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The long-term restoration of ecosystem complexity

David Moreno-Mateos[1,2,3], Antton Alberdi[4], Elly Morriën[5,6], Wim H. van der Putten[6,7], Asun Rodríguez-Uña[2] and Daniel Montoya[8]

Multiple large-scale restoration strategies are emerging globally to counteract ecosystem degradation and biodiversity loss. However, restoration often remains insufficient to offset that loss. To address this challenge, we propose to focus restoration science on the long-term (centuries to millennia) re-assembly of degraded ecosystem complexity integrating interaction network and evolutionary potential approaches. This approach provides insights into eco-evolutionary feedbacks determining the structure, functioning and stability of recovering ecosystems. Eco-evolutionary feedbacks may help to understand changes in the adaptive potential after disturbance of metacommunity hub species with core structural and functional roles for their use in restoration. Those changes can be studied combining a restoration genomics approach based on whole-genome sequencing with replicated space-for-time substitutions linking changes in genetic variation to functions or traits relevant to the establishment of evolutionarily resilient communities. This approach may set the knowledge basis for future tools to accelerate the restoration of ecosystems able to adapt to ongoing global changes.

Human activities have impacted every ecosystem on our planet[1–3]. In response to this situation, ecosystem restoration, defined as the process of assisting the recovery of ecosystems that have been degraded, damaged or destroyed[4], has become a global priority. This is exemplified by the upcoming United Nations Decade (2021–2030) of Ecosystem Restoration[5], as well as the multiple large-scale restoration strategies launched by international agencies and governments in the last decade[6–8] (Fig. 1). However, twenty years after the first studies that questioned what can actually be achieved by actively restoring ecosystems[9,10], ecosystem restoration still continues to be insufficient to offset the loss caused by anthropogenic development[11]. As ecosystem degradation and related biodiversity loss proceeds, the ability of ecosystems to maintain ecological functions and provide benefits to society declines[3,12], preventing us from achieving those international environmental goals set by 2020 and beyond[13].

Traditional approaches and metrics to assess ecosystem recovery focus on simple attributes such as taxonomic richness, or single functions such as carbon accumulation in soils[11,14]. Assessments of the restoration performance over different ecosystems worldwide show that, when traditional restoration guidelines based on the recovery of those simple metrics are followed; (1) restored ecosystems may only recover part of their lost biodiversity, functions and benefits to societies, even after decades or centuries; and (2) active restoration efforts may not yield better results than naturally regenerating ecosystems (Fig. 2). This suggests that traditional approaches are excessively simplified abstractions to achieve a sustained recovery of ecosystems and to provide guidelines for future restoration. Seminal studies aiming to increase our understanding of the effects of restoration on more complex attributes, for example, ecological networks[15], opened a new avenue to measure recovery that has slowly expanded, particularly in recent years[16,17]. Results from these studies have been addressed in recent restoration standards[4] to propose a more comprehensive approach than previous ones[18,19], by suggesting to focus efforts on restoring more complex attributes, such as trophic relationships, plant–animal interactions and gene flows[4]. However, these standards still ignore our emerging understanding of ecosystem complexity and its effects on the potential of species within ecosystems to adapt to ongoing changes. Restoration standards and strategies also ignore that the re-assemblage of damaged complexity and the recovery of adaptive potential occur at ecological timescales that may take centuries or more[20,21].

In order to advance restoration science, we suggest to focus on restored or recovering ecosystems to understand (1) how to measure complexity (Fig. 3); (2) how to identify changes in the adaptive potential of species and communities; and (3) how complexity and adaptive potential recover after anthropogenic disturbance over long time periods (centuries or more). To achieve these aims, we propose the following: First, based on the definition from information theory, we define ecosystem complexity as the amount of ecological information required to describe a metric (see Box 1). For example, a gradient of complexity could be: species richness, species composition, functional diversity, genetic diversity and interaction network structures. Each of these metrics require the information contained in the previous metric plus additional information. In this gradient of complexity, we focus on elements accumulating the largest amount of information (interaction networks). We propose to measure changes in ecosystem complexity in restored ecosystems as changes in (1) the structure of interactions networks; (2) functions emerging from those interactions; and (3) stability of those networks. Second, we propose to understand how species and the adaptive potential of communities responds to restoration actions

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[1]Department of Landscape Architecture, Graduate School of Design, Harvard University, Cambridge, MA, USA. [2]Basque Centre for Climate Change – BC3, Leioa, Spain. [3]IKERBASQUE, Basque Foundation for Science, Bilbao, Spain. [4]The GLOBE Institute, Faculty of Health and Medical Sciences, University of Copenhagen, Copenhagen, Denmark. [5]Department of Ecosystem and Landscape Dynamics, Institute of Biodiversity and Ecosystem Dynamics (IBED-ELD), University of Amsterdam, Amsterdam, The Netherlands. [6]Department of Terrestrial Ecology, Netherlands Institute of Ecology, Wageningen, The Netherlands. [7]Laboratory of Nematology, Wageningen University, Wageningen, The Netherlands. [8]Centre for Biodiversity Theory and Modelling, Theoretical and Experimental Ecology Station, CNRS, 2 route du CNRS, Moulis, France. ✉e-mail: dmoreno@gsd.harvard.edu

