Essay

Restoring complexity in a changing environment

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As land use leaves massive tracks of land vacant for recovery, restoration must undergo a substantial shift to incorporate a complexity perspective beyond the traditional community, biodiversity or functional views. With an interaction–function perspective, we may be able to achieve ecosystems with better chances to adapt to current environmental changes and, especially, to climate change. We explore combined approaches that include still unused and underexplored techniques that will soon go mainstream and produce massive amounts of information to address the complexity gap. As we understand how complexity reassembles after the end of agriculture, we will be able to design actions to restore or enhance it at unprecedented spatial scales while increasing its adaptability to environmental changes.

Land use change is dramatically reshaping the state of our terrestrial ecosystems, yet the compounding impacts of climate change on this shift are unclear. Changing locations of agricultural intensification leave massive amounts of abandoned land every year[1], leading to net gains of forested ecosystem globally in the last 40 years (27% in the case of temperate forests)[2]. As forests recover in post-agricultural lands, global biodiversity gains have the potential to increase ecosystem functions like nutrient retention and carbon (C) sequestration in above and belowground biomass over the long term (greater than 100 years), especially if they lead to recovery of ecosystem complexity, such as species interaction networks (Figure 1). Interactions may have low resilience to disturbance, but are key for certain critical ecosystem functions (such as tree–microbial relationships) and often better correlate with disease incidence[3], ecosystem productivity, and plant fitness[4]. Nevertheless, climate change can make the ability of ecosystems to evolve and adapt to further change increasingly uncertain[5,6]. Integrating the effects of both land use and climate change into our understanding of ecosystem recovery dynamics is critical to estimate the composition and functionality of future ecosystems and to design restoration and management actions that accelerate these trajectories.

To achieve this goal, we should set the basis of what we understand as recovery dynamics by including the reassemblage of the structure of interactions and related functions as metrics of ecosystem change[4]. However, recent theory and some evidence suggest a temporal decoupling between the recovery of biodiversity and species interactions[7]. 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. During recovery after restoration, the pattern is the inverse, however — generating interactions takes longer than recruiting species[8] (Figure 1). 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). Functions themselves also may not be positively correlated and may form synergies and trade-offs among them[9]. Although progress exists in measuring comprehensive sets of structural and functional ecosystem properties in recovering ecosystems (particularly in post-agricultural areas) at large spatial scales and reasonably long (~100 years) timescales[10,11], there is still a mechanistic disconnect between the reassembly of biodiversity, interaction complexity, and their functional implications over the long term (greater than 100 years). Building knowledge to fill the mechanistic gap to understand recovery dynamics would be a first step to then assess the roles of land use and climate change on the process.

Recovering in a changing environment

The arrival or loss of species in a recovering system will be affected by climate change factors, like changes in air temperature. Changes in air temperature will affect biotic factors including growth period, primary productivity, or herbivore population density, which in turn will also affect the arrival or loss of species. Evidence and theory support the idea that global climate change could alter equilibrium points in ecosystem recovery so that alternative, persistent combinations of ecosystem states would be possible (i.e., alternative transient states)[9,12]. In particular, warming initially benefits certain functional traits over others (e.g., larger leaves or smaller body sizes, copiotrophic strategies, greater capacity for cellulose decomposition in soils)[13,14], which may associate with species' dispersal and competitive abilities, as well as with species' evenness and patterns of abundance[15]. Warming can also produce range shifts, phenological mismatches, increased metabolic rates, and higher species turnover[16], and — along with changes in precipitation regimes — can accelerate ecosystem function**)**. However, ecosystems of different ages (i.e., those that have undergone recovery for different periods of time) can respond differently. Forests recovery rates consistently increase with temperature[5]. Some of the main causes of this pattern may include an extended growing season, and increased biogeochemical turnovers and metabolic rates[5,17,18]. Extended growing seasons could lead to increased annual assimilation of carbon and nutrients by plants, which, along with potential CO_2 fertilization effects, could increase primary productivity and carbon storage capacity[19]. This increased plant primary productivity is mediated to some degree by mycorrhizal associations, driven by fungi whose metabolic rates are also increased[20]. Faster biogeochemical turnover may also accelerate the conversion of unavailable forms of nitrogen and phosphorus to available ones, and their absorption and transfer between fungal communities and plants[18]. These results suggest that climate change has the potential to affect the reassemblage interaction networks (Figure 1).

