

Opinion

Adaptive Networks for Restoration Ecology

Rafael L.G. Raimundo,^{1,2,*} Paulo R. Guimarães Jr.,² and Darren M. Evans³

The urgent need to restore biodiversity and ecosystem functioning challenges ecology as a predictive science. Restoration ecology would benefit from evolutionary principles embedded within a framework that combines adaptive network models and the phylogenetic structure of ecological interactions. Adaptive network models capture feedbacks between trait evolution, species abundances, and interactions to explain resilience and functional diversity within communities. Phylogenetically-structured network data, increasingly available via next-generation sequencing, inform constraints affecting interaction rewiring. Combined, these approaches can predict eco-evolutionary changes triggered by community manipulation practices, such as translocations and eradications of invasive species. We discuss theoretical and methodological opportunities to bridge network models and data from restoration projects and propose how this can be applied to the functional restoration of ecological interactions.

Restoration Ecology: Developing the Application of Ecological Networks

With unprecedented biodiversity losses as a result of anthropogenic disturbance, restoration of many ecosystems is needed to re-establish the provision of valuable **ecosystem services** (see [Glossary](#)) [11,12]. Historically, restoration ecology has applied ecological theory to recover biodiversity and **ecosystem functions** [12]. Recent theoretical advances provide new ways to consider the restoration of community properties, such as **resilience** and **functional diversity** [13]. One such perspective is the ecological network approach to restoration, which benefits from a growing understanding of how species interactions affect community organization and dynamics [14]. Several studies show how ecological networks can link new ways of understanding and planning ecosystem management [13,15,16].

Ecological networks can be powerful tools for restoration because species interactions shape, and are shaped by, ecological and evolutionary processes that maintain biodiversity and its related ecosystem functions [17]. Networks are already used to provide informative assessments of restoration outcomes [13]. For example, the removal of invasive species from a plant-pollinator network has been shown to increase the number of interactions per species, which in turn enhanced pollination quality and functional diversity [16]. Importantly, networks can also be used to plan and better predict restoration outcomes [13,15,16].

The potential of using network models for restoration has been strengthened by novel sources of **biodiversity big data**, such as those created through **next-generation sequencing (NGS)** technologies that provide unprecedented amounts of information on species interactions, including their phylogenetic structure, in a cost-effective manner [1,5]. For example, ‘nested tagging’ DNA metabarcoding approaches can create highly-resolved, host-parasitoid networks using >1000 insect hosts in a single sequencing run [18]. We contend that using phylogenetically-structured species interaction data to inform dynamic network models is a major advance linking theoretical and applied research to support and predict the outcome of restoration strategies.

Highlights

A network approach to restoration ecology recently emerged as a tool for integrating methodological and theoretical advances to support environmental management and decision-making.

Adaptive network models allow us to better understand and predict how both ecological and evolutionary processes shape biodiversity and ecosystem functioning.

In adaptive networks, the feedback between the macroscopic dynamics of interaction structure and the microscopic dynamics of population-level processes shapes interactions, abundances, and traits, hence influencing resilience and functional diversity.

The increasing availability of phylogenetically-structured network data generated through next-generation sequencing techniques, alongside the standardization of biomonitoring protocols, can foster the integration of evolutionary principles into adaptive network models for ecological restoration, providing highly-resolved information for model parameterization and assessment across temporal and spatial scales.

Phylogenetically-informed adaptive network models can be used for the selection of alternative species sets to be added or removed from communities and hence can provide flexible strategies for functional biodiversity restoration that fits local socio-economic contexts.

Overcoming current theoretical and methodological gaps to build a two-way street between adaptive network models and experimental restoration ecology is now an achievable task, the resolution of which can broaden our ability to restore biodiversity and ecosystem functioning based on key ecological and evolutionary principles.

The manipulation of community composition is one pivotal aspect of restoration practices, which routinely add or remove species from communities, such as in species translocations (e.g., [19]) and in the eradication of invasive species (e.g., [20]). Network models can help to inform the selection of species to be added or removed by considering, for example, the expected outcomes under variable degrees of perturbations [21] or alternative restoration targets [15]. In order to improve the usefulness of ecological networks for restoration, we suggest that these models can readily incorporate evolutionary principles, which to date have mostly been overlooked.

Eco-evolutionary network models using phylogenetically-structured species interaction data can help to predict how the manipulation of community composition reshapes its resilience, **stability**, and functional diversity, which are key properties for setting restoration targets and biomonitoring assessment. Here, we (i) show that rapid evolution within ecological networks is an important consideration that is expected to affect restoration outcomes; (ii) present a theoretical background that underpins a restoration framework based on adaptive networks, a general class of dynamic network models; (iii) identify the steps required to merge adaptive network modelling with phylogenetically structured species interaction data; and (iv) discuss the opportunities and challenges to bridge network models and field data generated by restoration scientists in a mutually beneficial exchange between pure and applied researchers. Overall, we seek to stimulate integrative research on the mechanisms that drive restoration outcomes – an understanding that is fundamental for predictive restoration science [22].

Why Is Rapid Adaptive Evolution Important for Restoration Ecology?

Restoration ecology has historically overlooked evolutionary theory [23]. Nevertheless, compelling evidence shows that the rapid evolution of functional traits (Box 1) can affect community dynamics [24]. Indeed, traits that mediate species interactions can evolve even within a few generations [25]. For example, body mass evolution in reed warblers (*Acrocephalus scirpaceus*) that colonized a restored wetland in Malta was recorded over a period of just 19 years [26]. Rapid trait evolution can affect life histories [27], ecological dynamics [28], and ecosystem services [29]. In turn, such ecological changes reshape the local interplay of evolutionary processes, creating feedbacks between ecological and evolutionary processes [30]. Eco-evolutionary feedbacks might influence restoration outcomes as species that lack a coevolutionary history start to interact within degraded environments, triggering rapid adaptive evolution [31]. Strong trait selection in organisms used for restoration will often be predictable, as illustrated by repetitive evolution of small plants and seeds, and earlier flowering, in the grass *Elymus elymoides* ssp. *californicus* after post-fire restoration [32].

We next introduce adaptive network models (ANMs, Box 2, see [33]) to show how they can incorporate eco-evolutionary feedbacks to support ecological restoration strategies.

How Can Adaptive Network Models Be Used in Restoration Research?

ANMs are part of the ongoing integration of ecological and evolutionary theories of community dynamics, which include eco-evolutionary dynamics [30], evolutionary metacommunity theory [37], and the geographic mosaic theory of coevolution [2]. ANMs capture eco-evolutionary feedbacks that connect community-level dynamics of ecological interactions to the population-level processes that shape species abundances and trait evolution [33,36] (see Box 2). Within a restoration context, such trait-abundance-interaction feedbacks [36] can occur, for example, when selection favours taller individuals within a plant population: as the mean plant height increases, the population sizes of herbivores also increases due to higher food availability, triggering the adaptive evolution of novel forms of plant resistance (see [31]) and ultimately changing the interaction patterns at the community level.

