Trends in Ecology & Evolution

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Review

The Role of Evolution in Shaping Ecological Networks

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The structure of ecological networks reflects the evolutionary history of their biotic components, and their dynamics are strongly driven by ecoevolutionary processes. Here, we present an appraisal of recent relevant research, in which the pervasive role of evolution within ecological networks is manifest. Although evolutionary processes are most evident at macroevolutionary scales, they are also important drivers of local network structure and dynamics. We propose components of a blueprint for further research, emphasising process-based models, experimental evolution, and phenotypic variation, across a range of distinct spatial and temporal scales. Evolutionary dimensions are required to advance our understanding of foundational properties of community assembly and to enhance our capability of predicting how networks will respond to impending changes.

Highlights

Networks of ecological interactions define the way that ecosystems function. Network assembly and temporal persistence can be thought of as contemporary ecological functions but shaped by historical evolutionary processes.

Increasingly, researchers study networks within a phylogenetic comparative context, acknowledging that networks are sensitive to evolutionary constraints operating at regional or local scales.

Methodological progress in population genomics and molecular detection, combined with theoretical developments in modelling, now permit investigation of ecoevolutionary feedback loops within networks.

Although understanding of isolated parts of network assembly and persistence is developing, a unifying framework for making connections and predictions across evolutionary scales is lacking. Approaches are being developed on multiple fronts from which such a framework may well emerge.

Linking Evolution and Ecological Networks across Multiple Levels

There is growing interest in the role of evolutionary history in determining how species interact within communities [1]. At fine spatial scales, the evolution of one species is impacted directly by others through biotic natural selection and sometimes through reciprocal **coevolution** (see Glossary). Interacting species, however, do not persist as isolated pairs in time and space: they are embedded within **ecological networks** involving multiple positive and negative interactions. Such a network perspective is essential for understanding the arena within which species interact. Network structure itself feeds back to influence evolutionary outcomes [2], and ongoing **trait** evolution [3]. Here, we review the impact of evolution on ecological networks, taking a novel multiscale approach. We present a synthesis of previous work on the often-interlinked drivers of network structure across space (local to regional) and time (ecological to evolutionary) (Figure 1). While we appraise how an integrative and process-based approach will advance the understanding of network assembly and structure, we focus on how this has emerged from previous work through identifying current challenges and future directions.

Evolutionary Patterns in Large-Scale Networks

Macroevolution and Phylogeography

The availability of phylogenetic trees for entire clades allows identification of large-scale phylogenetic patterns within networks [4]. Large datasets from sequencing studies are providing the taxonomic breadth required to connect networks with **macroevolutionary** studies of diversification [5,6]. Many networks are phylogenetically [7] and spatially structured, shaped by both historical and ongoing selection [8], which may lead to topological convergence over evolutionary time (Box 1) [9,10]. For example, rapid adaptive radiations on islands produce networks of endemics rather than recurrent and recent invaders reflecting niche differentiation among close relatives, whereas sequential sympatric speciation on novel plant hosts can drive modularity in networks [11]. Network structure is dynamic through evolutionary time (Figure 1). In island chronosequences, older islands

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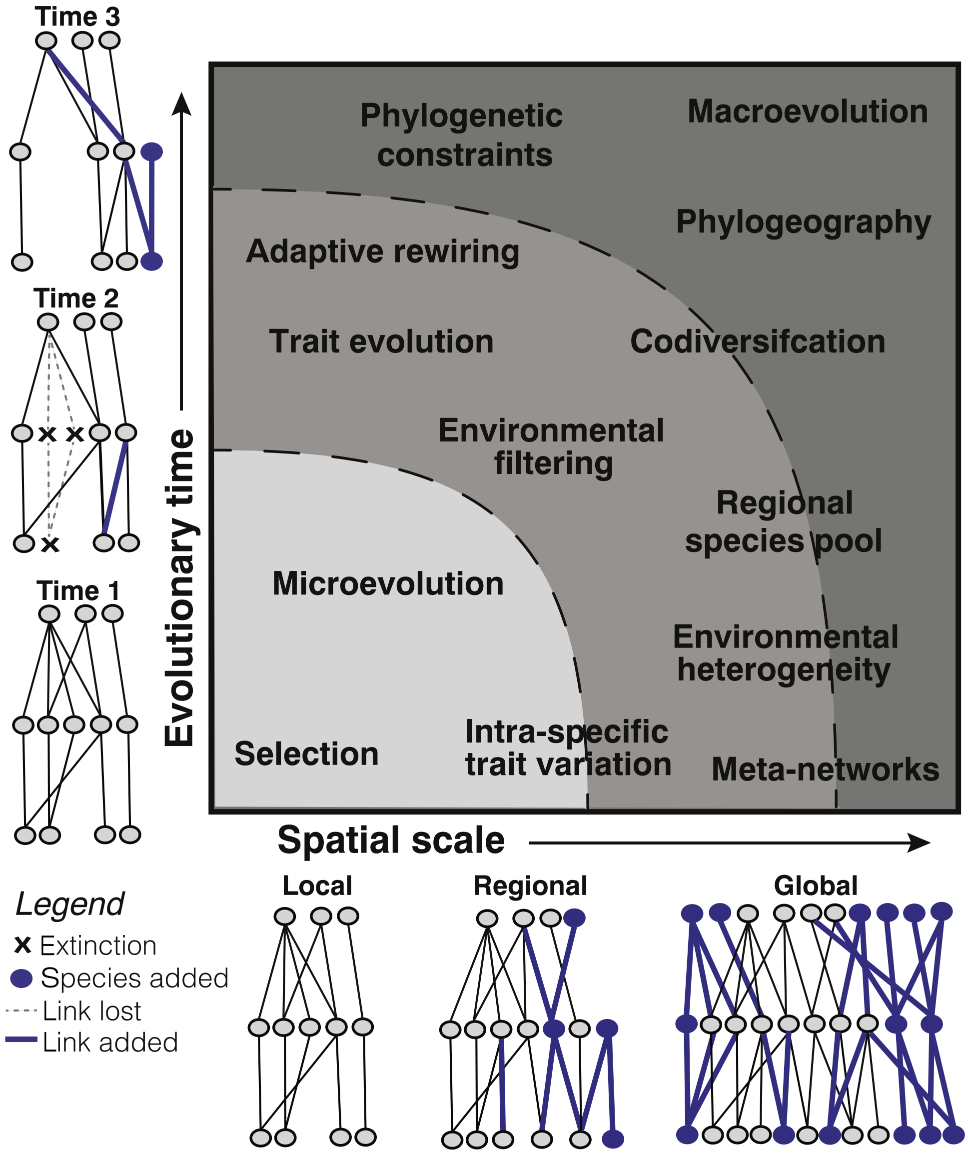

