indicator of ecological recovery than a list of species and their abundances. Secondly, interaction networks inform not only about how biodiversity is structured—i.e., which

> **Box 2. Theoretical foundations of restoration ecology**
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> The first theoretical basis of restoration ecology probably comes from the concepts of ecological development and ecosystem organization. The concept of ecological development was termed by Odum (1969),[26] who presented a tabular model of ecological succession whereby several ecosystem trends are expected from the early stages to mature developmental stages. Margalef (1968)[27] applied information theory to quantify the structural organization of ecosystems—ecosystem organization—represented by their taxonomic diversity, using species' diversity and connectivity as measures of ecosystem organization and complexity. A few years later, Connell and Slatyer (1977)[28] were among the first to gather these concepts and formulate a clear theory of ecological succession—the process by which the structure of a biological community evolves over time—that included the idea that species identity and the effects of the first-arriving organisms (i.e., priority effects) are important for a community's further development. Facilitation, inhibition, and tolerance were postulated as the main mechanisms to explain succession, and their relative importance changed as a community goes through succession. One of the best studies on succession is that of Chapin et al. (1994)[29] in Glacier Bay, Alaska, where both facilitation and inhibitory mechanisms were empirically documented. Although the process of succession has been studied by ecologists for several decades, it is still an active field of study.
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> Restoration also builds on assembly theory to determine fundamental assembly rules of recovering communities—i.e., those that result in persistent communities.[30] Different assembly models have been proposed, from conceptual (e.g., dynamic filter model[30]) to more quantitative ones.[31] Studies of community assembly have found that invasion resistance increases with time, and that different assembly sequences can result in different community endpoints. Perhaps the most interesting result is that assembly is a nonlinear process that can lead to different community trajectories (i.e., the sequence of species additions and subtractions) and thus stable endpoints. This is summarized by the concept of alternative states, a theory that supports that alternative, persistent combinations of ecosystem states and environmental conditions might be possible. Applied to restoration,[32] models of alternative states might explain why degraded ecosystems are resilient to restoration and how selected disturbances can release degraded ecosystems from strong internal feedbacks and drive them to successful recovery. Disturbance is an important part of ecological succession and community assembly, and thus represents a central concept in restoration. Disturbances vary in size and intensity, and not only are events that produce degradation or change of state, but also are an essential tool in ecological restoration for its ability to modify ecosystem dynamics.[33] More recently, there is a small, but increasing tendency to incorporate community ecology theory into ecological restoration.[34,35]

species interact with which others, and how often—but also about the functioning of ecosystems.[37] Studies demonstrate qualitative links between structure and function in multitrophic communities,[40] and how the loss of interactions between species threatens multiple functions, e.g., seed dispersal, primary productivity, carbon storage.[41–44] For their effects on functionality, restoring species interactions is a sign of the functional systems that restoration targets.

Species interactions are fundamental to understand the success (and failure) of restoration actions. The analysis of the role of predation in ecosystems illustrates this point, although examples of other interaction types are possible (e.g., mutualism, parasitism). The impact of predator loss caused by cascading effects down through the species interaction network are quantitatively similar to the impact derived from the transformation of a diverse plant community into a single crop.[45] Conversely, many changes in restored ecosystems are only understood through the lens of food web theory, i.e., as a cascade of interactions that begins with the reintroduction of a key-stone predatory species. For example, the reintroduction of wolves into Yellowstone in the mid-1990s recovered much of the biodiversity lost,[46] whereas the reintroduction of sea otters led to the recovery of biodiversity and biomass production of kelp forests in the North Pacific through its effects on sea urchins.[47] Both examples illustrate successful restoration programs where species interactions and their structure led to the recovery of other species and the functionality of the entire community.

Functionality

Restoration often focuses on single functions, e.g., carbon cycling, nitrogen cycling, soil erosion. This overlooks the fact that (1) ecosystems are multifunctional, i.e., they provide multiple functions and services, and (2) functions are not always correlated positively. Ecosystem functions interact with each other, forming synergies and trade-offs.[48,49] For example, the reintroduction of predators reveals parallel increases in the rates of predation and production of plant biomass (synergy) at the expense of a reduction in herbivory (trade-off). Similarly, crop production is favored at the cost of biodiversity and biodiversity-based services (e.g., pollination and pest control) in agricultural systems. Given the existence of such trade-offs, measuring various functions should be a priority in restoration, especially if we want to restore multifunctional landscapes. Recent works suggest that restoring multifunctional landscapes is possible if moderate service levels are deemed acceptable, even where there are trade-offs between services.[50] Methodologically, advances have recently been made to quantify multifunctionality,[51,52] and they could readily be used in ecological restoration.