The effects of the recovery of species interactions on ecosystem function may be also influenced by the functional and phylogenetic diversity of those species — that is, how different they are. This will affect how they will respond to changing climate conditions. Given that the gain and loss of species interactions are affected by eco-evolutionary relationships (i.e. certain clades have higher chances to be gained or lost[21,22]), using phylogenetically structured species interaction data can help to predict how the recovery process reshapes ecosystem resilience, stability, and functional diversity[23]. Integrating these network and eco-evolutionary approaches in analyzing recovering ecosystems could help us construct a new paradigm in ecosystem recovery that links realized interactions with its emerging functions as they relate to species traits and their position in the evolutionary tree. Existing recovery theory suggests that recovery will structure around certain clades with higher chances to interact first, and less frequently interacting clades will follow[24]. By integrating this approach into recovery studies, we could potentially predict clades with increased chances to respond positively to the combined effect of recovery and climate change.

Organismal interactions and function

The interactions between plants and root-associated microbial communities are key structural and functional components of ecosystems, influencing plant survival, productivity, fitness, and diversity through a belowground network of species interactions[25] (Figure 2). This network is formed by trees that associate with root endophytes, mycorrhizal fungi, and root- and fungal-associated bacteria and we are just beginning to understand the interactions between these players[26,27]. There is some evidence that these associations can allow the trade of C, N, and P between species or the signaling of adverse situations (e.g., allelopathy or herbivory) among existing plants and associated mycorrhizal fungi[28].These associations can then have direct effects on plant coexistence or population growth[25], as well as on resistance to insect herbivory[29]. Overall, belowground successional trajectories may increase reliance of plants on mycorrhizal fungi for nutrition over long periods of time[30]. Fungal and bacterial pathogens also have key effects on host fitness and ability to survive[31], potentially affecting the community composition and the structure of beneficial plant–microbial interaction networks. However, all these interaction dynamics are altered in post-agricultural areas, where both the richness and diversity of plants and microbes are significantly decreased, as are microbial functional genes involved in soil C, N, and P cycling[32]. Interaction dynamics can also be affected by high temperatures favoring pathogens over mycorrhizal symbionts, in part due to elevated soil N[33]. In recovering and restored ecosystems, we could expect warming to accelerate pathogen infection but slow development of mutualistic symbioses between trees and fungal root symbionts, delaying recovery of ecosystem functions like tree growth or carbon sequestration[34]. This supports the idea that climate change can potentially reduce or slow recovery (Figure 1) or support alternative transient states with lower mutualism.

Combining ‘omics’ technologies with field surveys and phylogenetic analysis may help us measure some of the elusive complexity needed to understand ecosystem recovery and restoration (Figure 3). Environmental DNA (eDNA) data has revealed shifts in unseeable organisms with both land use and climate change over the past three decades, showing us that some lineages and functional groups of fungi and bacteria are particularly sensitive to these changes[35,36]. Metagenomics (i.e., the suite of genes detected from all members of a microbial community) are beginning to reveal how functional potential of whole microbiomes responds to climate change[37], yet metagenomics has historically targeted only the prokaryotes. This has been happening in part because of their gene abundances in environmental systems (like soil) and because our computational tools and databases are biased against eukaryotic microorganisms[38]. In addition, one of the main limitations of standard metagenomic approaches is that they do not distinguish the active from inactive members of a microbiome, and thus cannot identify taxa contributing to observed ecosystem behavior.