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Figure 1. A Conceptual Framework for Drivers of Network Structure across Evolutionary and Spatial Scales. The pool from which interacting species are drawn is shaped by macroevolutionary processes (e.g., speciation, adaptation, and extinction), which are modified by species migration among regions as well as environmental and biotic heterogeneity. Here, we summarise important processes that lead to changes in network properties over evolutionary time (y axis) and with increasing spatial scale (x axis). Additional links (edges) and species (nodes) are introduced to networks over both evolutionary time and with increasing spatial scale. Links and species are also lost as a result of species extinction over evolutionary time. The x axis shows how both local and regional scale networks are embedded within the global network. These multilayered networks are linked by nodes shared across time and across space.

exhibit more modular networks, reflecting longer periods of *in situ* diversification [12]. Accordingly, a phylogeographic approach to network assembly is required, focusing on the distribution and evolution of species and their interactions across regions [13]. This will afford a greater understanding of pattern in ecology, as well as the underlying evolution of morphological, behavioural and ecological traits.

Box 1. Modelling the Evolutionary Processes That Determine Interaction Networks across Spatial and Evolutionary Scales

Evolution has been incorporated into models of network self-assembly by allowing macroevolutionary change in nodes [90]. The resulting networks are architecturally similar to real networks [66]. Such models have now been extended to include multiple traits with more realistic bounds on trait evolution [68,69]. The trait evolution of a given species can be affected by interactions with multiple species. More complex, nonadditive selection can occur when there are indirect interactions. These different selection pressures can be integrated into network models, at least for single trait coevolution, and simulations have shown that indirect interactions can be major selective agents for trait changes in mutualisms [3].

Links within ecological networks are frequently represented as between species-level nodes, but in fact individual and population level traits determine interactions and their frequencies. Furthermore, traits and abundances fluctuate in time and space resulting in nonstatic networks [91]. For example, a widespread generalist may be comprised of many local specialists in different parts of its range. Dynamic network models [49] are predictive, in that they build up networks according to point variation in phenotypic traits, individual abundance and feedbacks among individuals (including indirect interactions). Since they are process-based, niche or neutral mechanisms can be modelled. Importantly, this approach bridges the gap between local and regional scales, enabling the comparison of networks on a biogeographic scale while still being sensitive to regional variation. Adaptive network models [46] provide a link between population level processes driving trait evolution and the interactions that shape networks and communities. Evolving metacommunity models describe how ecoevolutionary feedbacks act across the selective landscape, resulting in changes in network organisation that alter the distribution of traits between interacting species in a reciprocal manner [47]. Inclusion of evolutionary history into dynamic models can help us to predict how species interactions may be rewired [48] and shed light on the processes shaping phylogenetic signal as a pattern in ecological networks. Fluctuations in phenotypic traits resulting from coevolution can also be integrated into dynamic and adaptive models, in combination with spatial variation in interaction strength. Metacommunity models facilitate the description of meta-networks and their derived local networks. Combining the metacommunity models [92] used to describe meta-networks and local networks with adaptive network models and **community phylogenies** will be important in linking processes across spatial and evolutionary scales.

Phylogenetic Network Signals

Phylogenetic patterns in networks are mediated by species-specific traits. As biotic [14] and abiotic conditions change so traits are modified, in turn producing network-level responses (Box 2). If traits are conserved within phylogenies they will act as proxies for phenotypic similarity by shared descent. Closely related species will often interact with sets of similarly closely related species [15] through **niche conservatism** (Figure 2). Strong **ecophylogenetic** patterns in extinction cascades and compartmentalisation of networks have been identified [7,16,17], indicating the network-structuring roles of conserved traits.

Under the assumption of niche conservatism, phylogeny should help predict both species interactions and overall network topology [18]. For example, traits with a phylogenetic signal (such as flower symmetry and pollinator size) accurately predict interactions in some plant–pollinator networks [19]. However, deviations from phylogenetic conservatism may occur (for instance via convergence) [20], suggesting that phylogenies should be combined with trait measurements [17,19].

Trait Evolution

To investigate the ecological influence of biotic drivers on trait evolution and network structure [21] we need to encompass ecological interactions and phenotypic evolution into phylogenetic comparative methods. Drury *et al.* [22] included competition when tracing the phylogenetic evolution of traits in *Anolis* lizards. Extending such an approach to predation, mutualism, and facilitation would help elucidate the assembly of interaction networks. Ancestral trait reconstruction may facilitate the modelling of trait transitions over time and, accordingly, the likelihood of interactions among species and lineages [23].

Although evolutionary processes within networks can lead to predictable structures [9], scaling **microevolution** in networks to macroevolutionary processes across phylogenies remains a challenge [5,24]. Intergenerational studies of phenotypic ecoevolution in one or two

Glossary

Adaptive network: ‘A network whose links change adaptively with respect to its states, resulting in a dynamical interplay between the state and the topology of the network’ [46].

Antagonistic networks: networks in which the links represent interactions with negative impacts on the fitness of one level of interacting species.

Brownian motion: evolution of a continuous trait across a phylogeny, modelled as a random walk for comparison with other processes [20].

Codiversification: simultaneous diversification (speciation) of two interacting lineages.

Coevolution: mutual and concurrent evolutionary adaptation of traits in a population of one species to individuals from another [34].

Community phylogenies: phylogenies pruned to include only cooccurring species rather than all species within a taxon or clade.

Ecoevolutionary feedback: ‘cyclical interaction between ecology and evolution such that changes in ecological interactions drive evolutionary change in organismal traits that, in turn, alter the form of ecological interactions, and so forth’ [87].

Ecological fitting: ‘process whereby organisms colonise and persist in novel environments, use novel resources or form novel associations with other species as a result of the suites of traits that they carry at the time they encounter the novel condition’ [88].

Ecological network: any depiction of a set of interindividual or interspecies interactions in nature, usually comprising nodes (the species themselves) and edges (the functional links among species).

Ecophylogenetics: field of study focused on exploring patterns and process in ecology through the combination of ecological data with phylogenetic and biogeographic data.

Interaction strength: frequency and/or fidelity of a connection between two nodes in a network when sampled at multiple points (across time and/or space).

Macroevolution: evolution on a scale at or above the level of species.

Microevolution: relates specifically to the turnover of allele frequencies within a population through inheritance, selection and drift.

Box 2. Evolutionary History as a Predictor of Network Responses to Human Impacts

The impacts of novel environmental gradients generated by humans on species composition are now relatively well known, and their effects on interactions between species are becoming apparent [93]. However, the influence of evolutionary history on network responses to global changes, the degree to which networks can adapt to global changes through evolution, and subsequent longer-term consequences for evolution of networks remain mostly unknown (but, see [94]).