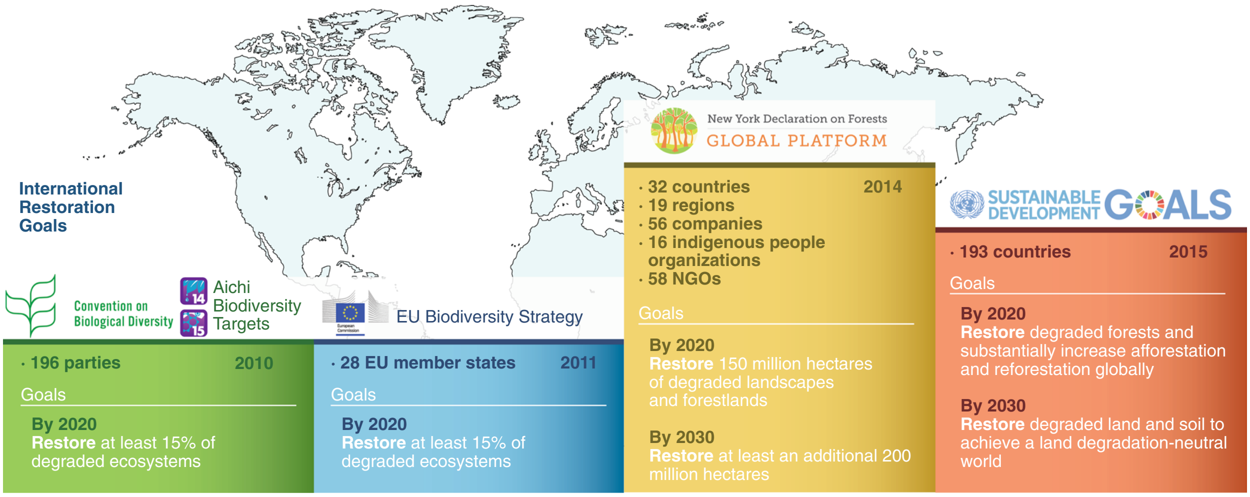


Fig. 1 | Global restoration initiatives. Some of the most important international restoration strategies launched in the last decade and their specific goals and timelines are shown. Credit: European Union, 1995–2020 (European Commission logo) under a Creative Commons CC BY 4.0 licence; New York Declaration on Forests Global Platform, United Nations Development Programme (New York Declaration on Forests Global Platform symbol); Convention on Biological Diversity (Convention on Biological Diversity symbol and Aichi Biodiversity Target symbols); United Nations (UN/SDG; SDG symbol)

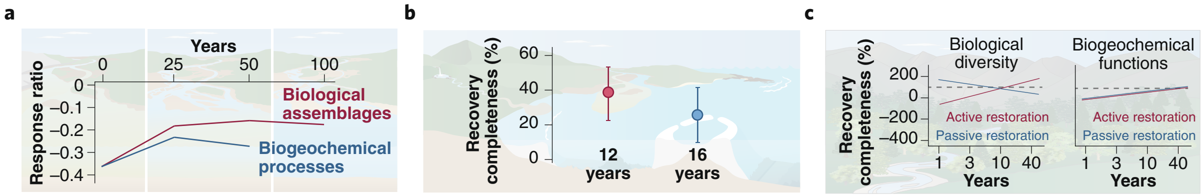


Fig. 2 | Meta-analyses on restoration performance. a, A meta-analysis of >600 restored wetlands showed that animal and plant assemblages and biogeochemical functions only recovered to 74% of the reference level after 50 to 100 years[81]. **b**, Another meta-analysis of 89 lake and coastal ecosystem restoration projects reported a recovery of 24% and 34% of their biodiversity and biogeochemical functions after 16 and 12 years, respectively[82]. Points are mean ± 95% confidence interval. **c**, A third meta-analysis on 166 forest studies reported that although plant and animal abundances recovered within a few decades, diversity and biogeochemical functions were not clearly affected by active restoration[83]. The dashed line indicates 100% recovery. Credit: The Integration and Application Network, University of Maryland Center for Environmental Science (background landscape elements; ian.umces.edu/symbols/)

over the long term. This approach requires long time periods not available today to solve the pressing issues found in restoration science. For this reason, we propose using space-for-time substitutions, providing a time approach to allow species genomes to respond to changes happening during the recovery process without waiting on evolutionary time periods. Third, we propose to understand the mechanisms regulating the re-assembly of interaction networks, functions and stability over the long term, again using space-for-time substitutions. Once the knowledge proposed here is generated, the next crucial steps are finding practical tools to implement this knowledge on the ground, and integrating the knowledge in the additional layer of complexity existing in socio–ecological systems in which restoration happens.

Measuring ecosystem complexity

In this section, we discuss methods for measuring ecosystem complexity from network and evolutionary perspectives.

Interaction network structure. The structure of ecosystems can be modelled as a network in which species (nodes) are connected by pairwise interactions (links). These interaction networks change in response to perturbations and along a recovery process. Traditional approaches to measure ecosystem complexity only quantify or list the species (nodes) while overlooking the interactions (links) interconnecting them. However, we now know that interaction networks within communities can change in response to perturbations without changes in species richness[22,23], and that the loss and gain of species and interactions can be decoupled[24]. Deficits in the number of interactions may occur when perturbations reduce the abundance of species down to a threshold below which the species no longer interact. This pattern is typical of systems in which a core group of strong mutualists or super-generalist species maintains many weak interactions[25] (for example, pollination and dispersal interactions). Hence, the extinction of interactions affects the provision of ecosystem functions and services at faster rates than species extinctions[26]. During recovery after restoration, the pattern is the inverse, as generating interactions takes longer than recruiting species[27] (Fig. 3). This happens because the realization of interspecific interactions requires the presence of species with a matching trait (limited by environmental filtering, dispersal limitation or historical contingencies), a phenological matching of the species (they must be present at the same time), and a high encounter probability (either because of high densities or effective location traits). Therefore, loss or gain of interactions, and the associated changes in network structure, are expected to be a better indicator of the ecosystem degradation and recovery than a list of species and their abundances. Studies on different kinds of networks report that restored communities are better connected than degraded ones[16],