Metatranscriptomics — or the analysis of all genes that are being expressed in a microbial community — is emerging as a powerful tool to identify plant–microbial interactions, allowing us to build interaction networks for eukaryotes (such as fungi and plants) and connect them to changes in ecosystem functional diversity[39]. Recently, advances in metatranscriptomics of tree roots have revealed the biochemical mechanisms of ectomycorrhizal host associations, identifying pathways for recognizing and initiating physical interaction with compatible partners (e.g., small secreted proteins) and pointing to specific sugar alcohols and amino acids as the agents of carbon and nutrient exchange between plant and fungal partners[27]. Using metatranscriptomics, genes expressed at relatively low levels can be detected, annotated, and mapped to metabolic pathways and specific functions[40]. These omics technologies allow us to peer into the metabolic potential of plant and microbial communities — including their growth, stress, and resource use metabolism — that may serve as proxies for actual activities in the field[39]. However, molecular analysis of environmental communities is most powerful when validated with careful measurements of biogeochemical activity. Stable isotope probing (SIP) metagenomics and metatranscriptomics[41] (Figure 3) could, for example, allow us to tie plant, fungal, bacteria, and other microbial expression of genes for N exchange (Table 1) to specific N uptake rates for individual taxa and the tree roots they associate with. This new and powerful approach of SIP metatranscriptomics to trace ^{15}N present in microbe-produced RNA can also allow us to identify the specific biochemical pathways that are actively using^{15}N (Table 1). While climate change and time since agricultural abandonment can impact many aspects of ecosystem biogeochemistry, a focus on N exchange could allow linking the well-characterized microbial genomics of fungal–plant N transfer[42] to ecosystem-level patterns of plant growth and nutrition. This approach has the potential to transform our understanding of how microorganisms and roots interact belowground and serve as key validation data for hypothetical interactions among species that define how ecosystem complexity responds to recovery and climate gradients.

Species interactions are highly dynamic and ecosystem complexity assessments need to accommodate the dynamic nature of interaction networks, as species interactions vary in time[43] and across space[44]. As the climate changes, interactions may reshape networks based on changes in species distributions, extinctions, or the increase in generalists[45]. However, the factors that trigger variability of ecological interactions along the recovery and climate gradients are unknown. One way to approach this could be looking into how interactions are affected by eco-evolutionary feedbacks that ultimately determine the structure of the resulting networks. For example, food webs like host–parasitoid and plant–herbivore tend to be modular, with stronger phylogenetic signals as a result of co-evolution[46]. However, mycorrhizal fungal–plant networks show more nested patterns as a result of the unusually highly connected species (i. e. metacommunity hubs)[4,47], with inconsistent phylogenetic signals[48]. Adaptive network models capture the eco-evolutionary feedbacks that link the dynamic nature of ecological interactions to the population-level processes shaping species abundances and trait evolution[23]. Adaptive network models are dynamic models that provide a natural framework for the ongoing synthesis of ecological and evolutionary theories and can be used to comprehensively explore network dynamics in the context of the recovery of ecosystem complexity and its potential response to climate change. As biotic and abiotic conditions change during recovery and along temperature increases, traits are modified, in turn, producing network-level responses[22,49]. In this context, closely related species often interact with sets of similarly closely related species[21] through niche conservatism. Under this assumption, phylogeny should help predict both species interactions and overall network topology[22]. This approach would involve assessing both the phylogenetic nature of these interactions (e.g., are particular plant clades associated with particular fungal clades?) as well as assessing the phylogenetic nature of functional trait associates outlined above. These efforts could help to bridge a major gap in our knowledge about such associations and contribute greatly to our understanding of the potential for such co-additions (as opposed to co-extinctions) in the recovery process to impact biodiversity, and specifically species additions, that may be phylogenetically nonrandom or non-uniform as traits respond to changing climate conditions.

Understanding network reassembly and its phylogenetic constraints can also help gain insights into the recovery of functional and phylogenetic diversity. For example, network structure is associated with the number of functional groups present and functional group diversity is heterogeneously distributed across spatial scales[50]. These functional groups form modules within the community so that food webs with more modular architectures have more functional group diversity. In the context of post-agricultural systems, we find specific, yet widespread, constraints. For example, the long-term use of fertilizers can decrease the complexity of networks between plant and microbial functional communities in terms of node numbers, connectivity, network density, and the clustering coefficient[32]. In 60-year post-agricultural restored sites, communities were still commonly composed of species that are more phylogenetically, and functionally, closely related to one another, relative to the species in undisturbed areas[51].