¹Departamento de Engenharia e Meio Ambiente, Centro de Ciências Aplicadas e Educação, Universidade Federal da Paraíba, Campus IV, Rio Tinto, PB, Brazil

²Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

³School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, UK

*Correspondence:
rafael.raimundo@cdae.ufpb.br
(R.L.G. Raimundo).

Box 1. Rapid Evolution, Ecological Dynamics, and the Restoration of Seed Dispersal Networks

Ecological interactions link selection and population dynamics and hence underpin ecological and evolutionary processes driving biodiversity. The subset of organisms bearing traits favoured by selection imposed by ecological interactions can show intrinsic growth rates that are higher than the average of the population [34]. The demographic consequences of rapid evolution on populations have repercussions on community structure and dynamics [24,28,30].

The rapid evolution of palm tree seed sizes following the extinction of large-gaped birds in the Brazilian Atlantic Forest [35] (Figure 1) illustrates how changes in community composition can trigger rapid evolutionary changes whose ecological effects can reshape the distribution of traits, abundances, and interactions at the community level [30,36]. In Atlantic Forest fragments where these large frugivores no longer exist, palm trees now produce smaller seeds, which can negatively affect seedling survival [35]. Accordingly, rapid trait evolution in human-modified environments can have broad effects on ecosystem functions, as illustrated by the seed dispersal deficit imposed by the evolution of smaller body sizes of frugivore fish species due to selective fishing [29].

Community manipulation for restoration purposes will often trigger feedbacks between trait evolution and population dynamics [31]. Understanding how such feedbacks change network structure [36] is relevant, for example, to support decision-making regarding whether to introduce or eradicate species for restoration. Similarly, the restoration of seed dispersal networks within Atlantic Forest fragments subject to defaunation [35] requires a predictive framework for the selection of frugivorous species whose reintroductions can recover the interactions of species that have lost their seed dispersers.



Trends in Ecology & Evolution

Figure 1. Effects of Rapid Evolution on Ecological Interactions. Rapid evolution led to reduced seed sizes in the *Euterpe edulis* palm, the plant depicted in both photos above, in Brazilian Atlantic Forest fragments that lost large-gaped frugivore species [35], such as (A) the black-fronted piping-guan, *Aburria jacutinga* (Cracidae). In such fragments, small frugivores, such as (B) the rufous-bellied thrush, *Turdus rufiventris* (Turdidae), became the prevalent seed dispersers of *E. edulis*. Photos by Mathias M. Pires, here used with permission from the author.

Knowledge Gaps and Emerging Research Directions**Restoration of Biodiversity Structure: Timescales and Dynamics of Interaction Rewiring**

Different types of ecological networks can be seen as building blocks of restoration strategies because they correspond to complementary ecosystem processes (Figure 1). For example, in oceanic islands, the taxonomic disparity between pollinators (mostly invertebrates, such as bees and beetles) and seed dispersers (mostly vertebrates, such as birds, bats, and lizards) requires compatible restoration strategies at distinct spatio-temporal scales; the small-scale and rapid restoration of plant populations and their pollinators can later benefit from the restoration of seed dispersal interactions at broader spatio-temporal scales, which in turn will increase the genetic diversity of previously restored plant populations [41]. The restoration of such ‘networks of networks’ [42] is a promising perspective, but currently we still need to understand the mechanisms of **interaction rewiring** that are relevant for the restoration of particular ecological networks. The incorporation of realistic rewiring mechanisms [43,44] into ANMs can help to predict when a restored ecological network will be able to absorb perturbations by the reconfiguration of its interaction patterns (Box 2) without changes to ecosystem functioning [7].

Glossary

Biodiversity big data: large datasets provided by a variety of sources, such as field surveys and next-generation sequencing technologies (e.g., environmental DNA), that can be used to describe ecological populations and communities [1].

Coevolutionary dynamics: the processes of local adaptation mediated by reciprocal natural selection between interacting species [2].

Ecosystem functions: biological and geochemical processes that govern biodiversity organization and the flow of matter and energy across ecosystems.

Ecosystem services: outcomes of ecosystem functions that have socio-economic value, such as crop pollination and pest control.

Forbidden links: interspecific interactions that do not occur due to trait incompatibilities of potentially interacting individuals, such as mismatching morphologies or phenologies [3].

Functional diversity: ‘the range and value of those species and organismal traits that influence ecosystem functioning’ [4]; a notion that relates to the extent to which species are functionally complementary (functional complementarity) or redundant (functional redundancy).

Interaction rewiring: the reconfiguration of an ecological network arising from the establishment or cessation of pairwise interactions as a consequence of adaptive or stochastic processes.

Next-generation sequencing (NGS): several novel techniques that allow the rapid, inexpensive, and genome-wide sequencing of DNA. These can be used to construct large, phylogenetically-structured species-interaction networks [5].

Resilience: the extent to which an ecological system absorbs disturbances without fundamental changes in its structure, dynamics, and feedbacks [6,7].

Rewiring rules: algorithms used to model the processes that drive interaction rewiring.

The tempo and mode of rewiring mechanisms are expected to vary between different types of ecological interactions across taxa and ecosystems (Figure 1). Hence, the design of rewiring algorithms should take into account similarities and dissimilarities of network dynamics expected from coevolutionary history, which may be partially encoded in the phylogenetic structure of ecological interactions [45,46] to inform restoration strategies. To date, ANMs have overlooked the role of phylogeny in rewiring dynamics (but see [47]). Instead, **rewiring rules** have applied several heuristic criteria, such as the optimization of species abundances [48], the number of interactions per species, and phenotypic similarity [43]. We propose that incorporating phylogenetic data and natural history knowledge into ANMs will help in predicting the outcomes of restoration practices, especially if in association with other constraints that shape network structure, such as **forbidden links** [3]. Ultimately, constraints to interaction rewiring might depend on the extent to which phylogenetic relatedness (i.e., phylogenetic signal) predicts interaction patterns [45,49]. Therefore, whenever phylogenetic signal matters, phylogenies will be helpful to inform rewiring models on which interactions are likely or unlikely to occur.

Phylogenetic signals are expected to be pervasive in reciprocally specialised mutualistic interactions, such as those between figs (*Ficus* spp.) and fig wasps (Hymenoptera: Chalcidoidea), as their codiversification history tightly connects species, and hence rewiring events are phylogenetically constrained [50]. Indeed, strong phylogenetic constraints on interaction rewiring partially explain the modular structure of many mutualistic networks (Figure 1G, [51,52]). Phylogenetic constraints also affect network dynamics in antagonisms, for example, limiting the range of plant species used by herbivores [47]. Phylogeny is expected to constrain network structure even in generalized ecological interactions, as illustrated by a study showing that phylogenetically related species tend to interact with similar partners in 42.7% of the 103 phylogenies of mutualistic networks considered [45]. Although phylogenetic signals are ubiquitous in ecological networks, their strengths vary across interaction types, species sets, and components of network structure [46]. In some generalized interactions, such as seed dispersal mutualisms, rewiring rarely requires further specializations [53]. In these interactions, the

Robustness: the 'ability of a system to maintain itself within a narrow range of function' [8].