Stability

Despite being very influential in global change biology, the concept of ecological stability has seldom been applied in restoration. This is intriguing, as one main goal of restoration is to restore stable, self-sustained ecosystems (without further human intervention), but comprehensible given that ecological stability is still an open field of research. The problem with stability is similar to that of functionality and to making general statements about the effects of biodiversity on ecosystem functioning: the answer depends on the function, and changes with increasing number of functions. Similarly, stability has multiple components, e.g., resilience, resistance, variability, persistence.[53,54] Most of them are strongly correlated in undisturbed ecosystems,

but disturbances can alter and decouple these correlations.[55,56] Restoration is a successional process involving changes in species numbers and composition, interactions, and environmental conditions, and active restoration imposes disturbances to accelerate recovery. Given that successional dynamics and active restoration efforts, either individually or in combination, might de-correlate the strong dependencies among stability metrics, recovering ecosystems are among the most interesting and relevant systems to analyze the strength of correlations among stability metrics.

Ideally, restoration studies should start considering multiple stability metrics and investigate how they vary along recovery. At the very least, the assessment of restoration outcomes should quantify both the mean values of ecological variables and their variability through time,[57] given that variability is a stability property that is integrative and much easier to measure empirically than other ones. Various approaches[58–60] are possible to add such temporal dimension and provide insights into the variability of different complexity facets along the recovery process. This information is key to assess the stability of restored ecosystems.

The challenge of space: Spatial scales of restoration?

Traditionally, restoration has been applied to specific locations, habitats, or habitat fragments. However, local-scale restoration might be inappropriate given differences in the spatial distribution between consumers and resources,[61] and the dependence of some species on different habitats that provide different resources. Metacommunity theory provides the ideal framework to understand the spatial scales of restoration. First, it shows that the structure of ecological communities changes with the spatial scale,[62–64] and that the relationships between habitat size and community structure are not necessarily linear (e.g., due to dispersal constraints). This indicates that restoration at the local scale does not always translate into landscape-scale restoration. Second, mobile organisms (e.g., pollinators, predators, and seed dispersers) actively move between habitat fragments, functionally connecting habitats in space,[65,66] and contribute importantly to ecosystem services.[67,68] These species are generalists in habitat range and interaction patterns and have clear spatial roles, e.g., core species form the core of the metacommunity, interacting consistently with multiple species in various habitats or habitat fragments, whereas connectors ensure community cohesion, typically within the same habitat or fragment of habitat.[69,70] These two types of species or spatial roles are key to understand the permeability of habitats to species, interactions and the functions they provide, and are thus particularly important for landscape-scale restoration.

Ultimately, a better understanding of what landscape configurations favor functionally important species is important in restoration. For example, a recent study shows that pollinators connect habitats at a regional scale by feeding on different plants in multiple habitats.[67] Landscape management is often focused on preserving and restoring connectivity between fragments of similar habitat,[71] but pollinators connecting various types of habitat indicate a dependence of species on multiple habitats.[72] In this case, the restoration of pollinator species and their pollination services should avoid a discontinuity in resource provision and adopt a multi-habitat perspective[73] that is the focus of metacommunity studies.

The challenge of global change

Because global change is a widespread phenomenon, global change factors will affect the recovery dynamics of ecological systems. However, aside from the recognition that historical ecosystem states prior to disturbances offer a biased target or reference of recovery,[74] little is known on the effects of global change on ecological recovery. Global change could be changing equilibrium points constantly so that alternative, persistent combinations of ecosystem states would be possible (i.e., alternative states, Box 2), compromising long-term restoration goals. In this context, it has been argued that "a more realistic goal is to move a damaged system to an ecological state that is within some acceptable limits relative to a less disturbed system," and that restoration can be viewed as "an attempt to recover a natural range of ecosystem composition, structure and dynamics."[75] If recovering ecosystems change substantially in their species composition and interactions, and therefore in their functioning and stability under global change, then restoration goals, currently based primarily on species persistence, should be adapted to include more general aspects of the metacommunity (i.e., holistic approach).

Global change drivers interact in different ways, and this has implications for restoration (Figure 1). For example, changes in dispersal due to climate interact with other global change drivers, e.g., habitat fragmentation. A recent study with butterflies reveals that dispersion distances are greater both at lower temperatures in a fragmented landscape and in continuous landscapes and warmer conditions, but lower in the opposite cases.[76] Dispersion thus depends on temperature when the landscape is fragmented, but is temperature-independent in continuous habitats. Understanding the effects of such complex, nontrivial interactions on recovery dynamics requires new research questions as well as models and experiments designed to investigate the individual and combined effects of global change drivers on recovery (see "directions toward a theory of recovery dynamics"). Here, I focus on two main global change drivers—climate warming and the loss and fragmentation of natural habitats.