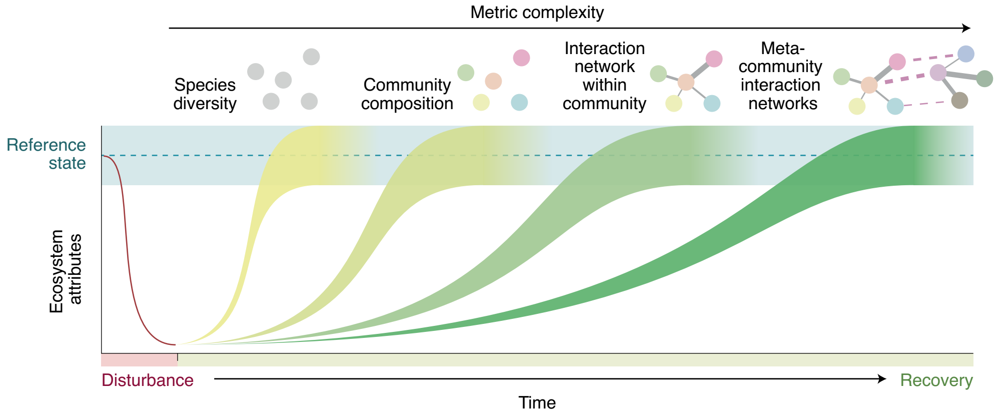


Fig. 3 | Measures of recovery through time. Higher metric complexity may involve longer recovery periods. Species diversity: measure of individual species presence and abundance. Community composition: assembly of unique species present in a community. Interaction network within community: structural metrics based on the links between species. Interaction networks between communities: metrics involving the nature and intensity of the links across multi-layered interaction networks.

yet have fewer interactions or are less resilient to further extinctions than undisturbed or pre-disturbance networks[15,17].

Ecosystem complexity assessments need to accommodate the dynamic nature of interaction networks, as species interactions vary in time[28] and across space[29]. Species may rewire their interactions when environmental variations change their local abundances and traits[30]. For example, the loss or weakening of strong interactions causes a decline in species abundances that in turn may lead to the extinction of co-occurring weak interactions[25], altering network structure. This is the focus of dynamic network models[31], which aim at understanding the factors that trigger variability of ecological interactions, specifically how trait-abundance-interaction feedbacks affect the structure of species interaction networks. Ecosystem degradation and restoration actions influence all these factors, analysing them would thus benefit from using this dynamic perspective of ecological interactions.

Interactions between species are also affected by eco-evolutionary feedbacks that ultimately determine the structure of the resulting networks. For example, differences in the architecture of antagonistic and mutualist networks may reflect different evolutionary processes. Food webs (predator–prey, host–parasitoid, plant–herbivore) tend to be modular with stronger phylogenetic signals as a result of 'arm races' and strong co-evolution[32]. Diffuse co-evolution is more common in mutualistic webs (pollination, seed dispersal, shelter and facilitation), which display more nested and less phylogenetically clustered interactions[33]. To capture these eco-evolutionary feedbacks that link the dynamic nature of ecological interactions to the population-level processes shaping species abundances and trait evolution, we can use adaptive network models (ANMs)[34,35]. ANMs are dynamic models that provide a natural framework for the ongoing synthesis of ecological and evolutionary theories (see a review by Raimundo et al.[35] about its application in restoration ecology), and can be used to comprehensively explore network dynamics in the context of the restoration of ecosystem complexity.

Although assessment of the changes on the complete interaction structure of an ecosystem is not feasible yet[36], partial structures or components with core roles in the ecosystem might serve as proxies of its overall complexity. One promising approach to make it feasible consists of selecting metacommunity hub species[29,37], which are species with core structural and functional roles within the metacommunity whose demographic and evolutionary effects control regional-scale dynamics[37]. For example, mobile consumers, such as predators, seed dispersers and certain pollinators moving across local communities are expected to couple different energy channels within the metacommunity (for example, a predator feeding on several prey species). These species can be generalists in habitat range and interaction patterns, thereby stabilizing the metacommunity at the landscape scale[38]. The definition of species roles within the metacommunity and the identification of hub species can be implemented with ANMs[35].

Ecosystem functioning. A key aspect in the integration of structure of biological communities and ecosystem functioning is to determine whether and how species interaction networks relate to functioning[16,27]. Recent studies have shown that ecosystem functioning is largely dependent on key structural components with major regulatory roles[39], such as species disproportionally well linked to other organisms[40] or species linking multiple networks, that is, metacommunity hubs. For example, studies on plant–animal interactions demonstrate that the loss of interactions of such organisms poses serious risks for the maintenance of ecosystem functioning. This has been shown for changes in seed dispersal dynamics due to extinction of large herbivores. Those changes simplify plant population structures[41] likely affecting their evolutionary potential. Also, carbon storage in tropical forests is known to be affected by the loss of key ecological interactions due to defaunation of large vertebrates[42].

While recent research enables to establish causal links between key organisms and functions, it is still not clear how the recovery of interactions structure impacts the ability of ecosystems to provide multiple functions. Species interactions provide insights into how communities are organized and how they function, yet the specific outcome of diversity–function relationships of recovering multispecies communities is difficult to predict. Such uncertainty could be reduced by implementing approaches based on multi-layered networks coupled with experimental modelling. Multi-layered networks (Box 2) are very useful to study the variability of communities and ecosystems under restoration[43], as they add temporal and spatial dimensions to study species interactions. This approach helps understand the relationships between biodiversity (species and their interactions), multifunctionality, and their variability along the recovery process. Combining multi-layered networks with ANMs could generate predictions on how different sequences of species addition or removal will affect the structure and functioning of the resulting community. For example, baseline ANMs could be built for a given community at time zero (right after restoration starts), with additional ANMs at different time steps along the

Box 1 | Definitions

Adaptive potential: the ability of populations to respond to natural selection by means of genotypic or phenotypic changes.