Stability: the ability of an ecological community to buffer disturbances and return to an equilibrium point after a small perturbation of population densities [9].

Topological roles: the patterns of interaction of a species within a network with regards to how its interactions are distributed within and among cohesive species groups, the so-called modules [10].

Box 2. Adaptive Network Models: Definition and Application to Restoration

Adaptive network models are a class of network models that incorporate feedback between patterns of interaction among elements (e.g., species) and the properties of these elements (e.g., species traits and abundances) [33,38]. Thus, when depicting ecological communities, ANMs capture trait-abundance-interaction feedbacks [36] (Figure 1A). Traits and abundances shape patterns of interaction because traits allow interactions to occur and abundances affect the encounter rates of potentially interacting species [36]. Patterns of interactions have eco-evolutionary effects that shape abundances and traits within populations. When one species rewires its interactions, the arising demographic and evolutionary effects can spread across the network via indirect interactions [28]. As a consequence, the community-level distribution of traits and species abundances will change, and further rewiring can be triggered.

ANMs account for the feedback loop between: (i) the dynamics of networks, which refers to temporal variation in the network structure due to interaction rewiring; and (ii) the dynamics on networks, which refers to changes in population-level properties of the species that form the network, such as mean traits and abundances (see [33,38], Figure 1B). ANMs can explore the relative roles of candidate mechanisms that produce biodiversity patterns, such as neutral and niche-based processes which can influence patterns of interaction among species [39]. ANMs can provide testable predictions for changes in biodiversity arising from restoration practices that add or remove species from communities and refer to: (i) network structure, which is a proxy for resilience [6]; (ii) the distribution of species abundances, which relates to stability [9]; and (iii) the community-level distribution of traits, which relates to both robustness [8] and functional diversity (e.g., [40]). As a simple example, the rewiring of seed dispersal networks with highly generalist animals might increase the number of interactions per species and ensure the persistence of plant species with a wide range of seed sizes (Figure 1C). Alternatively, the addition of a specialist plant species that connects only particular groups of highly interactive species (modules) within the network might increase modularity, promote trait divergence between unconnected network modules, and ultimately lead to the functional extinction of disconnected species (Figure 1D). Taken together, predictions provided by ANMs for the outcomes of community manipulation strategies can represent a broad support for the restoration of resilient and functionally diverse ecological networks.

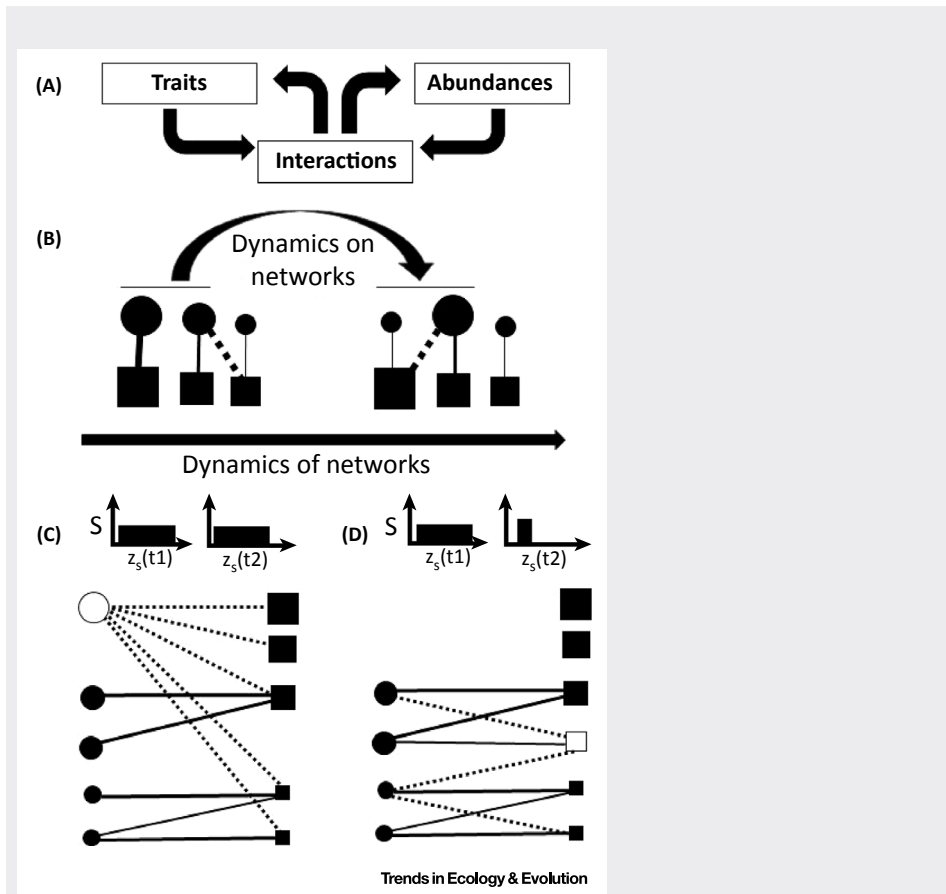
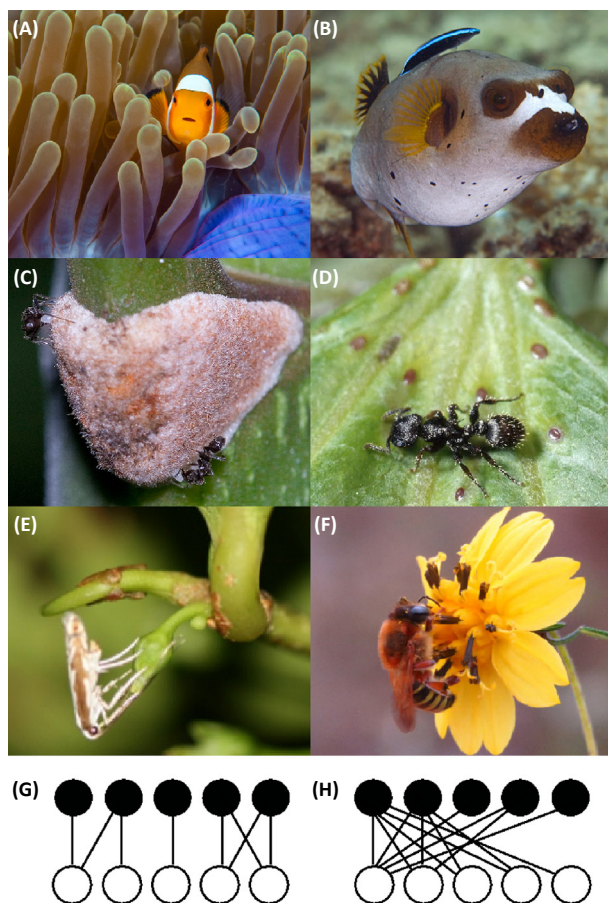