Climate warming

Climate warming impacts different facets of ecological complexity in multiple ways. Warming benefits certain functional traits over others, e.g., smaller body sizes, and these traits are associated with species' dispersal abilities and diet breadth,[79] as well as with species' evenness and dominance patterns of abundance.[80] These changes affect metacommunity dynamics (e.g., small-sized organisms usually disperse less), which in turn impact community structure and functioning, modifying biodiversity-ecosystem functioning (BEF) relationships. The consequences of varying environmental conditions on BEF relationships are nontrivial and depend on the function that is considered,[81,82] potentially generating trade-off responses among functions. Warming also produces range shifts,[83] trophic and phenological mismatches,[84–86] and higher species and interactions turnover in novel ecosystems, and can impact the stability of restored systems, e.g., by increasing the temporal variability of biomass production.[87] In sum, warming alters all three facets of ecological complexity (species interactions, functionality, and stability) and, consequently, will influence recovery dynamics.
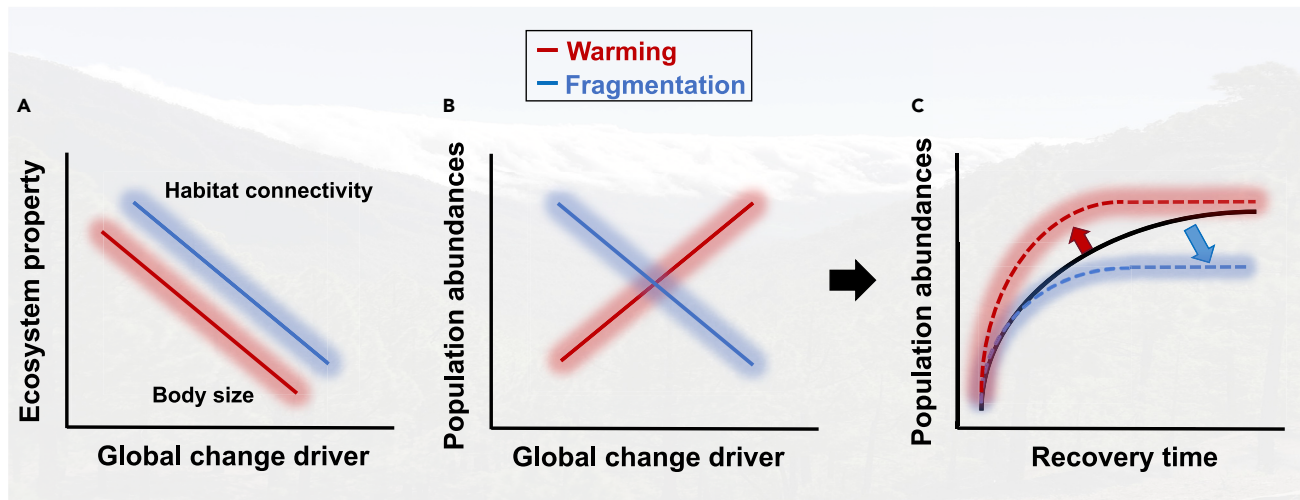
Figure 1. Effects of global change on communities and implications for their restoration

Two types of nonadditive effects are possible from interactions among global change drivers: either they combine synergistically (total effect is amplified), or antagonistically (total effect is reduced). Although there are multiple global change drivers, here I focus on two of them: climate warming and habitat fragmentation.

(A) Habitat fragmentation and climate warming can impact community properties in the same direction. Both drivers affect two properties (spatial connectivity, body-size distributions) in the same manner (fragmentation reduces spatial connectivity, warming favors small individuals), which reduces dispersal. If such reductions in dispersal are large, biodiversity decreases (number of species and the evenness patterns of abundance),[77] which ultimately decreases functionality.
(B) Opposite effects of warming and fragmentation are also possible. The example is based on opposite responses of British butterflies' abundances.[78]
(C) Restoration prediction assuming opposite effects of warming and fragmentation (taking the butterfly example from B). The temporal trajectory is assumed to be saturating for illustrative purposes. The black line represents recovery in the absence of global change. Because warming and fragmentation differ in their effect on butterfly populations (B), predictions on the combined effect of both drivers on the recovery rates and trajectories of butterfly populations are more complicated.

Habitat loss and fragmentation

The loss and fragmentation of natural habitats reduces the amount of suitable habitat for biodiversity, increasing the isolation of habitat patches and causing a dispersal limitation. The effects of limiting dispersal not only lead to species extinction,[88] but also causes ecosystems to change substantially beyond species numbers, e.g., modifying the structure of species interaction networks,[89,90] the frequencies of species interactions,[41] and the distribution of functional traits.[91,92] Human management of ecosystems, including restoration, often affects the amount and distribution of natural habitats. This generates trade-offs between functions that can affect the magnitude and stability of ecosystem services,[49], which in turn result in a wide range of BEF relationships.[93,94] In sum, dispersal limitation derived from the anthropogenic landscape management can have a huge impact on the structure, functioning, and stability of recovering communities.

DIRECTIONS TOWARD A THEORY OF RECOVERY DYNAMICS

A general theory of ecological recovery dynamics should be able to describe two fundamental phenomena: the recovery rates (speed of recovery) and recovery trajectories (shape of recovery, e.g., nonlinearities and thresholds) of ecological systems. Several combinations of recovery rates and trajectories are possible, might be context-dependent, and vary across complexity facets (Figure 2). Such general theory should also identify and understand the factors that alter those rates and trajectories; two such factors are discussed in this perspective:

space and global change. An overview of the type of questions (Box 3, Q1-Q4) and associated hypotheses for restoration ecology to address is provided in Box 3. The model and experiment in this section are designed to address these questions.