Chronosequence: a series of sites that are similar according to background attributes, but differ in the time since a certain event took place (for example, retraction of a glacier, abandoned agricultural land or abandoned mining practice). Effects of this event in time can be studied, where time is actually replaced by space.

Dynamic network models: type of models designed to understand the factors that trigger variability of ecological interactions. These models investigate how the feedbacks between functional traits, species abundances and their interactions in biological communities ultimately affect the structure of species interaction networks[34,35].

Ecosystem complexity: The amount of ecological information required to describe a metric or attribute of an ecosystem. This definition originates from the field of information theory, where complexity relates to the minimal length of a description of a system[84].

Ecosystem recovery: The process of re-organization—including re-assembly—of biotic and abiotic components that an ecosystem experiences once an anthropogenic disturbance ceases.

Ecological resilience: The capacity of a system to absorb disturbance and reorganize in time while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks[85]. It is one component of ecological stability.

Ecological stability: According to Pimm's definition[86], a system is deemed stable if the variables return to the initial equilibrium following perturbation. Stability is however a multidimensional attribute of ecosystems that involves its resilience, resistance, species turnover and variability (ratio of the standard deviation to the mean of a metric, for example, biomass and carbon storage)[47].

Evolutionary potential: The ability of a population to respond to selection pressures created by changing environmental conditions.

Multi-layered networks: Multi-layered networks consist of layers of several networks, where nodes appear in at least one of these layers. Layers are connected by intra-layer links (links in one layer) and inter-layer links (links between layers). Multi-layered networks provide a powerful approach to study ecological complexity as they can incorporate multiple types of interactions, interactions that vary in space and time and interconnected systems (for example, networks of networks)[43].

Whole genome (re)sequencing (WGS): The process of determining the (virtually) complete DNA sequence of an organism's nuclear and organellar genomes at a single time.

restoration process. This would provide a set of temporal trajectories of communities differing in species addition or removal sequences and functional outcomes. Such integration would also provide a framework for mapping ecosystem functions onto ecological networks[44] and investigating how functions interact with each other and form trade-offs or synergies[45,46] during the recovery process.

ANMs can also be used to better predict recovery trajectories and design improved future restoration actions. Once an ANM is defined for a certain community, species additions or removals can be simulated and their effects on the distribution of species abundances, traits and interactions investigated. This could be used as a predictive approach that, with caution, may serve as a guideline to determine which species should be introduced to or removed from the system in order to restore its functioning.

Ecosystem stability. Ecological stability is one of the most influential concepts in ecology and global change biology, yet it has rarely been applied to restoration ecology. Furthermore, restoration assessments should consider multiple forms of stability, for example, metric variance or species turnover[47] because general interpretations of ecological stability of recovering communities may vary depending on the stability component measured[47,48], and stability components may be decoupled during recovery processes. Restoration would benefit from quantifying changes in the mean values of ecological variables—species numbers and abundances, interactions, trait distributions and multiple functions—and their variability through time (dynamics models). Such a concept is encapsulated by the temporal coefficient of variation, a metric widely used as temporal variability in empirical studies[49,50]. This metric is a stability property that is integrative and more easily measurable at large scales by scientists and managers than, for example, resilience.

Ecosystem's adaptive potential

The pace of the ongoing global changes, including land degradation, climate change or increased pollution, requires local populations to adapt to the changing conditions. However, the ability of populations to evolve and adapt to environmental changes becomes increasingly uncertain when a sufficient gene pool is lacking[51,52]. Habitat fragmentation, biodiversity loss or population decrease promoting anthropogenic degradation of ecosystems may not only alter the population structure of species and their interactions, but often causes loss of genetic diversity of local populations as well[2]. Therefore, loss of genetic diversity can hamper the adaptive potential and resilience of species under future environmental changes[53,54]. Promoting evolutionarily resilient ecological communities in which adaptive potential is maximized is increasingly recognized as a conservation necessity[55], and desirable for the establishment of ongoing functional and stable ecosystems.

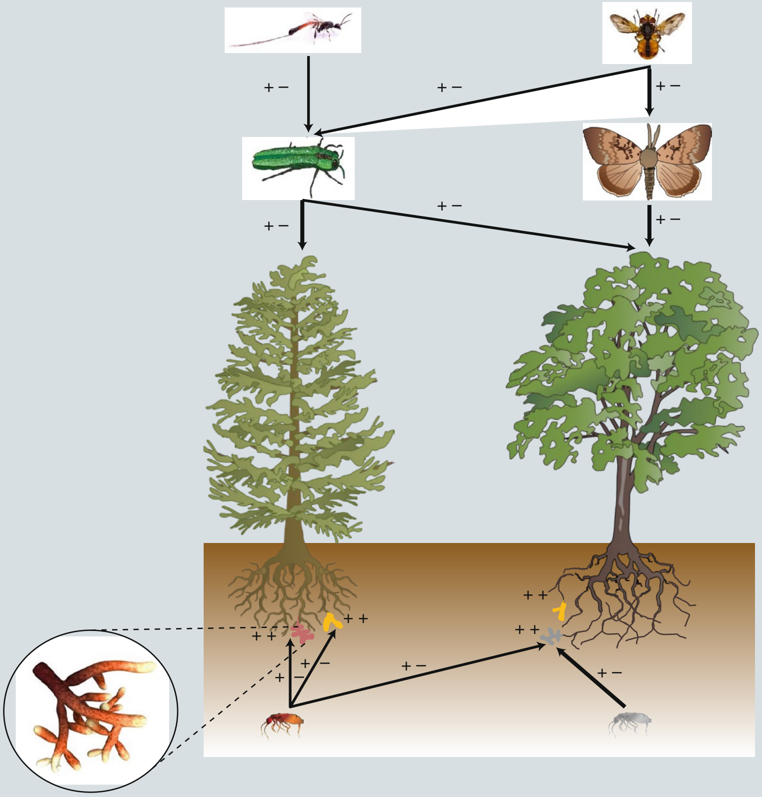
Recovery from anthropogenic disturbance is an untested opportunity to understand how the adaptive potential of populations changes through time during ecosystem recovery. The recovery of the adaptive potential is expected to be even slower than the recovery of interaction networks. This is because (1) increasing genetic diversity through neutral or selective processes might take centuries to millennia, especially when the generation times of some key structural species are very long, for example, tens or hundreds of years in the case of many trees or corals; and (2) selective pressures that produce directional shifts in favoured alleles are infrequent[54]. However, empirical evidence on recovery of adaptive potential is largely absent, likely due to two reasons.