Figure 1. Adaptive Networks Capture the Interplay of Processes Occurring at Different Levels of Biological Organization and Can Be Used to Predict How Restoration Practices Will Affect Community-Level Properties. (A) Trait-abundance-interaction feedbacks capture reciprocal causality between demographic and evolutionary processes and network structure. (B) The dynamics of networks [33,38] refers to the long-term rewiring of ecological interactions that drive network structure, whereas the dynamics on networks [33,38] describes changes in species abundances and traits that shape the population-level properties influencing adaptive and stochastic processes that drive network structure, closing the feedback loop. (C) Hypothetical example of a restoration strategy in which one generalist seed disperser is reintroduced into a local network, increasing the overall network connectivity and ensuring the persistence of plant species across the entire range of seed sizes (z_s). Here, (t1) is the original distribution of seed sizes and (t2) is the expected distribution of traits arising after the reintroduction of the generalist. The sizes of the geometric symbols are proportional to species abundances. White symbols indicate species added to the community for restoration purposes. Broken links represent the new interactions established by reintroduced species. (D) Hypothetical example of restoration strategy analogous to (C), but with the introduction of a more specialist plant that connects only particular modules within the network, triggering within-module trait convergence and reducing trait diversity at the community level. The community-level decrease in trait diversity is reinforced by the functional extinction of plants with large seed sizes that will remain disconnected. See the section 'Bridging Adaptive Network Theory and Experimental Restoration Research' for further details on predictions that can be provided by adaptive network models.

phylogenetic signal might be weak and selection should favour unconstrained interaction rewiring as individuals optimize their foraging strategies to face the spatio-temporal heterogeneity in resource availability [54].

Restoration of Ecosystem Functions: Dynamics of Abundances and Traits on Networks

Although changes in species abundances and traits are intertwined with trait-abundance-interaction feedback [36] (Box 2), most ANMs to date have explored ecological or evolutionary



Trends in Ecology & Evolution

Figure 1. Distinct Types of Bipartite Networks, Such As Those Depicting Specialized Obligate Ecological Interactions (A,C,E) or Generalized Facultative Ecological Interactions (B,D,F), Show Contrasting Structures and Relate to a Variety of Ecosystem Functions. (A) Mutualism between the anemonefish *Amphiprion percula* and the magnificent sea anemone *Heteractis magnifica*. Photo by João Paulo Krajewski. (B) Cleaning mutualisms between the blackspotted puffer, *Arothron nigropunctatus*, and the bluestreak cleaner wrasse, *Labroides dimidiatus*. Photo by João Paulo Krajewski. (C) Defensive mutualisms between ants, *Azteca cf. alfari*, and the tree *Cecropia pachystachya*. Photo by Ronaldo B. Francini. (D) Worker of *Procrystocerus* sp. visits the extrafloral nectaries of an Euphorbiaceae species. Photo by Paulo S. Oliveira. (E) Pollinating seed parasite, the moth *Epicephala* sp., pollinates a flower of the plant *Phyllanthus grayanus*. Photo by David H. Hembry. (F) The bee *Melipona quinquefasciata* visits a flower of *Aspilula jolyana*. Photo by Jeferson Vizontin-Bugoni. (G) Specialized obligate mutualisms often form modular network patterns in which subsets of species (represented by black and white nodes) are more interconnected among themselves than with the rest of the network. (H) Generalized facultative networks are frequently nested, that is, a core of generalist species interacts with most species within the network and a periphery of specialists mostly linked to the generalist core. All photos in this figure are used with permissions from the authors.

dynamics independently. The ecological dynamics of abundances on theoretical models of ecological networks has been studied for decades [9]. By contrast, we are only just beginning to understand how networks affect trait evolution. Models of coevolutionary networks show how selection and other mechanisms shape trait evolution underpinning network structure [55,56]. For example, coevolutionary convergence, that is, the evolution of similar traits in phylogenetically unrelated species as a result of selection arising from ecological interactions [2], can reinforce functional redundancy by increasing functional trait similarity among species [57]. Therefore, coevolutionary convergence might positively affect the resilience and **robustness** of ecosystem functions, such as pollination or seed dispersal. Another example of how coevolution on networks might influence ecosystem functioning is the addition of super-generalists to pollination networks. This is expected to enhance trait matching between plants and pollinators [56], which, in turn, enhances pollination quality [58]. For antagonisms, ANMs of host-parasite interactions predict that network structure shapes, and is shaped by, selection, with transient arms races being the prevalent **coevolutionary dynamics** driving trait diversity [59]. More generally, eco-evolutionary processes triggered by frequency-dependent selection shape genetic diversity, network dynamics, and adaptive diversification [60–62]. Despite such relevance, the ecological and socio-

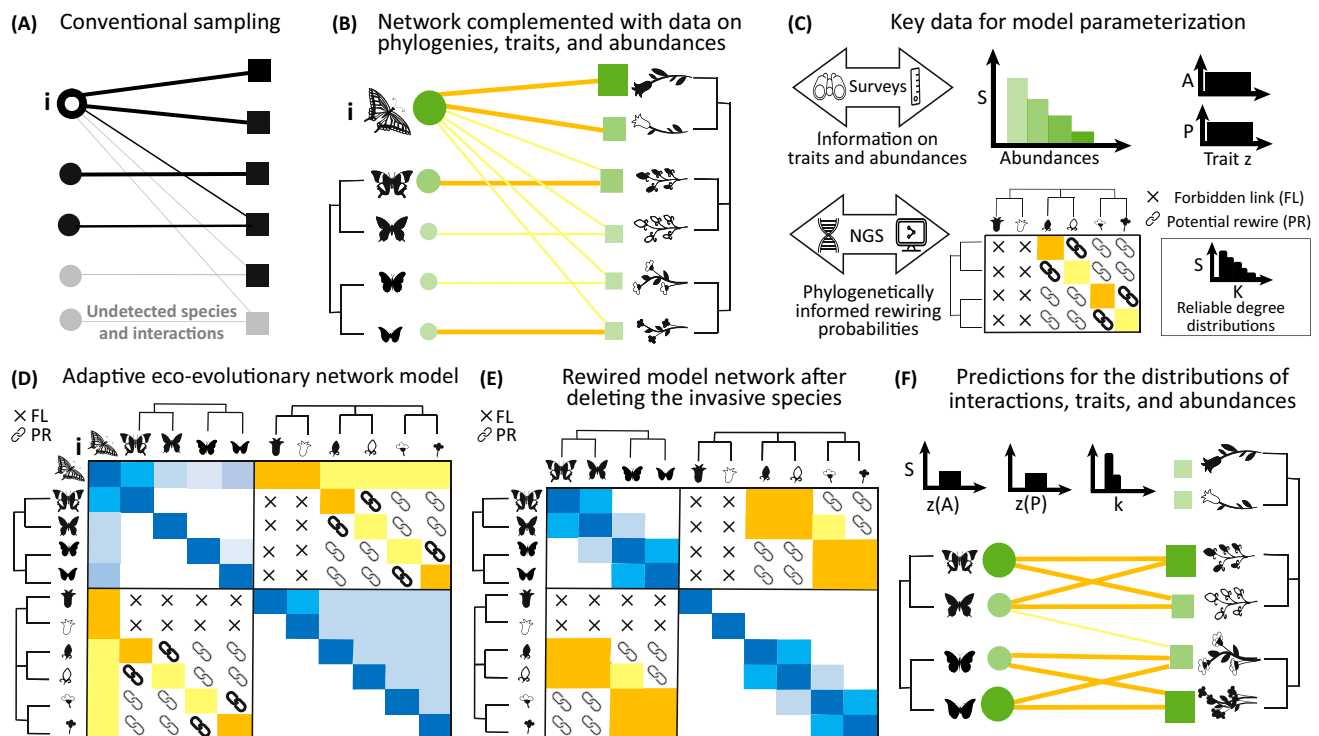
economic consequences of rapid evolution on networks remain largely unexplored (but see [2]). ANMs that incorporate both ecological dynamics and trait evolution are likely to better predict how species additions and removals will affect restoration outcomes. Such an integrative step requires the joint efforts of theoreticians and restoration ecologists to build an ANM approach to 'pre-restoration' [63], that is, the selection of species sets to ensure that the restored network structure and related ecosystem functions will persist over time.