Methodologically, a general theory requires a balance between observations, theory, and experimentation. Although restoration actions are necessarily idiosyncratic, this site-specific nature hinders comparisons among systems and synthesis efforts. Restoration ecology has made substantial advances in the past decades, and many datasets (from observational studies and meta-analyses) have been assembled that reveal universal patterns of recovery across ecosystems, disturbance types, and geographical locations, e.g., Moreno-Mateos et al.,[6,8] Curran et al.,[7] Rey-Benayas et al.,[9] and Jones et al.[10] However, quantitative, predictive restoration models are generally absent, and the type of large-scale, replicated experiments used in disciplines such as invasion ecology[95] and community ecology[96] are still seldom applied in restoration. For models and experiments to be reliable, and their predictions representative of natural systems, we need "coupled" designs where models are implemented in parallel with ad hoc experiments designed to test model predictions, e.g., Gilarranz et al.[97]

Metacommunity theory provides a useful framework to investigate temporal changes in the recovery rates and trajectories (Figure 2) of various complexity facets (challenge #1), across space (challenge #2) and under global change (challenge #3). The model and the experiment proposed below are generic and show how this framework is used to explore (1) the recovery of ecological systems after anthropogenic disturbances, and (2)
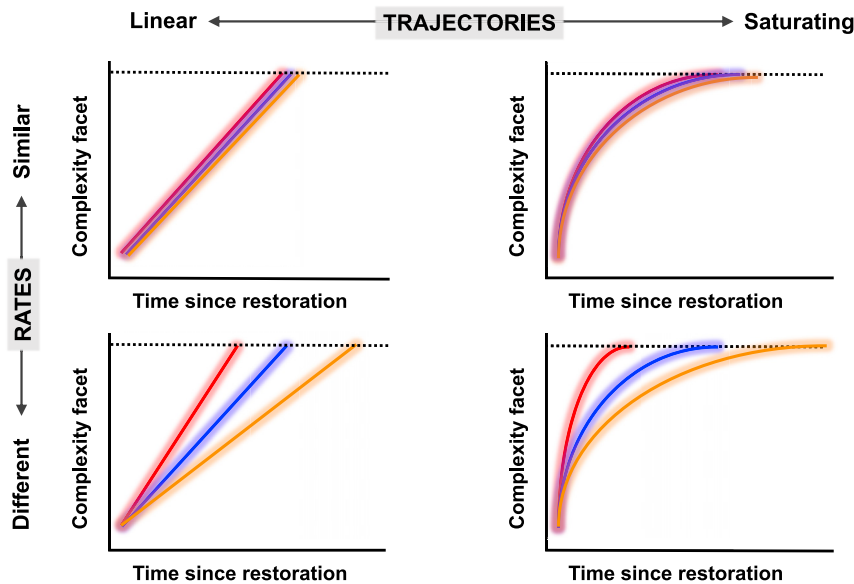
Figure 2. A diversity of recovery patterns in ecological systems
Different rates and trajectories result in different recovery patterns. Multiple recovery patterns are observed in meta-analyses (D. Moreno-Mateos and A. Rodríguez-Uña, personal communication). The figure shows four example scenarios corresponding to four general recovery patterns, from linear/similar to different/saturating (the rates and curves have illustrative purposes only). For simplicity, all scenarios assume the restored system eventually reaches the reference state. Different colors represent different complexity facets.

the impact of global change on recovery dynamics. Recovery dynamics are quantified after an initial disturbance, which varies depending on its intensity, size, and frequency. Both the model and experiment quantify changes in several complexity facets along restoration (Table 1). Q1–Q4 refer to the research questions presented in Box 3. Box 1 illustrates how metacommunity theory can complement existing restoration programs.

What type of models?
Despite theoretical models have largely been used in restoration ecology (see Box 2),[30,74,98] the type of model that I propose, and that is seldom used in restoration, is a dynamic one, considers spatial and trophic dynamics, diverse stability metrics, and multiple species and functions. The scientific literature, especially in ecological networks, provides examples of this type of modeling framework, e.g., multilayer/multiplex models, dynamic network models, and adaptive network models.[58–60,99] The backbone of these models is that they can explore temporal changes in recovery rates and trajectories of several complexity facets (Figure 2). They, however, differ on the identity and range of variables they measure, so model choice depends on the specific restoration goal or question. Here, I focus on metacommunity models,[62] which provide a framework for assessing the roles of local and regional-scale dynamics in determining diverse complexity facets (challenge #1 and #2). In these models, communities consist of spatially distinct local habitats or assemblages linked through the dispersal of multiple interacting species. These models can also investigate the effects of global change on ecological recovery dynamics (challenge #3).