First, experimental studies of ecosystem recovery and restoration processes are limited at most to a few decades. While useful for capturing features of ecosystem recovery that occur in such short time periods, these approaches do not enable to assess the recovery of ecosystem properties that require many decades, centuries, or even

Box 2 | Measuring the recovery of complexity

Representative networks in restoration are those encapsulating a large amount of diversity and functionality and that are also potentially more resilient to change and recovery. Among the many networks ecologists could monitor, an example are the multilayered weighted networks formed by fungivore collembolans, mycorrhizal fungi, plants, herbivore insects, and their parasitoids; see Box Figure). This network example provides a wide spectrum of biological interactions, including three kingdoms of organisms (that is, plants, fungi and animals), two types of networks (antagonistic and mutualistic), and four kinds of interactions (herbivory, fungivory, parasitism and mycorrhization) linking above- and below-ground organisms. Mycorrhizal associations influence plant survival, productivity and diversity of 86% of terrestrial plants through an underground network allowing the movement and retention of resources among coexisting plants[87]. This exerts a direct effect on resistance to insect herbivory[88] and an indirect effect on parasitism[55]. Collembola grazing on mycorrhizal fungi may increase extra-radical mycelium nutrient sequestration, particularly phosphorus, and in turn plant performance[89]. Overall, belowground successional trajectories may take millennia, becoming more complex and stable, with increasing food chain length, and greater reliance on mycorrhizal fungi for plant nutrition over time[90], which makes this system especially interesting for assessing recovery. The architecture of these networks regulates major ecosystem functions, including primary productivity (via plant performance and herbivory)[88], population control (via herbivory, fungivory and parasitism)[91], nutrient cycling (N and P absorption by plants), and C cycling (C absorption by fungi)[92].

Measuring changes in this or any other multi-layered network could focus on the structure of the network and the related functioning and stability. In the present case, one could study how changes in the structure of the network (for example, robustness, modularity or nestedness) affect the use of nitrogen and phosphorus facilitated by the mycorrhizal fungi to the plant and how it affects plant growth or resistance to herbivory. In the opposite direction, one could measure how much carbon is facilitated by the plant to the mycorrhizal fungi and how they affect fungal predation by collembolans. Through time, an asymptotic approach of these functions to a reference or stable condition will help ecologists and practitioners to monitor the recovery of restored ecosystems.



Conceptual description of the selected interlinked weighted networks. Arrow line thickness represents interaction strength and symbols indicate mutualistic (++) or antagonistic interactions (+–). Credit: Viter8/Dreamstime (wasp image); Alexander Hasenkampf/Dreamstime (fly image); Bearsky23/DreamsTime (borer image); 7active Studio/Dreamstime (Mycorrhiza image); the Integration and Application Network, University of Maryland Center for Environmental Science (collembola, tree and moth images; ian.umces.edu/symbols/)

millennia to develop. Thus, understanding the effects of ecosystem degradation on successional, assembly and evolutionary processes at ecologically relevant scales[20,21] may be challenging. This hinders the development of knowledge on the real magnitude of ecosystem degradation and the recovery potential of ecosystems. A careful use of space-for-time substitution approaches can provide the timescale required to understand recovery trajectory of adaptive potential and the other ecological attributes proposed.

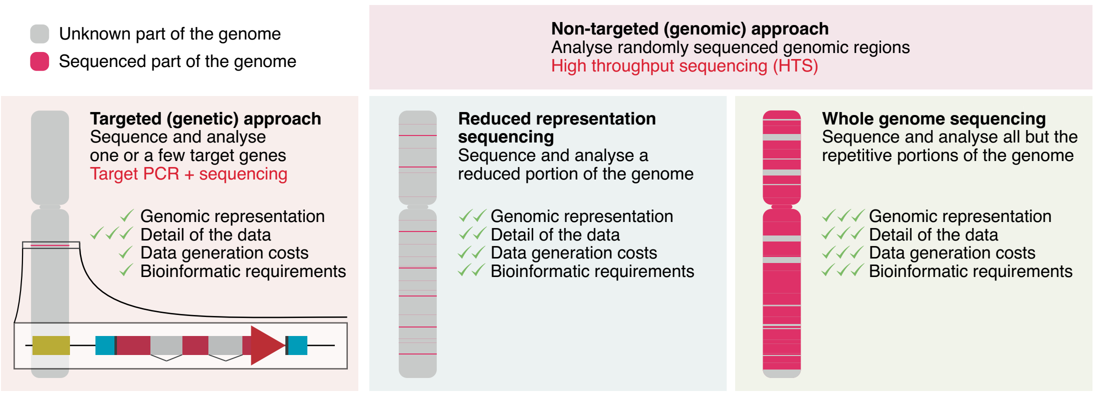


Fig. 4 | Approaches to analyse genomic variation. Targeted approaches (genetics) are usually based on polymerase chain reaction (PCR) and traditional Sanger sequencing. Although they might yield highly detailed information, the scope is limited to a few genes or regions. In contrast, non-targeted approaches (genomics) based on high throughput sequencing (HTS) enable analysing a larger quantity of genomic information at once. While reduced representation sequencing approaches just cover a fraction of the genome and thus have limited capacity to identify relevant loci, whole genome sequencing approaches enable a much more complete characterization of the genomic variation.