Bridging Adaptive Network Theory and Experimental Restoration Research

Network models can be applied to different restoration problems, such as predicting which subsets of candidate species can be added to a network to improve its resilience [21] or whether (and which) invasive species should be eradicated to favour the persistence of species and interactions [64]. For example, network models suggest that the consequences of species additions depend on their specialization and on the extent to which introduced species compete for interactions [65]. Simulations also suggest that introducing many generalist species can prevent network collapse [21]. Regarding species removals, models suggest that the eradication of highly connected non-native species from plant-pollinator assemblages can increase extinctions driven by ecological dynamics [66]. Together, these results support the concept that species' **topological roles** within networks (e.g., network 'hubs' that connect multiple modules, see [10]) are relevant for the selection of species that will persist together in the long term. A challenge to consider is that both species roles and network properties change as species rewire their interactions. For example, in species removal simulations, the vulnerability of plant-pollinator networks to secondary extinctions decreases if species rewire interactions following the extinction of their mutualistic partners [44]. Again, predictions derived from ANMs can help to unravel the consequences of interaction rewiring for restoration, whilst simultaneously informing pre-restoration strategies.

A framework that combines ANMs, phylogenetically-structured species-interaction data, and biodiversity monitoring (Figure 2) can improve network approaches to predictive restoration in several ways. First, it can improve network data completeness as conventional network sampling, based on field observations, often misses species and interactions (Figure 2A). NGS cost-effectively enhances species-interaction data completeness and, moreover, provides information on the phylogenetic structures of ecological networks (Figure 2B). Second, ANMs can be immediately parameterized to assess predictions by combining data provided by NGS plus a variety of existing data on species abundances, trait distributions, and patterns of interactions (Figure 2C). Phylogenetically-structured network data can improve network rewiring rules by incorporating evolutionary constraints on network dynamics. This requires the development of new methods to allow the assignment of rewiring probabilities based on different components of phylogenetic signals [46], forbidden links [3], and trait matching [67].

Phylogenetically-informed ANMs can predict the outcomes of species additions and removals in terms of resilience, stability, and functional diversity via the integrative modelling of the dynamics of species abundances (Figure 2D, see [48]) and trait evolution [56,59]. Once a baseline ANM is defined for a focal community, simulations of species additions or removals, such as the eradication of invasive species (Figure 2E), can be used to predict changes in the distribution of interactions, abundances, and traits (Figure 2F). Our example in Figure 2 refers to the eradication of an invasive species, but a similar approach can predict structural and functional outcomes of adding species with contrasting topological roles. We suggest that plant-insect networks are ideal study systems to begin the operationalization of the framework because they: (i) encompass a wide variety of complementary ecosystem functions and services; (ii) have well known structural patterns that represent references for restoration targets; and (iii) have been well studied from



Trends in Ecology & Evolution

Figure 2. A Roadmap for the Predictive Restoration of Ecological Networks Illustrated by a Hypothetical Case of Eradicating an Invasive Species, the Larger Butterfly (i), without a Direct Phylogenetic Relationship with the Other Native Species That Form the Assemblage. (A) A conventional sampling of ecological networks often provides incomplete datasets as observational field efforts often lack species and interactions. (B) Next-generation sequencing (NGS) improves network data completeness, informs the subjacent network structure and, combined with field surveys, provides additional information on the community-level distribution of traits and abundances. (C) Network data, improved by NGS and systematic, long-term biomonitoring, provide information for the parameterization of adaptive network models, including species abundances, trait distributions, and rewiring probabilities derived from phylogenetic distances or trait-based criteria. The symbols S and k indicate the number of species and the number of mutualistic interactions per species, respectively. (D) The adaptive network model is implemented as a dynamic system in which the temporal variation in species abundances is governed by the negative and positive effects of several types of ecological interactions on population sizes. The gradient of hot colours depicts the strength of the positive demographic effects imposed by each mutualistic interaction, and the gradient of cold colours represents the negative effects of interspecific competition. The diagonal represents the negative effects of intraspecific competition. (E) Simulated rewired system after the removal of the invasive species (i), according to phylogenetically-informed rewiring rules based on phylogenetic distances and trait-defined forbidden links. The rewiring of mutualistic interactions also reorganizes the structure of interspecific competition, which is defined as the overlap in resource use between species within the same trophic level. (F) Predictions for the distributions of interactions, abundances, and traits after the removal of the invasive species (i). In this hypothetical example, the removal of the invasive species led to competitive release and interaction rewiring within phylogenetically defined modules, resulting in within-module trait convergence, decreased trait diversity at the community level, and changes in abundances and in the number of interactions per species. The ecological traits that mediate the mutualistic interactions between animals and plants are indicated by $z(A)$ and $z(P)$, respectively.

ecological and evolutionary perspectives. Moreover, due to their short lifespans, many insect and plant species are suitable for monitoring trait evolution, which is a key but challenging aspect of empirically assessing predictions of changes in functional diversity within restoration contexts.