General model
Metacommunity models typically simulate communities consisting of a set of M patches that hold multiple species and trophic groups, where species disperse among patches (i.e., trophic and spatial dynamics). A first step consists on defining what feeding interactions actually occur (e.g., as many food webs are size-structured,[100] restrictions to feeding interactions are imposed based on

the body size of consumers and resources[101]). Once the fully connected network is established, ordinary differential equations are assigned to each species i of the community to calculate changes in species i biomass in patch j, B_{ij}, through time, t[102] (biomass units are easily transformed into numerical abundances by dividing by species body mass). For example, in a two-trophic level metacommunity, Equations 1 and 2 give the rate of change in biomass for producers and consumers, respectively:

$$\frac{dB_{ij}}{dt} = r_i B_{ij}\left(1 - \frac{B_{ij}}{K_{ij}}\right) - \sum_s F_{is}B_{ijs} - \delta B_{ij} + \frac{\delta}{M-1}\sum_{k \neq j}^{M} B_{ik}$$

(Equation 1)

$$\frac{dB_{ij}}{dt} = \sum_s e_s F_{is}B_{ijs} - B_{ij} + \frac{\delta}{M-1}\sum_{k \neq j}^{M} B_{ik},$$ (Equation 2)

where s represents the subset of all species that interact with species i, given by the niche model. Basal species grow logistically with an intrinsic net growth rate, r_i, and a carrying capacity, K_i. Species gain and lose biomass by feeding, F_{is}, and assimilate consumed biomass with a ratio of e_s (assimilation efficiency). Consumers additionally lose biomass through respiration, x_i (sometimes considered as mortality rate; respiration can also be estimated scaling up from individuals using abundance data). Species disperse at rate δ, and different dispersal scenarios can be explored (e.g., global dispersal is assumed in Equations 1 and 2, but other regimes are possible: density-dependent, body size-dependent, distance-dependent). For example, in case of density-dependent dispersal, the last two terms in Equations 1 and 2 are substituted by $\frac{\delta}{M-1}(B_{ik} - B_{ij})$.[103] The functional response F_i describes the feeding dynamics. Holling type II-III functional responses are used:

$$F_i = \frac{a_i B_{ij}^h}{(1 + a_i)B_{ij}^h},$$ (Equation 3)

Box 3. Overview of potential research questions

This box includes examples of the type of questions (Q1–Q4) and some associated hypotheses (in *italics*) to investigate the temporal changes in the recovery rates and trajectories of several complexity facets (challenge #1), across spatial scales (challenge #2), and under global change scenarios (challenge #3). The model and experiment in the main text are designed to address these questions.

Question 1: Metacommunity recovery dynamics in the absence of global change: assembly versus recovery and spatial scales.

What are the rates and trajectories of different ecological complexity facets along restoration?

Different facets recover at different rates. These differences determine BEF relationships along restoration.

Generalist species colonize first. Functional complementarity of species and interactions increases with recovery time, thus leading to more linear BEF relationships.

What are the similarities and differences between natural (i.e., seasonal) assembly and recovery dynamics?

Whereas naturally assembled ecosystems typically respond fast to climate-driven seasonal changes, slow and abrupt responses characterize ecosystem recovery.

Recovery dynamics take longer to stabilize due to the effects of anthropogenic disturbances.

What are the adequate spatial scales for restoration?

Larger spatial scales with >1 habitat type (i.e., landscape) result in faster and more efficient restoration.

Dependent on organism type (dispersal capacity and resource demands) and/or the ecological process(es) or function targeted for restoration.

Question 2: Effects of climate change on metacommunity recovery.

What are the effects of increasing temperature regimes on metacommunity recovery?

Climate change alters BEF relationships due to changes in the distribution of functional traits, and species' diet breadth (which affects interactions). Such changes ultimately determine recovery rates and trajectories.

Climate change alters a number of ecosystem functions, such as biomass production and respiration; this generates functional trade-offs that influence global functionality in recovering systems.

Question 3: Effects of fragmentation on metacommunity recovery.

What are the effects of habitat loss and fragmentation on metacommunity recovery?

Fragmentation reduces functioning of recovering ecosystems due to diversity loss.

Fragmentation decreases the stability of recovering ecosystems due to changes in dispersal and species interaction strengths.

Is there a maximum level of habitat loss (minimum number of intact habitat patches) and/or maximum level of fragmentation for community recovery?

The rates of passive recovery are determined by the regional species pool, which in turn depends on the number of intact fragments.

Maximum fragmentation levels differ across organisms (e.g., due to differences in dispersal capacity).

Question 4: Effects of climate change + fragmentation on metacommunity recovery.

What is the combined effect of warming and fragmentation on the restoration of communities?

Trade-offs and synergies among functions, and between the average provision and stability of these functions, are expected under the combined effect of warming and fragmentation. The global effect on BEF relationships depends on the directionality of the effect of warming and fragmentation (Figure 1).

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where a_i is the maximum consumption rate of i, h is the Hill's exponent, that determines the shape of the functional response (type II while $h = 1$; type III while $h = 2$).