Network structure can predict impacts of cascading extinctions [95] or identify keystone species. Most simply, phylogenetic relatedness has been incorporated into models simulating the impacts of species extinctions on networks. If there are phylogenetic signals in the network then cascading extinctions are predicted to lead to nonrandom loss of species from phylogenies, with greater risk of entire clades going extinct [18]. For example, pollination networks in smaller and less isolated forest fragments show a lower degree of phylogenetic matching, presumably owing to extinction of more specialised species and invasion by generalists [7]. This is of concern because conservationists often assign high value to phylogenetic diversity and hence prioritise to reduce its loss [96]. Furthermore, the effects of biodiversity on ecosystem functioning depend critically on how species reorganise within networks following species loss [97].

An important next step in understanding species' responses to global changes will be to incorporate traits into such analyses. This approach is already being used regarding individual species' responses to global changes, with impacts of multiple traits on fitness of species in new abiotic environments being calculated to describe dynamic adaptive landscapes [98]. This approach could be profitably extended to novel biotic assemblages, by quantifying fitness changes in a focal species due to shifts in its inclusive network.

An additional complication is that species may evolve in response to altered biotic and abiotic environments [99]. However, it is often challenging to determine whether observed changes are due to existing **phenotypic plasticity**, or to changes in genotypes [100]. For example, mutualists may shift to become more antagonistic, or even abandon interactions completely [94]. If the fitness outcomes of being involved in an interaction shift, though not to the extent that species go extinct in the short term, then we would expect them to adapt to their novel biotic environment.

species [25] must be connected to trait evolution and processes such as speciation and extinction [26–28]. Widely used neutral models of trait evolution (e.g., the **Brownian motion** model) can be extended to include processes such as stabilising selection, which generates a weak phylogenetic signal [20]. The parameterisation of relatively simple models of trait evolution with ecologically relevant data (e.g., heritability, and effective population size and selection) across networks of species and across scales, remains a major challenge [29]. Extending the phylogenetic comparative approach is essential for exploring trait evolution in networks.

Codiversification and Coevolution

Congruence between network and phylogenetic tree structures likely depends on the type and intimacy of interactions (e.g., mutualistic or antagonistic; obligate or facultative). Phylogenetic patterns of two connected trophic levels may be asymmetric or reciprocal. Asymmetrical phylogenetic patterns in networks [30] may result from **phylogenetic tracking** rather than reciprocal coevolution [31]. Furthermore, even when network patterns reflect phylogeny, reciprocal coevolution may not always be the driver. Congruence in phylogenetic branching among trophic levels may simply reflect biogeographic vicariance. Moreover, coevolution does not always produce trait and network correlations [32–34].

Comparing different network types provides strong evidence for evolution in networks. **Phenotypic matching** among interacting species leads to more modular networks and cycles of increased specialisation. In contrast, nested structures arise when interactions are mediated by **phenotypic differences**, particularly in **mutualistic networks** when coevolutionary selection is weak [35]. Food webs (antagonistic trophic networks) are often modular [36] with a strong phylogenetic signal [30]. Mutualistic pollination and dispersal networks are often nested [36], with fewer, frequently asymmetric, phylogenetically clustered interactions [30] often with convergent traits. These patterns conform with the predictions of coevolutionary theory derived from pairwise and small group interactions [30,37].

Mutualistic networks: networks in which the links represent interactions with positive impacts on the fitness of both sets of interacting species.
Network phylogenetic signal: statistical nonindependence, and phylogenetic clustering, among interactions in a network due to the phylogenetic relatedness of nodes (modified from [20]).
Network stability: multidimensional component (metrics include persistence, robustness, resistance, resilience and variability) that quantifies the ability of a network to resist restructuring or collapse following perturbation.
Niche conservatism: tendency of species to retain ancestral traits.
Phenotypic differences: extent to which a trait in one species exceeds or overcomes a corresponding trait in another (e.g., animal gape must exceed fruit diameter in seed dispersal mutualisms) [35].
Phenotypic matching: phenotypic resource traits that match those of consumers, (e.g., phenological cooccurrence of plants and pollinators).
Phenotypic plasticity: 'ability of individual genotypes to produce different phenotypes when exposed to different environmental conditions' [89].
Phylogenetic tracking: 'phylogenetic tracking occurs if there is strong asymmetry in the interaction between two species, implying one species is much more dependent on the other. This leads to parallel phylogenetic trees' [31].
Trait: morphological, behavioural, ecological, or chemical features of a species reflecting both its evolutionary history and its local phenotypic adaptation.