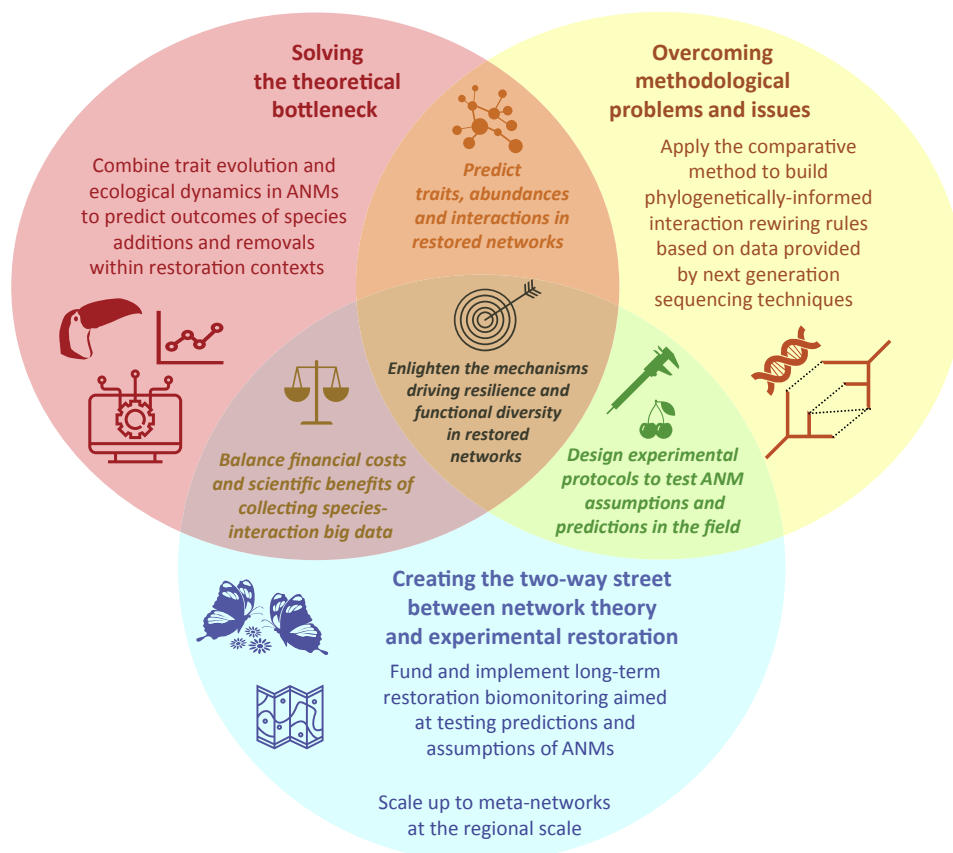
Challenges and Ways Forward

We argue that merging the evolutionary ecology of species-interaction networks [17], adaptive network modelling [33,38], molecular techniques [5], and novel biomonitoring methods [1,18] can predict how restoration strategies will affect resilience and functional diversity (Figure 2). ANMs provide predictions to improve the functional restoration of ecological networks. In turn, data from restoration projects can validate predictions, assess modelling assumptions, and inform

parameterization [68]. Improved models can then guide field trials to elucidate eco-evolutionary mechanisms driving resilience and functional diversity within restored networks. The success of this framework depends upon collaborations between network and restoration ecologists. We see this as a two-way street between theory and practice, resulting in mutually beneficial partnerships. However, there are still several theoretical and methodological bottlenecks to overcome.

Overcoming Theoretical Bottlenecks and Methodological Issues

We identify three interlinked challenges to overcome in order for adaptive networks to be successful in restoration (Figure 3). First, evolutionary and ecological dynamics need to be merged into ANMs to elucidate trait-abundance-interaction feedbacks [36], particularly when considering species additions and removals within communities. This is achievable, as ANMs have already been used to model ecological (e.g., [48]) and evolutionary dynamics (e.g., [59]) independently. Second, work is needed to translate phylogenetically-structured network data into rewiring rules driving ANM dynamics (Figure 3). Although studies on phylogenetic signals in ecological networks [46], mechanisms driving forbidden links [3],



Trends in Ecology & Evolution

Figure 3. Key Challenges to Be Solved for the System-Specific Implementation of the Interface between Adaptive Network Models and Field Data on Species Traits, Abundances, and Interactions. The partial intersections of the Venn diagram depict general goals to be achieved on the interfaces between (i) theory and modelling methods, (ii) modelling methods and field research, and (iii) field data and theory-building. The central intersection of the diagram represents the general expected result, which is the improvement of our mechanistic understanding of the eco-evolutionary processes driving the outcomes of community manipulation for restoration.

and linkage rules across different types of species-interactions [67] provide a starting point, a general synthesis is needed. Third, the success of this approach requires new, mutually beneficial collaborations between network scientists and restoration ecologists. The funding of co-designed, long-term restoration experiments and the systematic monitoring of species interactions is key (Figure 3). Persuading restoration scientists and practitioners, who are likely to be operating on limited budgets and facing urgent decisions, of the benefits of using ANMs is achievable through improved communication. With the growth of field-based NGS technology and specific development of network analysis software, it will not be long before these challenges are resolved and adaptive networks become mainstream in restoration ecology.

Achievable Benefits of Using Adaptive Networks for Restoration Research and Practices

ANMs can help restoration planning because they can infer the structure and dynamics of ecological networks even in the absence of detailed information [9,69]. Ideally, however, the better the description of the system, the better the inferences for restoration. The collection and standardisation of long-term abundance and interaction data to inform ANMs requires only small modifications to existing sampling and biomonitoring protocols [1]. NGS techniques can complement network data with a balance between financial costs, which are continuously decreasing, and the expected scientific benefits (Figure 3). Concomitantly, trait-based metrics used in restoration (e.g., [70]) can be used in trait-evolution models to predict changes in functional diversity.

The ANM framework can improve the efficiency of restoration practices in several ways. For example, it should be feasible to select multiple bio-control agents with complementary topological roles whose introduction will affect invasive taxa, mitigating their deleterious impacts [23,71]. ANMs can also improve restoration planning by considering the key role of functional trait diversity for the management of invasive species, an issue that was brought to the attention of restoration ecologists over a decade ago [72]. Finally, ANMs can also extend synthetic biology principles [73,74] to restoration by showing, for example, when non-native species could be incorporated as novel biological elements that contribute to resilience and functional diversity [41,64,74].

In the long-term, the scaling up of ANMs to address the functional restoration of landscapes is possible, linking the spatial planning of restoration to eco-evolutionary processes at the metacommunity scale [2,37]. Habitat patches can be modelled as adaptive meta-networks defined by nodes that represent local species-interaction networks, which are linked via species' dispersal [75]. Each link within the spatial meta-network has multiple layers of information due to interspecific heterogeneity in dispersal abilities. Hence, multilayer links describe species-specific flows of individuals that connect, at the meta-community scale, the local dynamics of interactions, abundances, and traits. Recent work is unravelling how the dynamics of spatial and ecological networks together shape the turnover of ecological interactions and ecosystem functioning across landscapes (e.g., [76]). The empirical parameterization of multi-layer links that define adaptive meta-networks is straightforward, as illustrated by the application of DNA-based genotype techniques to describe the differential contribution of frugivore species to the dispersal of seeds connecting different sites [77]. The empirical description of meta-networks requires sampling effort that balances the completeness of local network structures and the availability of information for multiple sites, which can be improved by the large-scale application of NGS technologies. A further application of ANMs is the management of multi-layer ecological networks (see [78]) that takes into account feedback among multiple interaction types.

Together, these ideas converge with the growing notion that new syntheses, which extend existing theoretical foundations to account for eco-evolutionary feedback that pervade the hierarchical organization of biodiversity (e.g., [17,79]), combined with biodiversity big data provided by advances in molecular ecology, are urgently required to improve ecosystem management [80]. We contend that combining ANMs with phylogenetically-structured species-interaction data provides a much needed basis for integrating ecological and evolutionary dynamics to elucidate the mechanisms driving restoration outcomes (see Outstanding Questions). This can contribute to the expansion of the decision-space of restoration practitioners, which is key to ensure the adaptation of restoration strategies into local socio-economic contexts and to enhance ecological resilience in human-dominated landscapes [81].