Different alternatives to include functionality are possible. The most straightforward way is to assume that all species contribute to all functions and that their contribution is proportional to their abundance.[104] Functionality can be included more explicitly, e.g., total productivity at the metacommunity level ($\sum_{S, M} B_{ij}$), primary productivity (biomass of the basal species), secondary productivity (biomass of consumer species), and respiration ($\sum_{S,M} x_i B_{ij}$). Ecological stability is measured as the coefficient of variation of several complexity facets (Table 1). In sum, this simple metacommunity model allows to study the temporal dynamics of structural, functional, and stability variables (challenge #1) as well as their spatial dynamics (e.g., by varying the number of patches, the distance between them, and the dispersal ability of organisms; challenge #2).

Metacommunity recovery dynamics

Challenges #1 and #2; Box 3, Q1. One difficulty when modeling restoration is to differentiate natural assembly dynamics (i.e., those derived from seasonal changes or natural disturbances) from recovery dynamics. Ecosystem components recover differently[36]; this is what has been conceptualized as the filter model,[30] whereby the process of community assembly after disturbance involves a series of filters (biotic and abiotic) that must be passed. Besides, recovery depends on disturbance type, which varies in size (regional versus local scale; affecting one, several, or all populations or trophic levels), intensity (pulse [fire, flooding] versus press [global warming, exploitation]), nature (natural versus anthropogenic), and frequency (e.g., one pulse versus multipulse). For example, local disturbances affect individual habitat patches (and the communities inhabiting them) within the metacommunity, whereas regional disturbances affect a larger number of patches and, therefore, a larger fraction of or the entire metacommunity. This multifaceted

Table 1. Example of variables measured in model and experiment (complexity facets)

Diversity and interactions
• α-diversity, β-diversity
• Abundance distributions
• Species interactions (network properties, interaction strengths)
Functionality
• Production (e.g., primary, secondary)
• Biomass (total, pyramid structure)
• Other: biogeochemical functions, pollination, herbivory control
Stability (i.e., invariability)
• Population stability
• Compositional stability
• Functional stability

nature of disturbances hinders the study of recovery dynamics, but several alternatives are possible. For example, the metacommunity model can sequentially restore habitat patches after an initial disturbance. Meta-analyses show that recovering ecosystems accumulate a recovery debt,[8] and this likely influences certain model parameters. Several hypotheses can be tested, e.g., disturbances mostly impact growth rates or the system's carrying capacity. As empirical studies accumulate, models can be fed with information on how ecological communities recover, and what parameters are mostly affected by the disturbance. Alternatively, the metacommunity model can simulate a naturally fluctuating background environment that mimics seasonality and that determines metacommunity dynamics and their seasonal assembly. On top of seasonal dynamics, different disturbances can be added (pulse, press, multipulse, affecting either or both trophic levels, local or metacommunity scales, environmental stochasticity) and compare the temporal dynamics of systems undergoing seasonal dynamics versus systems experiencing both seasonal dynamics and different types of anthropogenic disturbances. This type of approaches allows establishment of a theoretical differentiation between natural assembly and recovery dynamics, and to assess the roles of local and regional-scale dynamics in determining the recovery of different complexity facets (challenge #1). The model can simulate spatially explicit landscapes at different spatial scales (challenge #2): varying the spatial scale results in landscapes with local communities inhabiting habitat patches that differ in their number, size, distribution, and interpatch distances. Differences in landscape characteristics across spatial scales have direct effects on species diversity and their interactions,[67,105,106] which in turn determine the functioning and stability of recovering metacommunities. This model is generic but can be adapted to reflect a particular disturbance, community, habitat, or spatial scale.

Global change effects on metacommunity recovery dynamics

Challenge #3; Box 3, Q2–Q4. To investigate how increasing temperature regimes affect local and metacommunity recovery dynamics (Box 3, Q2), the model includes temperature dependencies of several population rates and trophic interactions. All parameters, except for assimilation efficiency, e, and the hill exponent, h, scale with species' body mass and tempera-

ture.[107,108] To achieve a deeper understanding of temperature effects on recovery dynamics, and in line with recent literature, different temperature dependencies with and without optimum thermal values can be used, i.e., monotonic (i.e., based on Arrhenius equation)[107,109,110] and unimodal dependencies.[111,112] For example, in the case of temperature-dependent metabolic rates, r_i (growth rate), a_i (maximum consumption rate) under a monotonic dependence:

$$r_i = f(m_i, T) = cm_i^b e^{E\frac{T_0-T}{kTT_0}} \tag{Equation 4}$$

$$a_i = f(m_i, m_{i'}, T) = cm_i^b m_{i'}^g e^{E\frac{T_0-T}{kTT_0}}, \tag{Equation 5}$$

where c and T_0 are constants, k is the Boltzmann constant, m_i and $m_{i'}$ are the average body mass of species i and i', respectively, b and g are allometric exponents, E is the activation energy, and T is the temperature. Model parameterization is feasible because of the availability of high-quality data (e.g., activation energies and assimilation efficiencies).