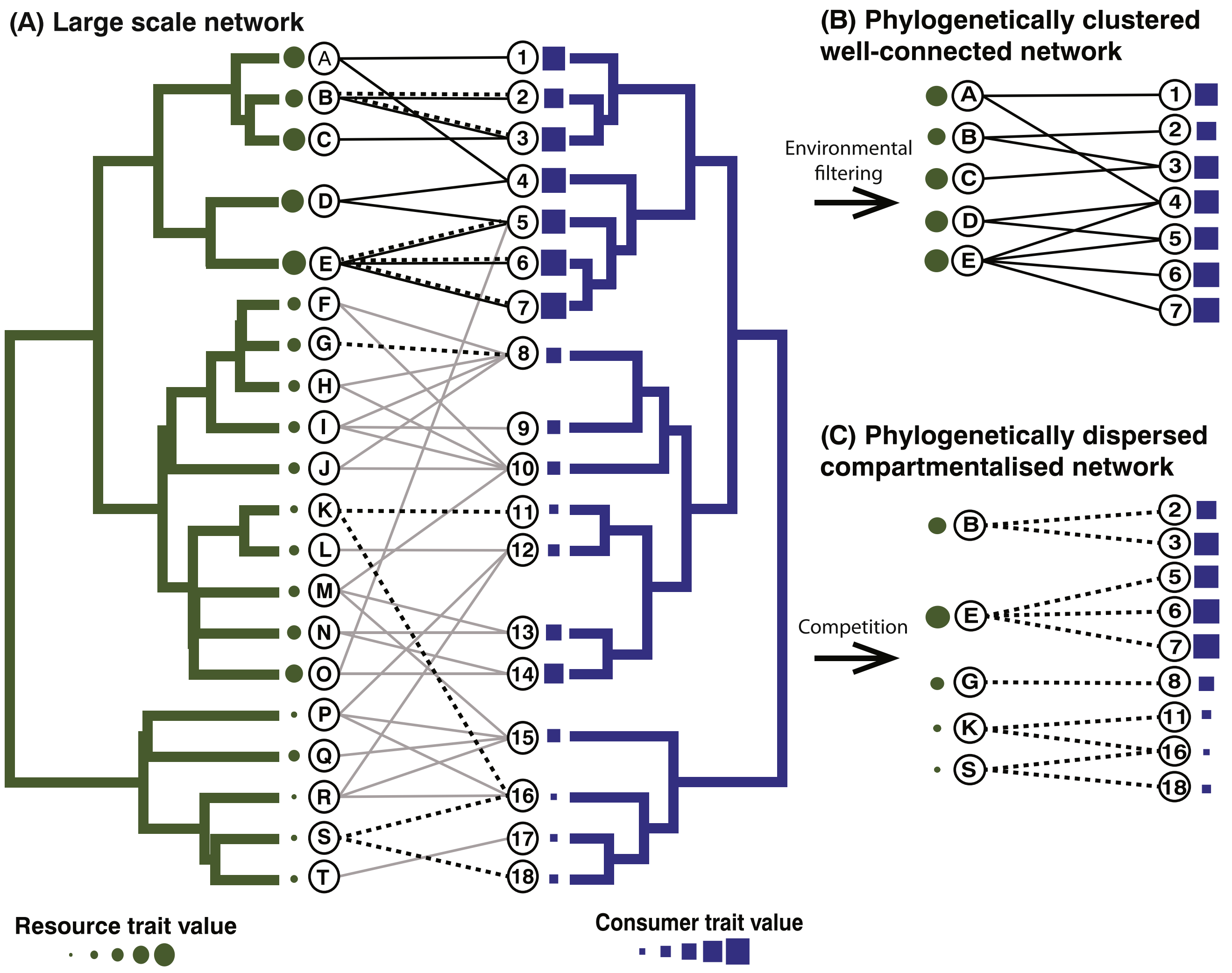

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Figure 2. Pathways to Network Assembly I: from Regional to Local Scales. A hypothetical bipartite regional network (A) consisting of resource species (letters in circles) and consumer species (numbers in circles). The evolution of a hypothetical continuous trait is illustrated for each set of interacting nodes. Optimal phenotypic matching occurs between producer and consumer traits, such that there is **network phylogenetic signal** and interactions are determined by phylogenetically conserved phenotypic matching. Processes such as environmental filtering (B) and competition (C) influence the draw of species from the available pool, in turn affecting local network structure.

Classically, antagonistic coevolution leads to an 'arms race' with escalation of defensive *contra* offensive phenotypes. This can lead to modular networks [38], particularly at larger phylogenetic scales. For example, Brassicaceous plants and pierid butterflies have undergone cyclical escalations of defence and detoxification traits, driving butterfly host specificity [39]. Such an outcome is most likely in highly modular networks [40]: indeed, increased selection pressure on lower trophic levels and specialisation [31] of higher trophic levels favour the emergence of modularity. Additional mechanisms, such as coevolutionary alternation (where predator–prey preferences fluctuate through time) are also likely to influence network structure over longer timescales [41].

Coevolution can follow multiple alternative trajectories in mutualistic and **antagonistic networks**, influenced by and influencing network structure and evolutionary feedbacks [3,35]. When many specialist species are reliant on a few persistent generalist species (as in nested networks), coevolution in mutualistic networks may lead to increased resilience [42], connectance and ‘coevolutionary rescue’ through rewiring [35]. Within a single network type, distinct structures can arise from differing evolutionary processes. Using simulations, Braga *et al.* [43] found that adaptive radiation in butterflies following a host shift led to modular networks, whereas nested networks only arose during periods of expansion in host range. This combination of theoretically derived predictions with directed empirical studies is pivotal in the comparative approach we advocate. Since network structure is itself a meta-trait, a cross-community approach provides a perspective for understanding such structures as outcomes of particular selective processes [44].

The clearest examples of phylogenetic pattern in networks result from **codiversification** among clades of interacting species. This is seen in entire clades of insects that are restricted to a particular clade of plants. Such strong signals in entire lineages in networks imply underlying coevolutionary processes. An extreme example is that of figs (Moraceae) and their pollinating wasps (Agaonidae). Genera of mutualistic, pollinating wasps and figs display phenotypic matching and congruence in clade ages. In contrast, networks of parasitic wasps derived from only distantly related clades invaded the fig–pollinator mutualism following phenotypic convergence, exhibiting more limited coevolution [45]. Phylogenetic tracking is likely to be more prevalent than codiversification, which is evident in the mismatch of phylogenetic timescales among trophic levels. This reflects the fact that ecological processes including network assembly may change over relatively short temporal and spatial scales, whereas macroevolutionary patterns emerge over much larger scales.

Phylogenetic Constraints and Adaptive Rewiring in Networks

Linking microevolution to macroevolutionary theory is central to the integration of network analyses across scales (see Trait Evolution). Explicit inclusion of trait evolution using phylogenetic comparative methods is essential because traits are the outcome of macroevolution that determine current species interactions [21]. Modelling networks as adaptive landscapes is one way of linking phenotype, measures of fitness and network structure (Box 1). **Adaptive networks** [46] model the feedbacks between the states of each node and the topology of the network. By integrating ecoevolutionary, metacommunity [47], and geographic theories, adaptive network models can connect population and community-level processes (Box 1) [48]. Interactions are modulated by species-specific abundance dynamics and traits and may feed back to modify network structure [49]. Incorporating phylogeny into adaptive network models can improve predictions of network ‘rewiring’ in response to perturbation, if species interactions evince phylogenetic signals [48]. Incorporating traits and their variance with phylogeny can tease apart the relative contribution of phylogenetic constraints (when certain traits and interactions cannot occur due to the phylogenetic history of the interacting clades), **ecological fitting** and evolution in determining this adaptive rewiring. Modelling networks as evolving entities becomes possible through incorporating the mechanisms by which interactions themselves evolve [50] and are inherited as speciation proceeds.

Phylogenetic Determinants of Network Structure across Different Spatial Scales

Evolutionary and Environmental Filters

The evolutionary history of interacting lineages filters regional species pools. For example, specialised natural enemies may be capable of suppressing range expansion of their hosts but not of invasive species. In an elegant laboratory experiment, Carrasco *et al.* [51] demonstrated the impacts of separate or concurrent arrival of an invasive herbivore (*Spodoptera littoralis*) and its associated parasitoid (*Microplitis rufiventris*) on a native herbivore (*Mamestra brassicae*) and its parasitoid (*Microplitis mediator*) in determining fitness costs within a tritrophic network. *M. rufiventris* varied in its negative impact on both native species according to the presence of *S. littoralis*. A second level of filtering by ecological processes sifts phylogenetically determined regional species pools into local networks of interacting species (Figures 2 and 3). The local species pool constrains realised interactions, but is itself constrained by proximal processes such as biogeography, physiological traits and interspecies dependencies superimposed on evolutionary history. A key task, therefore, is to elucidate and predict how local pools assemble (Figure 2). Habitat filtering can lead to phylogenetic clustering, whereas competition can lead to overdispersion. However, interactions and ecological processes cannot be inferred solely from phylogenetic patterns [52] because assumptions of trait conservatism are not always met, and species interactions need not persist over evolutionary time [53].