Acknowledgments

R.L.G.R. was supported by the São Paulo State Research Foundation (FAPESP, grant #2014/21106-4), by CAPES (Brazilian Ministry of Education), and by a URC Visiting Fellowship awarded by Newcastle University. D.M.E. and P.R.G.Jr were supported by a Royal Society Newton International Exchanges Scheme Mobility Grant. P.R.G.Jr was further supported by FAPESP (grant #2017/08406-7) and CNPq. We thank J.N. Thompson, S.A. Evans, and two anonymous referees for suggestions on the manuscript. We also thank Clive Emary, Pedro Jordano, John N. Thompson, Jens M. Olesen, Mauro Galetti, Rodolfo Dirzo, and Kate P. Maia for discussions on the application of ecological networks. We are grateful to Mathias M. Pires, João Paulo Krajewski, Ronaldo B. Francini, Paulo S. Oliveira, David H. Hembry, and Jeferson Vizentin-Bugoni for kindly providing the photos used to illustrate this article (see the figure legends for credits).

References

1. Derocles, S.A.P. *et al.* (2018) Biomonitoring for the 21st century: integrating next-generation sequencing into ecological network analysis. *Adv. Ecol. Res.* 58, 1–62
2. Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*, University of Chicago Press
3. Olesen, J.M. *et al.* (2011) Missing and forbidden links in mutualistic networks. *Proc. R. Soc. B* 278, 725–732
4. Tilman, D. (2001) Functional diversity. In *Encyclopedia of Biodiversity* (2nd edn) (Levin, S.A., ed.), pp. 587–596, Academic Press
5. Evans, D.M. *et al.* (2016) Merging DNA metabarcoding and ecological network analysis to understand and build resilient terrestrial ecosystems. *Funct. Ecol.* 30, 1904–1916
6. Holling, C.S. (1973) Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23
7. Walker, B. *et al.* (2004) Resilience, adaptability and transformability in social–ecological systems. *Ecol. Soc.* 9, 5
8. Mumby, P.J. *et al.* (2014) Ecological resilience, robustness and vulnerability: how do these concepts benefit ecosystem management? *Curr. Opin. Environ. Sustain.* 7, 22
9. Allesina, S. and Tang, S. (2015) The stability–complexity relationship at age 40: a random matrix perspective. *Popul. Ecol.* 57, 63–75
10. Olesen, J.M. *et al.* (2007) The modularity of pollination networks. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19891–19896
11. Normile, D. (2010) U.N. Biodiversity summit yields welcome and unexpected progress. *Science* 330, 742–743
12. Falk, D.A. *et al.* (2006) *Foundations of Restoration Ecology*, Society for Restoration Ecology
13. Montoya, D. *et al.* (2012) Emerging perspectives in the restoration of biodiversity-based ecosystem services. *Trends Ecol. Evol.* 27, 666–672
14. Harvey, E. *et al.* (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.* 54, 371–379
15. Devoto, M. *et al.* (2012) Understanding and planning ecological restoration of plant–pollinator networks. *Ecol. Lett.* 15, 319–328
16. Kaiser-Bunbury, C.N. *et al.* (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature* 542, 223–227
17. Toju, H. *et al.* (2017) Species-rich networks and eco-evolutionary synthesis at the metacommunity level. *Nat. Ecol. Evol.* 1, 24
18. Kitson, J.J.N. *et al.* (2018) Detecting host–parasitoid interactions in an invasive Lepidopteran using nested tagging DNA-metabarcoding. *Mol. Ecol.* Published online February 27, 2018. <http://dx.doi.org/10.1111/mec.14518>
19. Bullock, J.M. (1998) Community translocation in Britain: setting objectives and measuring consequences. *Biol. Conserv.* 84, 199–214
20. Pyšek, P. and Richardson, D.M. (2010) Invasive species, environmental change and management, and health. *Annu. Rev. Environ. Resour.* 35, 25–55
21. LaBar, T. *et al.* (2014) Restoration of plant–pollinator interaction networks via species translocation. *Theor. Ecol.* 7, 209–220
22. Brudvig, L.A. (2017) Toward prediction in the restoration of biodiversity. *J. Appl. Ecol.* 54, 1013–1017
23. Stockwell, C.A. *et al.* (2016) Evolutionary restoration ecology. In *Foundations of Restoration Ecology* (Falk, D.A., ed.), pp. 427–454, Island Press
24. Koch, H. *et al.* (2014) Why rapid, adaptive evolution matters for community dynamics. *Front. Ecol. Evol.* 2, 17
25. Thompson, J.N. (1998) Rapid evolution as an ecological process. *Trends Ecol. Evol.* 13, 329–332
26. Lo Cascio Sætre, C. *et al.* (2017) Rapid adaptive phenotypic change following colonization of a newly restored habitat. *Nat. Commun.* 8, 14159
27. Dlugosch, K.M. and Parker, I.M. (2008) Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecol. Lett.* 11, 701–709
28. Barraclough, T.G. (2015) How do species interactions affect evolutionary dynamics across whole communities? *Annu. Rev. Ecol. Syst.* 46, 25–48
29. Costa-Pereira, R. and Galetti, M. (2015) Frugivore downsizing and the collapse of seed dispersal by fish. *Biol. Conserv.* 191, 809–811
30. Fussmann, G.F. *et al.* (2007) Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* 21, 465–477
31. LaRue, E.A. *et al.* (2017) Eco-evolutionary dynamics in restored communities and ecosystems. *Restor. Ecol.* 25, 19–26

Outstanding Questions

Adaptive network models (ANMs) informed by biodiversity big data can foster novel research programs at the interface between evolutionary ecology and restoration science. Fundamental questions for the development of such an interface include: what are the effects of species introductions and removals on the organization of ecological interactions? How does the manipulation of community composition for restoration affect species traits, abundances, and ecological dynamics? How does this then impact upon natural selection in the course of ecological restoration? Evolution can change traits rapidly, but how does adaptive trait evolution propagate at the community level to redefine network structure, resilience, and functional diversity? How fast is adaptive network rewiring in the course of ecological restoration and which dynamics can be expected depending on the interaction types considered?

In order to facilitate the operationalization of novel research programmes based on the ANM framework, a key methodological issue to be resolved is the application of the comparative method to translate phylogenetically-structured interaction data to inform rewiring rules. This is necessary in order to describe and understand variation in the strength of phylogenetic signals across different types of ecological interactions and its consequences for rewiring mechanisms. In many cases, phylogenetic information can promptly inform forbidden links as well as the ranges of potential interactions. Overall, a general synthesis of key concepts and methodological issues is required in order to elucidate the time-scales and long-term dynamics of network rewiring over different types of ecological networks and ecosystems.