In terms of the restoration challenges mentioned earlier, habitat fragmentation can be considered as a spatial characteristic of the landscape (linked to challenge #2) and/or a global change driver (challenge #3), i.e., a global change factor that modifies the spatial structure of the habitat where communities live. In either case, fragmentation (Box 3, Q3) is implemented by limiting connections between habitat patches, so the impacts of dispersal limitation on metacommunity recovery are assessed. Patches are removed sequentially to study the effects of habitat loss on the metacommunity. To investigate fragmentation (or landscape configuration), patches can be defined in a spatially explicit manner (x, y coordinates), with dispersal being constrained to the nearest neighbor patches and/or decrease with distance from source patch.[113] In a restoration scenario, recovering patches might have different values for certain model parameters (see above) than nonperturbed and destroyed patches, allowing to address questions such as: what is the maximum level of habitat loss (minimum number of intact patches), or the maximum level of fragmentation, for metacommunity recovery? These are also the sort of questions associated with the challenge of space (challenge #3). Finally, the combined effects of warming and fragmentation (Box 3, Q4) are investigated by integrating temperature dependencies and dispersal constraints.

What type of experiments?

As with models, communities of multiple species and interactions should be experimentally assembled and manipulated under different global change scenarios in order to address the above-mentioned challenges. Restoration would benefit from two classes of experiments. First, small-scale experiments should be designed to study what particular parameters of the models are affected by disturbances. For example, in the case of the metacommunity model, these experiments would determine the mechanisms that drive changes in complexity facets subjected to disturbances, i.e., which model parameter/s (e.g., growth rates, carrying capacities) is/are mostly affected by disturbances and, therefore, how recovery dynamics are influenced by disturbances. This would
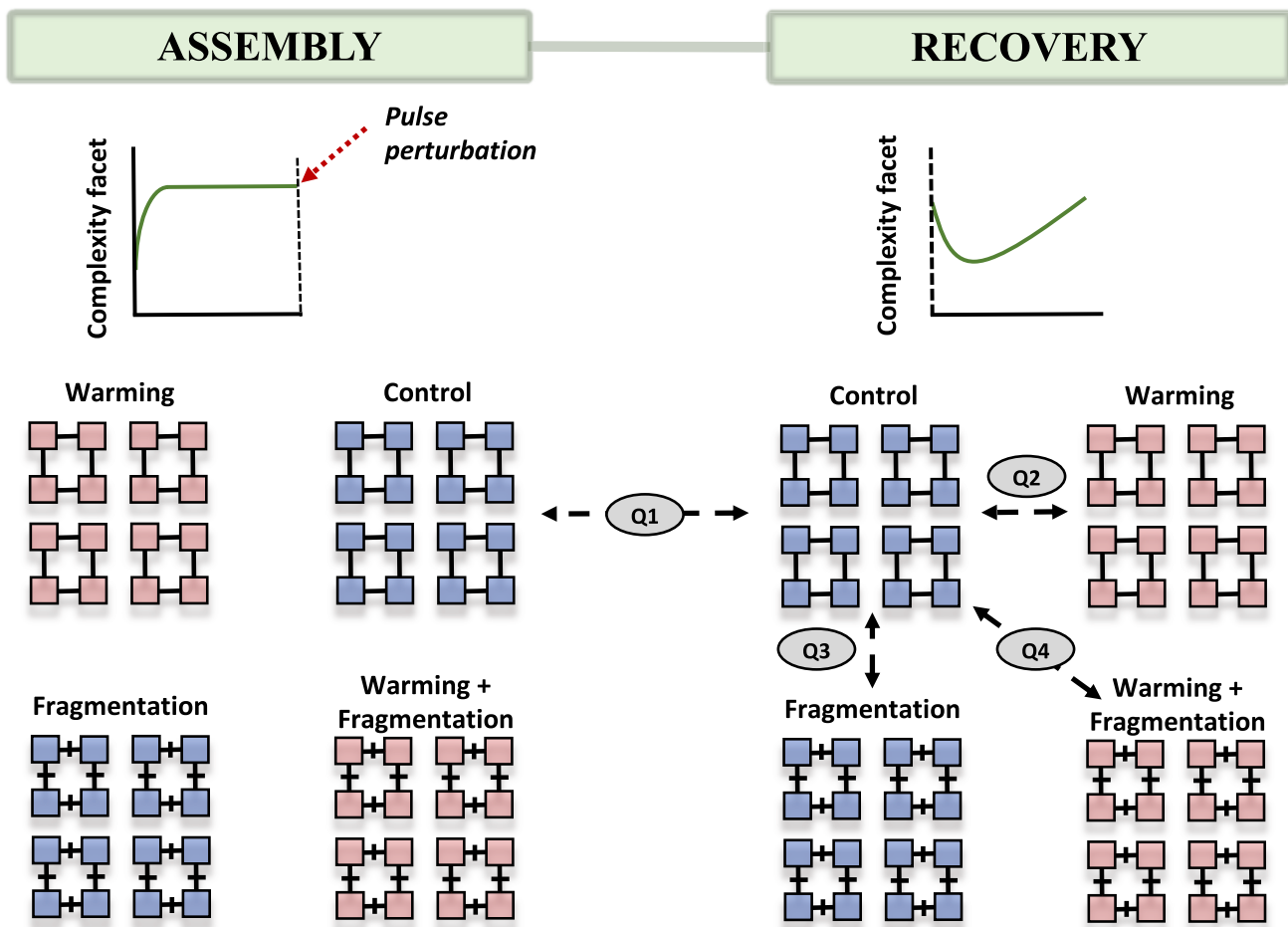
Figure 3. General mesocosm setting to study metacommunity recovery dynamics
For simplicity, experimental units have the same size and number (to address challenge #2, the mesocosm should replicate this setting for different unit sizes and numbers). The relationships drawn in the figures have only illustrative purposes.