Regional Species Pools and Meta-networks

Most existing phylogenetic studies of local networks comprise incomplete, taxonomically unbalanced subsets of diversity. Only sampling over wider spatial and phylogenetic scales will document regional pools of potential interactions from which locally recorded examples are drawn (see Macroevolution and Phylogeography). Moreover, potential meta-networks (Figure 1) constructed mechanistically from the total species pool (Figure 2) [54] allow us to model assembly through processes such as dispersal and extinction. Such modelled meta-networks are templates from which local networks can be extracted, conditional on evolutionary history and phenotypic matching. They also enable predictions of which species will not interact. In this way, inclusion of coevolution, ecological processes and life history traits into network hypotheses can take account of incompatibilities and ‘forbidden links’ [55].

Phylogenetic patterns within networks can change with downscaling from regional to local species pools as sets of available species diminish, and interactions vary with local conditions (Figure 2). In other words, evolutionary history may predominate in shaping regional pools but will be harder to detect in local networks. Ponisio and M’Gonigle [33] modelled both coevolving and non-coevolving networks, and concluded that the topological legacy of coevolution within networks does not always reflect interaction intimacy. Increased knowledge of biogeographic ranges of species, as well as their interactions and phylogenetic histories, will enable assessment of the relative contributions of evolutionary and ecological conditions to observed network structures.

Realised Networks and Ecoevolutionary Feedbacks

Microevolution

Two advances have fuelled understanding of **ecoevolutionary feedbacks** within networks. First, coevolution is now broadly accepted as a selective force comparable in importance to the abiotic environment [56]. Second, we can model phenotypic evolution in multiple interacting species over ecological timescales [57,58]. Studies that quantify genotypic frequencies, phenotypic change and resultant **interaction strengths,** in the short term, have resulted in compelling evidence for this ecoevolutionary feedback [57,59]. Advances in modelling evolution in networks have not only generated hypotheses for empiricists but facilitate better connections across spatial and temporal scales (Box 1).

Outcomes of Ecoevolutionary Feedbacks

Ecoevolutionary feedbacks link simple systems with few components to complex networks [60,61]. Evolution among ecologically linked genotypes can influence emergent network properties propagating selective pressures on other species within the network. This should be observable in natural systems, particularly those susceptible to rapid genetic change (e.g., with short-lived species and/or strong selective pressures).

Microcosm and mesocosm experiments involving short-lived organisms, especially microbes, provide a long-overdue integration of experimental evolution and network ecology informing

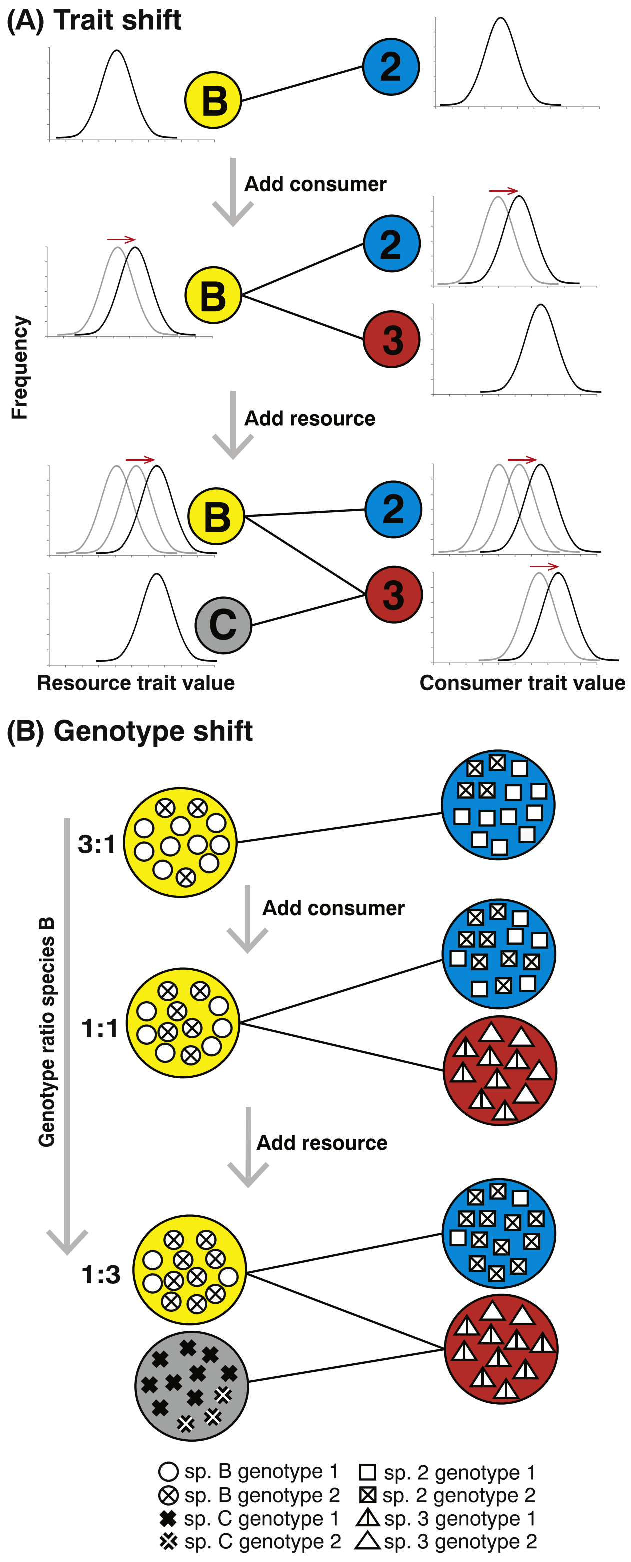

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Figure 3. Pathways to Network Assembly II: from Local Scales to Realised Networks. (A) Hypothetical changes in trait values based on a subset of interactions depicted in Figure 2. Trait values are represented by a normal distribution on the x axis. Interactions are mediated by trait matching, such as that which may occur in a plant–pollinator network, but trait values are modified as new species (with slightly different trait values) are added to the network. The arrival of a new consumer might select for modified traits in producers and the arrival of a resource might select for modified traits in consumers depending on the realised encounter frequency between consumers and producers, and on consumer preferences. (B) Phenotypes can be plastic, determined largely by the environment, and/or have a strong genetic component. This scheme focuses on genetic determination. As selection acts on individuals within a population, the frequency of genotypes related to adaptive traits will change. In this case the arrival of a consumer (sp. 3) causes a genetically determined shift in producer phenotype (sp. B) and selection acts against genotype 1 of species B. Subsequent selection results in convergence or divergence in traits between consumers (sp. 2 and sp. 3) and a corresponding reshuffle of genotype frequencies. In the final network module, a resource arrives (sp. C) that can be used only by consumer sp. 3, reducing competition between consumer species and modifying the selective landscape for sp. 2.