Second, the molecular approaches employed to measure adaptive potential have been quantitatively and qualitatively limited. Two approaches have dominated efforts to understand changes in genomically hardwired adaptive potential of populations: (1) targeting specific genes with well-known function; and (2) screening genomes to measure overall genetic variation. These approaches have limitations that prevent nuanced analyses of ecosystems' adaptive potential (Fig. 4). Targeting genes associated to specific traits is only reasonable when the traits are controlled by a small number of genes[56]. However, the traits that confer adaptive potential tend to be polygenic quantitative traits[57], and the identification of the loci that govern variation in such traits is extremely challenging with limited genomic resources[58]. In addition, such approaches limit the analysis to a priori selected loci, thus overlook the rest of genomic variation. The alternative approach is to employ non-targeted approaches. Reduced representation sequencing methods such as genotyping by sequencing (GBS) and restriction site-associated DNA sequencing (RADseq)[56,59] have considerably improved the resolution of traditional approaches (for example, microsatellites and restriction fragment length polymorphisms (RFLPs)), yet these still cover a small (1–5%) random fraction of the genomes of interest[60]. Therefore, these novel approaches still overlook most of the genetic background of organisms[61]. Consequently, all these approaches provide limited capacity to address critical issues such as finding genomic signatures of selection, accounting for contributions of small-effect loci that may contribute to adaptive potential, or predicting the specific adaptive variant(s) that will be required for foreseen environmental changes[56,60,62].

High throughput sequencing and related laboratory and bioinformatics technologies allow to overcome many of these limitations through implementing whole genome (re)sequencing (WGS) approaches (Box 3). While until recently prohibitively expensive[56,60], its costs are drastically decreasing[63] and will likely keep decreasing in the upcoming years, turning WGS affordable for many research groups. The advantages of WGS to gain a more complete understanding of the genetic variation caused by ecosystem degradation and recovery, and assess the adaptive potential of populations in those ecosystems are boundless. Critically, sequencing virtually the entire genomic information of organisms does not only enable accounting for the diversity encoded in neutral markers, a priori chosen protein-coding genes or a small genomic sample, but enables examination of a wider variety of genetic variants, from single base changes to structural changes[60,64]. It also enables screening intergenic and intronic regions that are increasingly regarded as key elements for evolution[65–67]. Furthermore, if the reference genome is annotated so that structural and functional information of each of the genomic regions is known, it is possible to assess the actual biological impact of diversity loss by measuring diversity variation in genes with specific functions that might be relevant for foreseen environmental changes. Similar high throughput sequencing approaches also enable analysing epigenetic mechanisms, transposable elements and symbiotic microbial communities, which could be used to assess their contribution to the adaptive potential of populations[68,69].

Coupling space-for-time substitution approaches with WGS would enable contrasting the evolutionary potential of populations under long-term recovery from human disturbance and undisturbed populations through time. One example using this approach could be finding differences in adaptive potential between populations of domesticated species that are recovering after being released from selection for many decades or centuries (in the case of trees) and wild populations. Domesticated populations, once selected for larger fruits in tropical trees or more palatable leaves in prairie grasses, would have seen other traits, for example, related to pest or drought resistance, reduced or lost, decreasing their resilience and resistance to environmental changes. After they are released from that pressure, part of the lost resilience and resistance may recover and can potentially be measured. Once we know how to find sources of genetic variation that enhance traits responsible for adaptive potential using domesticated species over the long term, we could use the same approach in other species of interest in restoration (for example, metacommunity hubs) that have been impacted in other ways beyond domestication (for example, selective logging in tropical forests or grazing in temperate grasslands). This would allow restoring ecosystems whose populations are best adapted to change, increasing their chance to thrive in current changing environmental conditions. Growing population sizes of hub species would increase the probability of interaction with other species, accelerating the recovery of complexity.

Assessing recovery over the long term

Using chronosequences for the study of recovery trajectories of the proposed ecosystem attributes should ideally be contrasted with undisturbed reference sites. These sites can provide key information about target features of ecosystems to guide restoration towards historic ecological trajectories[70]. Recovery could then be assessed by comparing the values of all metrics at each site with those of reference undisturbed sites. Alternatively, recovery could

Box 3 | Measuring changes in evolutionary potential by generating WGS data

Population-level genomic analyses based on WGS can be split in two main groups: those requiring reference genomes and those that do not. Some analyses, such as estimates of inbreeding or relatedness, or characterizing demographic events could be done without a reference genome[64]. Most applications, however, require a high-quality reference genome to which sequence reads of individual organisms are mapped to, so that low depth (usually 5–10×, that is, each position in the genome covered on average by 5–10 sequencing reads) whole genome re-sequences of each individual are generated. The reference genome should ideally belong to the species under study, although genomes of close relatives might also be valid in most cases. The reference sequences of many common species can be found in genome databases such as the National Center for Biotechnology Information (NCBI) Genome or Ensembl. As the quality of genomes available in reference databases can differ considerably, it is advisable to perform a quality assessment to ensure the genome meets the quality standards required for the analysis. In general terms, complete or chromosome level genomes (with no gaps) are not strictly necessary to perform such analyses, as a scaffold level genome with good quality parameters (for example, N50 and N90) could be good enough to cover >95% of the coding genes.