help differentiate natural assembly from recovery dynamics (Box 3, Q1).

The second class of experiments are mesocosms. In general, experimental mesocosms lie within two extremes of a trade-off defined by the size/area of the single experimental unit/patch, and the number of replicates. To investigate metacommunity recovery, ideal mesocosms would have individual experimental units with a relatively large patch area and sufficient replication, although this depends on the particular type of local communities under study, e.g., organism size and dispersal (see Haddad[114] for a review of the existing terrestrial mesocosm designs). For feasibility purposes, the studied communities would consist of relatively small-sized organisms with short-intermediate dispersal capacities. For example, in the case of terrestrial communities, the mesocosm can host insect-plant communities of three trophic levels: plants, herbivores (e.g., aphids, caterpillars)/pollinators (e.g., butterflies and bees), and their parasitoids. The interactions among these taxonomic groups affect plant growth, and thus directly influence functions related, among others, with biomass production at different trophic levels.

Figure 3 introduces an example mesocosm design of an adequate size and replication to study metacommunity recov-

ery dynamics under global change, and that is therefore valid to test predictions of the metacommunity model. The proposed experimental setting consists of simulated temperature-controlled units (cages for terrestrial systems, tanks for aquatic systems), each hosting a community of multiple species and trophic levels. These units are connected by corridors that allow migration from one environment to another, thus enabling metacommunity dynamics similar to those in the model. The experimental system without disturbance reflects natural assembly (e.g., seasonal) dynamics (Figure 3, left-hand side) and serves as the control treatment with which the metacommunity recovery dynamics are compared (Box 3, Q1). In the recovery treatments (Figure 3, right-hand side), a disturbance is induced experimentally. Variables in Table 1 are sampled to generate time-series of the assembly and recovery dynamics of metacommunities; these variables are similar to those quantified by the model, so its predictions can be tested. Therefore, this experimental design investigates the recovery rates and trajectories of several complexity facets (challenge #1). By varying the number and size of experimental units, the mesocosm allows investigation of different spatial scales and their effects on metacommunity recovery dynamics (challenge #2).

In Figure 3, for simplicity, experimental units have the same size and number.

The experimental design to address the effects of global change on metacommunity recovery dynamics (challenge #3) can comprise different levels for dispersal (e.g., low/null, intermediate/high), and different levels for warming (e.g., ambient, increased temperature), plus the combined effect of dispersal and warming on recovery (Box 3, Q2-4). Global change treatments in the assembly scenario are useful to investigate potential differences between assembly and recovery trajectories of metacommunities under global change. As an example, in Figure 3 each unit is connected to two other units, and a replicate consists of four units. This results in four replicates per treatment, and 128 units. Depending on the availability of funding and space to set up the mesocosm, the size of the experiment in Figure 3 can be modified. For example, it can be reduced by removing global change treatments in the assembly scenario and/or decreasing the number of *units* per treatment. Conversely, it can be enhanced by increasing the number of treatment levels for warming and fragmentation and/or simulating several types of anthropogenic disturbances (e.g., pulse, press, multipulse).

CONCLUSIONS

A deeper understanding of the ecological recovery dynamics must address three fundamental challenges that correspond to three main components of ecological systems: the challenge of complexity (how do we quantify restoration of ecological systems?), the challenge of space (what are the spatial scales of restoration?), and the challenge of global change (how does global change determine the reference state of restoration?). In this perspective, I have contended that a dynamical, holistic approach is fundamental to achieve this goal, and have proposed a generic type of model and experiment to illustrate how these challenges can be addressed from a metacommunity perspective, and to contribute toward a general theory of ecological restoration. Future research must start to develop this general theory, which will help reveal the patterns and processes underlying recovery, and move restoration from an idiosyncratic, phenomenological discipline to a more predictive science. Such increased predictive ability will allow us to anticipate restoration outcomes more accurately and implement active restoration more successfully. Given the extent of ecosystem degradation, the international consensus to restore ecosystems[1–4] manifested by the UN Decade of Ecosystem Restoration,[5] and the upcoming UN Biodiversity Conference (COP15), developing such a general theory is a fundamental and timely issue.

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