models of network assembly and dynamics [62]. Microcosms are testing grounds for theoretical predictions by, for example, confirming that resistance genes can structure entire communities [63] and are potentially important drivers of coevolutionary dynamics in networks [56]. Modelling these in a network superstructure suggests that evolution can lead to increased network diversity and **network stability** [64]. Diversity likely insures ecosystem function at larger scales [65], although a general rule for diversity–stability relationships remains elusive [66]. Linking phenotypic adaptation with genotypic evolutionary change is challenging because the exact genetic control of most phenotypic traits is unknown. Most current models consider quantitative traits linking individual genotypes to phenotypic population means [9,66,67], subsequently scaled up to include multiple traits and more realistic bounds on trait evolution [68,69]. Developments in whole-genome sequencing, transcriptomics and gene editing also bridge this gap. For example, gene editing in *Drosophila melanogaster* has indicated the evolutionary pathway leading to cardiac glycoside resistance in *Danaus plexippus* [70]. Resistance to host defences is a key predictor of host use in food webs. A marriage of comparative and experimental approaches will bridge the micro-macroevolutionary divide [71].

Ecoevolutionary Feedbacks in Spatial Networks

Ecoevolutionary feedbacks in ecological networks will operate spatially as well as temporally. Both ecological and microevolutionary processes show strong spatial dependence. Spatial heterogeneity in abiotic conditions results in species sorting within metacommunities, with consequent variation in the relative fitness of genotypes [72]. Dispersal of individuals among local networks in a metacommunity can affect both the species composition of networks (since individuals represent potential colonists) as well as the ability of species to adapt to local conditions (because colonists carry alleles that could either facilitate or swamp local adaptations). These spatial effects can have important ecoevolutionary feedbacks, within so-called evolving metacommunities [47]. Early colonisation of a habitat leading to rapid local adaptation may exclude subsequent colonists: an ecoevolutionary priority effect [73,74].

The geographic mosaic theory of coevolution predicts that the genotypes of coevolving species will be impacted as species interactions are moulded by environmental heterogeneity [37]. In consequence, interaction strengths and species persistence in local networks may change [75]. In partial support of this prediction, environmental gradients that correlate with genotype change in host plants have been shown to affect interaction strengths within associated arthropod networks [76] as well as species composition [77]. Full integration of ecoevolutionary feedbacks into spatially structured and speciose networks is a problem of high dimensionality and, in the short term, empirical progress will likely focus on the hub species that connect local networks in space [75].

Intraspecific Variation

We have increasing understanding of how genes coding for phenotypic traits affect fitness outcomes within interactions, and how intraspecific variation contributes to network persistence [78]. Incorporating genotypic diversity into empirical and simulation studies will help us to understand how networks themselves evolve and persist [79]. For example, plant genotypes can determine the level of resistance to herbivory, affecting networks of insect herbivores and even their parasitoids [80]. Linking the genotypic composition of interacting species and, thereby, identifying networks of interacting genes across species via gene expression, allows genotypic change to be studied in the same detail as population change [39]. Hitherto such studies have focused on pairwise interactions. By scaling up to networks, we can explore whether genotypes are important predictors of multispecies interactions and network structure (Figure 3) and, conversely, which biotic interactions generate and are affected by genotypic diversity. This is now central to understanding how evolutionary processes permeate and reflect network configurations. Phenotypic evolution also can be mediated by ecological interactions, a process increasingly being modelled within networks (Box 1). Emergent phenotypes can also be modelled along the branches of phylogenetic trees under fluctuating ecological conditions. This continuum provides a natural connection to macroevolutionary temporal and spatial scales.

Prospects for Tighter Cohesion across Network Levels

Multilayered Networks

A significant step will be to build ecoevolutionary models that span a range of levels across the biological hierarchy. We can now model how gene interaction networks (i.e., evolutionary networks) predict phenotypic trait variation which, in turn, determines interactions within networks [81]. The next step is to expand the focus to encompass multilayer networks. Promising approaches include the integration of different network layers through shared nodes, where layers represent different spatial or temporal dimensions or interaction modes [82,83] (Figure 1). An example involving diverse interaction modes would be a network comprising layers for plants, their antagonistic insect herbivores, and their mutualistic pollinators [84]. Adding a spatial dimension can be achieved by linking interactions occurring in a habitat patch to those occurring within wider landscapes [85]. Intersections of these spatial scales offer prospects for exciting future work which will elucidate how changes in phenotypes cascade up to the regional species pool.

Concluding Remarks and Future Perspectives

Emergent properties of complex networks of interacting species are a result of evolution. Interactions within any given network are embedded in large and complex networks of networks. Therefore, a larger spatiotemporal scale is required to understand fully the evolution of the regional species pool, the raw material for all such networks. Evolutionary change, often acting through biotic interactions, shapes phenotypic traits and, in turn, influences future species interactions. Simultaneously, trait trajectories are further modified by reciprocal selection among networks. Macroevolutionary change is most easily linked to phylogenies using the phylogenetic comparative method, which provides a tractable approach for detecting the signature of evolution at regional scales [24]. Three major research developments are helping to link networks with microevolutionary processes: (i) increasingly realistic, process-based models of indirect coevolution that link network layers across evolutionary and spatial scales; (ii) studying evolution in networks across ecological scales in tractable experimental systems that enable better separation of cause and effect; and (iii) explicit inclusion of phenotypic variation as the raw material on which selection acts within networks to maximise fitness, for example adaptive models of network assembly that consider variation in individual trait values and species' abundances (see Outstanding Questions).

We propose that the linkage of evolutionary processes and their ecological consequences across spatial and temporal scales is an obligate component of future research. Progress in this area will be achieved by exploring selective landscapes and their inherent fluidity, facilitated by individual-level adaptive simulations of network assembly. Ecoevolutionary feedback can be incorporated into network studies by mapping traits onto phylogenies. A major focus of new research should be modelling heritable trait changes within networks, between generations or after speciation events, permitting prediction of interactions and network topology [24]. By modelling using multiple real-world parameter sets, realistic trait values and variable interaction types we can simulate sets of interconnected [84] meta-networks, allowing them to undergo *in silico* selection together with periodic rewiring based on realistic levels of perturbation [48]. This process-based

Outstanding Questions

How can we best model the ecoevolutionary feedbacks and indirect interactions embedded in complex networks?