The development of models with parameters that can be easily estimated in the field, such as fundamental network metrics depicting resilience and feasible measures of trait diversity within communities, is essential for the validation of assumptions, testing predictions, and for the refinement of network models supporting predictive restoration. In the long-term, the operationalization of the ANM framework

32. Kulpa, S.M. and Leger, E.A. (2013) Strong natural selection during plant restoration favors an unexpected suite of plant traits. *Evol. Appl.* 6, 510–523
33. Gross, T. and Sayama, H. (2009) *Adaptive Networks*, Springer Science & Business Media
34. Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*, Oxford University Press
35. Galetti, M. *et al.* (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340, 1086–1090
36. Poisot, T. *et al.* (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos* 124, 243–251
37. Urban, M.C.C. and Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* 87, 1616–1626
38. Gross, T. and Blasius, B. (2008) Adaptive coevolutionary networks: a review. *J. R. Soc. Interface* 5, 259–271
39. Vázquez, D.P. *et al.* (2009) Uniting pattern and process in plant-animal mutualistic networks: a review. *Ann. Bot.* 103, 1445–1457
40. Pillar, V.D. *et al.* (2013) Functional redundancy and stability in plant communities. *J. Veg. Sci.* 24, 963–974
41. Kaiser-Bunbury, C.N. *et al.* (2010) Conservation and restoration of plant-animal mutualisms on oceanic islands. *Perspect. Plant Ecol. Evol. Syst.* 12, 131–143
42. Pocock, M.J.O. *et al.* (2012) The robustness and restoration of a network of ecological networks. *Science* 335, 973–977
43. Ramos-Jiliberto, R. *et al.* (2012) Topological plasticity increases robustness of mutualistic networks. *J. Anim. Ecol.* 81, 896–904
44. Kaiser-Bunbury, C.N. *et al.* (2010) The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecol. Lett.* 13, 442–452
45. Rezende, E.L. *et al.* (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448, 925–928
46. Rohr, R.P. and Bascompte, J. (2014) Components of phylogenetic signal in antagonistic and mutualistic networks. *Am. Nat.* 184, 556–564
47. Pearse, I.S. and Altermatt, F. (2013) Extinction cascades partially estimate herbivore losses in a complete Lepidoptera-plant food web. *Ecology* 94, 1785–1794
48. Suweis, S. *et al.* (2013) Emergence of structural and dynamical properties of ecological mutualistic networks. *Nature* 500, 449–452
49. Ibanez, S. *et al.* (2016) How phylogeny shapes the taxonomic and functional structure of plant-insect networks. *Oecologia* 180, 989–1000
50. Cook, J.M. and Rasplus, J.-Y. (2003) Mutualists with attitude: coevolving fig wasps and figs. *Trends Ecol. Evol.* 18, 241–248
51. Fonseca, C.R. and Ganade, G. (1996) Asymmetries, compartments, and null interactions in an Amazonian ant-plant community. *J. Anim. Ecol.* 65, 339–347
52. Guimarães, P.R., Jr *et al.* (2007) Interaction intimacy affects structure and coevolutionary dynamics in mutualistic networks. *Curr. Biol.* 17, 1797–1803
53. Camicer, J. *et al.* (2009) The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology* 90, 1958–1970
54. Agosta, S.J. and Klemens, J.A. (2008) Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecol. Lett.* 11, 1123–1134
55. Nuismer, S.L. *et al.* (2013) Coevolution and the architecture of mutualistic networks. *Evolution* 67, 338–354
56. Guimarães, P.R., Jr (2011) Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14, 877–885
57. Winemiller, K.O. *et al.* (2015) Functional traits, convergent evolution, and periodic tables of niches. *Ecol. Lett.* 18, 737–751
58. Garibaldi, L.A. *et al.* (2015) Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *J. Appl. Ecol.* 52, 1436–1444
59. Andreazzi, C.S. *et al.* (2017) Network structure and selection asymmetry drive coevolution in species-rich antagonistic interactions. *Am. Nat.* 190, 99–115
60. Nosil, P. (2012) *Ecological Speciation*, Oxford University Press
61. Dieckmann, U. *et al.* (2004) *Adaptive Speciation*, The Press Syndicate of the University of Cambridge
62. McQuaid, C.F. and Britton, N.F. (2013) Host-parasite nestedness: a result of co-evolving trait-values. *Ecol. Complex.* 13, 53–59
63. Butterfield, B.J. *et al.* (2016) Prestoration: using species in restoration that will persist now and into the future. *Restor. Ecol.* 25, S155–S163
64. D'Antonio, C. and Meyerson, L.A. (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor. Ecol.* 10, 703–713
65. Russo, L. *et al.* (2014) Patterns of introduced species interactions affect multiple aspects of network structure in plant-pollinator communities. *Ecology* 95, 2953–2963
66. Valdovinos, F.S. *et al.* (2009) Structure and dynamics of pollination networks: the role of alien plants. *Oikos* 118, 1190–1200
67. Bartomeus, I. *et al.* (2017) A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.* 30, 1894–1903
68. Servedio, M.R. *et al.* (2014) Not just a theory—the utility of mathematical models in evolutionary biology. *PLoS Biol.* 12, e1002017
69. Pires, M.M. *et al.* (2017) The friendship paradox in species-rich ecological networks: Implications for conservation and monitoring. *Biol. Conserv.* 209, 245–252
70. Derhé, M.A. *et al.* (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. *J. Appl. Ecol.* 53, 1714–1724
71. Palumbi, S.R. (2001) Humans as the world's greatest evolutionary force. *Science* 293, 1786–1790
72. Funk, J.L. *et al.* (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends Ecol. Evol.* 23, 695–703
73. Redford, K.H. *et al.* (2014) Synthetic biology and the conservation of biodiversity. *Oryx* 48, 330–336
74. Svenning, J.C. *et al.* (2016) Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Natl. Acad. Sci. U. S. A.* 113, 898–906
75. Hagen, M. *et al.* (2012) Biodiversity, species interactions, and ecological networks in a fragmented world. *Adv. Ecol. Res.* 46, 89–210
76. Emer, C. *et al.* (2018) Seed-dispersal interactions in fragmented landscapes - a metanetwork approach. *Ecol. Lett.* 21, 484–493
77. Jordano, P. *et al.* (2007) Differential contribution of frugivores to complex seed dispersal patterns. *Proc. Natl. Acad. Sci. U. S. A.* 104, 3278–3282
78. Pilosof, S. *et al.* (2017) The multilayer nature of ecological networks. *Nat. Ecol. Evol.* 1, 101
79. Melián, C.J. *et al.* (2018) Deciphering the interdependence between ecological and evolutionary networks. *Trends Ecol. Evol.* Published online May 24, 2018. <http://dx.doi.org/10.1016/j.tree.2018.04.009>
80. Bernatchez, L. *et al.* (2017) Harnessing the power of genomics to secure the future of seafood. *Trends Ecol. Evol.* 32, 665–678
81. Hiers, J.K. *et al.* (2016) The precision problem in conservation and restoration. *Trends Ecol. Evol.* 31, 820–830

will allow us to address questions with immediate consequences for restoration practices within specific socio-economic contexts, such as: whether (and which) invasive species should be removed from native habitats and which alternative sets of interacting species could be added into communities to improve ecosystem resilience?