If the reference genomes are not available in public databases, or the quality of the reference genome is poor, researchers might opt for generating a high-depth (>50×) de novo genome. Library preparation and sequencing could rely on traditional approaches in which DNA fragments of different sizes (0.2–40 kb) are sequenced from both ends, or by novel, more robust approaches such as long molecule sequencing coupled to Hi-C scaffolding[93]. Generating genomic sequences is the beginning of a long process in which reads first have to be quality-filtered, assembled and later annotated[64]. Each of these steps require deep knowledge on the underlying methods and assumptions, thus are usually beyond the range of non-specialists. Alternatively, this approach is an opportunity to get evolutionary and genomic scientists involved in restoration science.

To optimize WGS-based studies, target species should be chosen based on ecological criteria and practical reasons. The resequencing effort will depend on the genome size of the studied species; that is, the cost of resequencing a species with a genome size of 5 Gb (gigabases) is twice as expensive as resequencing another species with a 2.5-Gb-long genome. Hence, non-polyploid species should be prioritized, or alternatively, implement target capture approaches to enrich the genes or genomic regions of interest[94]. Using WGS on agricultural (plant) species that have been released from domestication along a chronosequence of abandonment would allow addressing a range of questions on the effects of the release on the recovery process of the adaptive potential. For example, if neutral loci can act as a record of demographic history (bottlenecks, range expansions or human disturbances)[95], how adaptive loci can be associated with natural selection, fitness or adaptation through time[60], and when those events happen through time. Examples of ancient agricultural selected species that have been released from selection for centuries that could be used with this approach exist in the Amazon basin[96], Central America[97], Central Africa and Southeast Asia[98].

be assessed using changes in variation of the recovery metrics. A recovered ecosystem would be that where metrics reach constant values of their variation, that is, stabilize in the chronosequence. This could involve substantial changes in the community composition or other attributes if systems enter alternative states. Using chronosequences can also allow comparisons among recovery trajectories of different metrics and environmental conditions—for example, understanding the effect of climate on the recovery of plant–fungal network stability and nitrogen absorption in plant–fungal associations.

Space-for-time substitutions must be carefully used, as their use has been questioned in relation to non-stationary conditions of the environment[71]. This condition can make recovery processes change to different endpoints with the result that sites within the chronosequence are hardly comparable and thus provide unreliable results[71,72]. This is particularly relevant in the Anthropocene, where multiple impacts simultaneously affect the environment of restored ecosystems. Given that centennial time series for complex ecosystem attributes of recovery do not exist, and that we need to understand and plan restoration at those timescales, chronosequences can help to solve this. We could reduce existing caveats of chronosequences in two ways: first, using replicated chronosequences with similar environmental conditions and covering the same period or, alternatively, having replicates of each point in the chronosequence. Second, using time series of a similar length provided by palaeoecological records located in the same area as the chronosequence (for example, sediment cores) that provide ecological information of species composition and processes in ecosystems from the past. Finding temporal patterns consistent between at least two independent time series, either from replicated chronosequences or from palaeoecological records, will increase the reliability of our space-for-time substitution approach.

Challenges

Sampling the ecological complexity of ecosystems may be time-consuming, especially considering the multitude of species, co-existing interaction types (for example, mutualistic and antagonistic), functional traits, and related ecosystem functions and services. The identification of metacommunity hubs could skip some, but not all parts, of this process. Further, stability assessments of restored ecosystems require multiple observations (time series) in order to explore temporal dynamics and variability patterns. Once mechanisms of recovery of complexity are better understood, a next research step should focus on finding operational tools for implementing the proposed approach on the ground.

Although genomic advances enable direct estimates of key quantitative genomic parameters (for example, additive genetic covariance and genetic correlations), assessing the evolutionary relevance of the observed variation is challenging[56,73]. For example, measures based on additive genetic variation ignore dominance (interactions between alleles in a locus) and epistatic effects (interactions among loci)[74], and information about how traits link to fitness is also limited in most scenarios[56].

Finding areas that were disturbed in ancient times (>100–1,000 yr) and that have never been degraded afterward can also be challenging. Probably, the greatest challenge is to find enough replicated sites that have not been disturbed after abandonment, as well as comparable reference sites, to build reliable chronosequences. This may be particularly difficult in temperate areas, given the intense use of land caused by the high human population density (but see Box 3). Further, as the data in chronosequences are collected independently for each network in the impacted and reference sites, one could only compare estimates of structural metrics that explain the distribution of interactions (degree distribution, nestedness and modularity)[75] and of interaction strengths[76], in addition to the values of several ecosystem