How should interactions between nodes be modelled as evolving traits across a phylogeny?

Can we scale up existing meso- and microcosm experiments to focus on more complex metazoan-dominated networks over a range of spatial scales, from regional to continental?

How does spatial (patch, habitat, or landscape) structure influence or modify the ecoevolutionary dynamics of interactive networks?

Does simulation of network assembly using phylogenetically derived rules produce networks with realistic network properties?

approach will produce insights into species coexistence and diversity-stability relationships. Synthetic (and empirical) networks can then be compared in a likelihood framework [23] as sets of alternatives, themselves part of a wider pool of selective regimes [81]. Adding the requisite spatial dynamics can be achieved by allowing transfer of individuals between networks [47,86], so that transitions across scales will become part of a natural continuum. Network structure itself will inform the probability of persistent interactions in subsequent generations. Such an integrative approach will provide incentive for empirical ecologists to consider intraspecific variation (and its genetic basis) as an additional parameter for predicting interaction matrices and trait values within networks. Studies of experimental evolution in networks will gain a powerful predictive approach and unified framework.

Networks lie at the heart of ecosystems, therefore the advances we outline and envisage will enhance ecology as a predictive discipline. Through connecting the evolution of species-interaction networks to the most foundational issue in ecology – the recognition and understanding of pattern across multiple scales – we expect that a more complete understanding of fundamental processes in community ecology will emerge. For example, the processes of community assembly and succession are driven by strong ecoevolutionary and spatial components played out across networks of networks. On a larger scale, species pools and standing diversity are greatly influenced by biotic selection over evolutionary time.

Ecological networks, when viewed as the coincident products of sets of evolutionary processes, are necessarily dynamic: as their selective environment responds to change, so will the configuration of the network. Adoption of a network framework will inevitably benefit our understanding of trait evolution itself and, at the other extreme, of ecosystem level responses to perturbations. Predictions of how networks will be rewired as a result of environmental, especially human-driven changes (such as species introductions and their local adaptation) must take evolutionary relationships and phenotypic evolution into account [42]. The stability of local networks will, *inter alia*, reflect the degree of coevolution among participating species. Understanding and predicting how evolutionary processes interact with network structuring and persistence will play a major role in understanding and managing such changes.

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References

1. Mouquet, N. *et al.* (2012) Ecophylogenetics: advances and perspectives. *Biol. Rev.* 87, 769–785
2. de Andreazzi, C.S. *et al.* (2018) Eco-evolutionary feedbacks promote fluctuating selection and long-term stability of antagonistic networks. *Proc. R. Soc. B Biol. Sci.* 285, 20172596
3. Guimarães, P.R. *et al.* (2017) Indirect effects drive coevolution in mutualistic networks. *Nature* 550, 511–514
4. Ponisio, L.C. *et al.* (2019) A network perspective for community assembly. *FEVO* 7, 103
5. Weber, M.G. *et al.* (2017) Evolution in a community context: on integrating ecological interactions and macroevolution. *Trends Ecol. Evol.* 32, 291–304
6. Hinchliff, C.E. *et al.* (2015) Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci. U. S. A.* 112, 6
7. Aizen, M.A. *et al.* (2016) The phylogenetic structure of plant-pollinator networks increases with habitat size and isolation. *Ecol. Lett.* 19, 29–36
8. Peralta, G. *et al.* (2015) Phylogenetic diversity and co-evolutionary signals among trophic levels change across a habitat edge. *J. Anim. Ecol.* 84, 364–372
9. Loeuille, N. and Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proc. Natl. Acad. Sci. U. S. A.* 102, 5761–5766
10. Pascual, M., Dunne, J.A., eds (2005) *Ecological Networks: Linking Structure to Dynamics in Food Webs*, Oxford University Press
11. Forbes, A.A. *et al.* (2009) Sequential sympatric speciation across trophic levels. *Science* 323, 776–779
12. Rominger, A.J. *et al.* (2016) Community assembly on isolated islands: macroecology meets evolution. *Glob. Ecol. Biogeogr.* 25, 769–780