Climate change can critically impact the recovery of interacting species via spatial and temporal mismatches in the occurrence and abundance of species, the formation of novel interactions and secondary extinctions, and alterations of the dispersal ability of plants and microbes[52]. These pathways are mediated by three kinds of functional traits: response traits, matching traits, and dispersal traits. In simulated scenarios of environmental change, phylogenetic relationships are a constraint in the rewiring of mycorrhizal networks, so that rewired interactions (i.e., with non-preferred hosts) tend to involve close relatives of preferred hosts[47]. Despite this constraint, rewiring increased the robustness of the fungal community to the simulated loss hypothetically caused by environmental change of their host species. These studies overall reinforce the importance of understanding the effects of species traits and phylogenetic relationships on the reassembly of interaction networks. A next step would be to predict how this reassembly process responds to the potential trait changes caused by changing environmental conditions.

Future perspectives

Based on the data emerging from these approaches, it should be possible to estimate future recovery trajectories of the forest built based on the IPCC Representative Concentration Pathways climate scenarios and predicted scenarios of land use change for the region (Figure 1). Given that trajectories of forest recovery would go beyond the IPCC scenarios of climate change that only cover until 2100, this approach should use longer-term models (several centuries) of climate change estimations[53]. The network approach could also expand aboveground to look at the effects of belowground changes caused by land use change (agricultural abandonment) along a climatic gradient on the aboveground community (e.g., leaf inhabiting microbial communities and its effects on insect herbivory and leaf disease). This would allow us to understand, for example, whether belowground increases in functionality caused by reassembling interactions could increase plant fitness affecting aboveground interaction and function[29].

These kinds of approaches can provide quantifiable information to understand the ability of post-agricultural lands to recover and resist further impacts caused by land use and climate change. They may also help understand the effects of the recovery of the structure of interactions on forest functional and phylogenetic diversity and tree health (nutrition and growth), and the ability of those interactions to respond to increasing temperatures. This can help identify species interaction modules, structures, and combinations of interactions with targeted functional responses that if used in the context of ecosystem restoration and management could accelerate the recovery process and increase the adaptability of current and future forests to increasing temperatures.

Declaration of Interests

The authors declare no competing interests.

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Table 1. Molecular targets to identify symbiosis and C/N nutrient cycling for amplicon and metatranscriptomic sequencing.

Ecological Interactions/Actions	**Targeted genes**
Fungal pathogenesis of roots	Fungal effector genes on transposable elements and accessory chromosomes[54] glycosyltransferases, secretory lipases, alpha-kinase, cutinase[55]
Plant root defense against pathogens	Plant synthesis of metabolites for antioxidants, lipid signaling; terpenes, and growth hormones[56]
Plant-fixed C allocation to ECM fungi	Plant genes involved in C production (e.g., glucose, sucrose, fructose) and C exchange (sugar alcohols such as mannitol, arabinitol)[27]
ECM fungal C uptake (from root)	ECM fungal production of trehalase, D-xylulose-5-phosphate cytidylyltransferase; CDPD-xylulose reductase; mannose 6- phosphate reductase; mannose-1-phosphate phosphatase; mannose-6-phosphate;

	Isomerase, enzymes for Fructose biosynthesis), as well as potential genes involved in EMF-plant symbiosis and signaling exchange (e.g., small proteins; low molecular metabolites)[27]
ECM fungal N exchange with plant	ECM fungal production of N-transporters/transferase for amino acids, oligopeptides, ammonium, nitrate and intracellular N process (e.g., synthesis/metabolism of glutamine, leucine-aminopeptides)[57]
Plant N uptake in roots	Plant genes involved in intracellular N process (e.g., amino acid transporters, nitrate and ammonium transporters)

Measuring ecosystem change

Figure 1. Measures of recovery through time.

The response of complex metrics to the combined effects of recovery and climate change may be slower than ‘simpler’ metrics only related to species numbers and abundance or biomass production (Moreno-Mateos *et al.*[4]). Symbol color represents species diversity. RCP, representative concentration pathways.

Figure 2. Restoration unit.

Once we understand how to restore interactions, we can design restoration units including modules of species with targeted functions that we know have key roles in the recovery process.

Figure 3. Conceptual integration of approaches to study the combined effect of land-use and climate change on ecosystem recovery and restoration.

The combination of approaches is represented as the central dark circle. Blue shading indicates global changes. Purple shading indicates target properties to be measured. Pink shading indicates key methodological approaches (in parenthesis examples of metrics that will be estimated).

In Brief

Moreno and Bhatnagar argue in favor of using an ‘interaction–function’ perspective to understand the dynamics of ecosystem recovery after land use change, especially in the light of climate change.