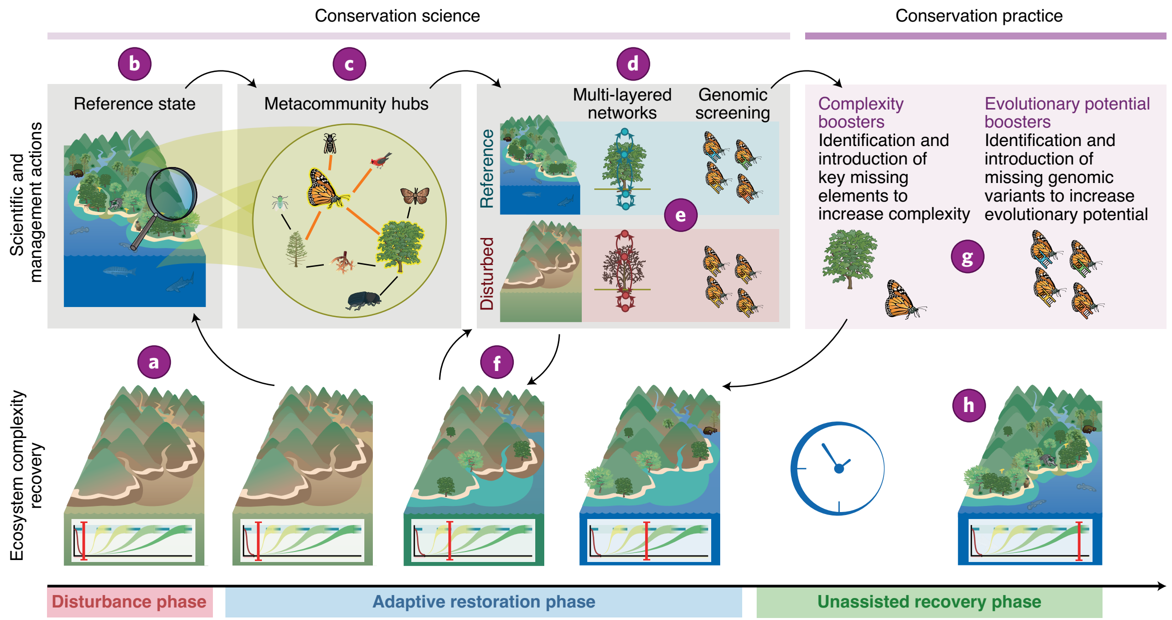


Fig. 5 | Future steps to improve restoration science and derived management actions. **a**, An ecosystem affected by anthropogenic impacts typically shows simplified interactions and functionality (see Fig. 2), which gradually increase during the recovery period. **b**, A reference undisturbed site with a priori similar ecological characteristics to the disturbed ones will help understand the recovery process. **c**–**e**, This reference site can be used to identify metacommunity hubs (**c**), that is, species with exceptional ecological relevance within the ecosystem, upon which, multi-layered network (**d**) and genomic analyses (**e**) are made. Results from this analysis can then be compared with similar analysis in disturbed sites to assess changes in the complexity and evolutionary potential of ecosystems. **f**, The level of variation of the analysed elements through time can provide insights into the stability of the ecosystem. **g**, Finding key species and genomic variants with exceptional roles in the recovery of the complexity and evolutionary potential lost in the disturbed site would enable actively introducing them to boost ecosystem recovery. **h**, The aim of this approach is to accelerate the recovery of ecosystem complexity and, subsequently, the recovery of ecosystem functionality, stability and resilience to current environmental change. Credit: The Integration and Application Network, University of Maryland Center for Environmental Science (background landscapes elements, tree and insect images; ian.umces.edu/symbols/)

functions. However, one could not compare estimates of network stability, for example, temporal variability or robustness[77]. This network independence prevents comparing raw data, requiring the implementation of standardization methods (for example, residual variation, null models or hypothesis-based meta-webs) to compare parameters among networks[78].

Future steps to restore complexity

From a practical perspective, we envision that future on-the-ground restoration could follow the next steps (Fig. 5). First, a previous study on the ecology of the site to be restored based on references will help finding species with unusually strong roles on ecosystem structure, function and stability (metacommunity hubs). Ideally, if using a space-for-time substitution approach of reference sites, a sequence of metacommunity hubs may be identified. The re-introduction or facilitation of metacommunity hubs, either once or along a temporal sequence, can accelerate the restoration of the meta-network by ensuring persistent connections between local communities, which may trigger eco-evolutionary and co-evolutionary cascades and rapidly reshape patterns of interactions, abundances and functional traits. The restoration of metacommunity hubs can also help establish the spatial and temporal scales of the restoration program. For example, restoring single habitats might be inappropriate in many cases given the differences from local to landscape scales in the spatial distribution between consumers and resources[79], and the dependence of some species on a mosaic of different habitats that provide different resources[80]. This first step will take between two and three years to be completed. Second, once metacommunity hubs are identified, WGS will help in finding their sources of genetic variation that increase adaptive potential. As other genomic techniques, WGS cost is expected to decrease substantially in the coming years. Then we would select propagules (for example, seeds, soil inoculum and animal specimens) from populations with highest adaptive potential for restoration. This second step will involve one to two years of work. The third step will involve the sequential implementation of restoration actions required to: (1) create environmental conditions (for example, soil, topography and hydrological dynamics) that facilitate the settlement of the selected propagules; (2) if necessary, reintroduce the selected propagules given the landscape context and the dispersal capacity of the species selected; and (3) assess the requirements and limitations existing in the socio–ecological context.

Conclusions

Long-term ecosystem restoration requires moving beyond traditional biodiversity and functional assessments to a broader perspective that considers the full complexity of ecosystems (that is, their structure, functioning and stability), the adaptive potential of species, and the fact that restoration is, in most cases, a centennial process. Such a complex and long-term perspective is necessary to restore the temporal and spatial variation of communities and the feedbacks between species, their abundances, trait distributions, interactions and the deriving functions. Also, this perspective is necessary to restore the genomic variation responsible for the adaptive potential of populations and the eco-evolutionary feedbacks that ultimately shape the structure of the interaction networks. We suggest approaching this perspective by using adaptive network models able to dynamically incorporate trait- and abundance-based processes shaping ecological networks. Within those networks, metacommunity hub genomes can then be scrutinized to understand loci particularly responsible for traits and functions that increase the adaptive potential of species and communities to ongoing global changes. Replicated space-for-time substitutions are ideally suited to address the centennial scale of the ecosystem recovery process and (1) help make projections of how future ecosystems will respond to increasingly changing environmental conditions; and (2) help restoration strategies and funders understand the real timescale at which restoration takes place.

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D.M.-M. and A.A. conceived the idea and wrote the manuscript. D.M., E.M., A.R.-U. and W.H.v.d.P. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Correspondence should be addressed to D.M.-M.

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