13. Bunnefeld, L. *et al.* (2018) Whole-genome data reveal the complex history of a diverse ecological community. *Proc. Natl. Acad. Sci. U. S. A.* 115, E6507–E6515
14. Pearse, I.S. and Altermatt, F. (2013) Predicting novel trophic interactions in a non-native world. *Ecol. Lett.* 16, 1088–1094
15. Ives, A.R. and Helmus, M.R. (2011) Generalized linear mixed models for phylogenetic analyses of community structure. *Ecol. Monogr.* 81, 511–525
16. Rezende, E.L. *et al.* (2007) Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos* 116, 1919–1929
17. Rezende, E.L. *et al.* (2009) Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecol. Lett.* 12, 779–788
18. Rezende, E.L. *et al.* (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448, 925–928
19. Chamberlain, S.A. *et al.* (2014) Traits and phylogenetic history contribute to network structure across Canadian plant–pollinator communities. *Oecologia* 176, 545–556
20. Revell, L.J. *et al.* (2008) Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* 57, 591–601
21. Pennell, M.W. and Harmon, L.J. (2013) An integrative view of phylogenetic comparative methods: connections to population genetics, community ecology, and paleobiology. *Ann. N. Y. Acad. Sci.* 1289, 90–105
22. Drury, J. *et al.* (2016) Estimating the effect of competition on trait evolution using maximum likelihood inference. *Syst. Biol.* 65, 700–710
23. Manceau, M. *et al.* (2017) A unifying comparative phylogenetic framework including traits coevolving across interacting lineages. *Syst. Biol.* 66, 18
24. Harmon, L.J. *et al.* (2019) Detecting the macroevolutionary signal of species interactions. *J. Evol. Biol.* 32, 769–782
25. Schoener, T.W. (2011) The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* 331, 426–429
26. Arnold, S.J. *et al.* (2001) The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* 112, 9–32
27. Arnold, S.J. (2014) Phenotypic evolution: the ongoing synthesis: (American Society of Naturalists address). *Am. Nat.* 183, 729–746
28. Uyeda, J.C. *et al.* (2011) The million-year wait for macroevolutionary bursts. *Proc. Natl. Acad. Sci. U. S. A.* 108, 15908–15913
29. Uyeda, J.C. and Harmon, L.J. (2014) A novel bayesian method for inferring and interpreting the dynamics of adaptive landscapes from phylogenetic comparative data. *Syst. Biol.* 63, 902–918
30. Rohr, R.P. and Bascompte, J. (2014) Components of phylogenetic signal in antagonistic and mutualistic networks. *Am. Nat.* 184, 556–564
31. Russo, L. *et al.* (2018) Quantitative evolutionary patterns in bipartite networks: Vicariance, phylogenetic tracking or diffuse co-evolution? *Methods Ecol. Evol.* 9, 761–772
32. Nuismer, S.L. *et al.* (2010) When is correlation coevolution? *Am. Nat.* 175, 525–537
33. Ponisio, L.C. and M'Gonigle, L.K. (2017) Coevolution leaves a weak signal on ecological networks. *Ecosphere* 8, e01798
34. Janzen, D.H. (1980) When is it coevolution? *Evolution* 34, 611–612
35. Nuismer, S.L. *et al.* (2013) Coevolution and the architecture of mutualistic networks: coevolving networks. *Evolution* 67, 338–354
36. Thébault, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853
37. Thompson, J.N. (1994) *The Coevolutionary Process*, University of Chicago Press
38. Beckett, S.J. and Williams, H.T.P. (2013) Coevolutionary diversification creates nested-modular structure in phage-bacteria interaction networks. *Interface Focus* 3, 20130033
39. Edger, P.P. *et al.* (2015) The butterfly plant arms-race escalated by gene and genome duplications. *Proc. Natl. Acad. Sci. U. S. A.* 112, 8362–8366
40. Andreazzi, C.S. *et al.* (2017) Network structure and selection asymmetry drive coevolution in species-rich antagonistic interactions. *Am. Nat.* 190, 99–115
41. Nuismer, S.L. and Thompson, J.N. (2006) Coevolutionary alternation in antagonistic interactions. *Evolution* 60, 2207–2217
42. Nuismer, S.L. *et al.* (2018) Coevolution slows the disassembly of mutualistic networks. *Am. Nat.* 192, 490–502
43. Braga, M.P. *et al.* (2018) Unifying host-associated diversification processes using butterfly–plant networks. *Nat. Commun.* 9, 5155
44. Borrelli, J.J. *et al.* (2015) Selection on stability across ecological scales. *Trends Ecol. Evol.* 30, 417–425
45. Segar, S.T. *et al.* (2013) Convergent structure of multitrophic communities over three continents. *Ecol. Lett.* 16, 1436–1445
46. Gross, T. and Sayama, H. (2009) Adaptive networks. In *Adaptive Networks*, pp. 1–8, Springer
47. Urban, M. *et al.* (2008) The evolutionary ecology of metacommunities. *Trends Ecol. Evol.* 23, 311–317
48. Raimundo, R.L.G. *et al.* (2018) Adaptive networks for restoration ecology. *Trends Ecol. Evol.* 33, 664–675
49. Poisot, T. *et al.* (2015) Beyond species: why ecological interaction networks vary through space and time. *Oikos* 124, 243–251
50. Poisot, T. and Stouffer, D.B. How ecological networks evolve. *bioRxiv*. Published online August 29, 2016. https://doi.org/10.1101/071993.
51. Carrasco, D. *et al.* (2018) With or without you: effects of the concurrent range expansion of an herbivore and its natural enemy on native species interactions. *Glob. Chang. Biol.* 24, 631–643
52. Godoy, O. *et al.* (2014) Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.* 17, 836–844
53. Mayfield, M.M. and Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities: phylogeny and coexistence. *Ecol. Lett.* 13, 1085–1093
54. Dunne, J.A. (2006) The network structure of food webs. In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, pp. 27–86, Oxford University Press
55. Strona, G. and Veech, J.A. (2017) Forbidden versus permitted interactions: disentangling processes from patterns in ecological network analysis. *Ecol. Evol.* 7, 5476–5481
56. Brockhurst, M.A. and Koskella, B. (2013) Experimental coevolution of species interactions. *Trends Ecol. Evol.* 28, 367–375
57. DeLong, J.P. *et al.* (2016) How fast is fast? Eco-evolutionary dynamics and rates of change in populations and phenotypes. *Ecol. Evol.* 6, 573–581
58. Govaert, L. *et al.* (2019) Eco-evolutionary feedbacks – theoretical models and perspectives. *Funct. Ecol.* 33, 13–30
59. Govaert, L. *et al.* (2016) Eco-evolutionary partitioning metrics: assessing the importance of ecological and evolutionary contributions to population and community change. *Ecol. Lett.* 19, 839–853
60. De Meester, L. *et al.* (2018) Analyzing eco-evolutionary dynamics – the challenging complexity of the real world. *Funct. Ecol.* 33, 43–59
61. terHorst, C.P. *et al.* (2018) Evolution in a community context: trait responses to multiple species interactions. *Am. Nat.* 191, 368–380
62. Weitz, J.S. *et al.* (2013) Phage–bacteria infection networks. *Trends Microbiol.* 21, 82–91
63. Bohannan, B.J.M. and Lenski, R.E. (2000) Linking genetic change to community evolution: insights from studies of bacteria and bacteriophage. *Ecol. Model.* 3, 362–377
64. Mougi, A. (2020) Natural selection contributes to food web stability. *PLoS ONE* 15, e0227420
65. Yachi, S. and Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1463–1468
66. Loeuille, N. (2010) Influence of evolution on the stability of ecological communities. *Ecol. Lett.* 13, 1536–1545
67. Loeuille, N. and Loreau, M. (2009) Emergence of complex food web structure in community evolution models. In *Community Ecology* (Verhoef, H.A. and Morin, P.J., eds), pp. 163–178, Oxford University Press
68. Allhoff, K.T. *et al.* (2015) Evolutionary food web model based on body masses gives realistic networks with permanent species turnover. *Sci. Rep.* 5, 10955
69. Ritterskamp, D. *et al.* (2016) A new dimension: evolutionary food web dynamics in two dimensional trait space. *J. Theor. Biol.* 405, 66–81

70. Karageorgi, M. *et al.* (2019) Genome editing retraces the evolution of toxin resistance in the monarch butterfly. *Nature* 574, 409–412
71. Weber, M.G. and Agrawal, A.A. (2012) Phylogeny, ecology, and the coupling of comparative and experimental approaches. *Trends Ecol. Evol.* 27, 394–403
72. Gómez, J.M. and Perfectti, F. (2012) Fitness consequences of centrality in mutualistic individual-based networks. *Proc. R. Soc. B Biol. Sci.* 279, 1754–1760
73. Loeuille, N. and Leibold, M.A. (2008) Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. *Am. Nat.* 171, 788–799
74. Urban, M.C. and De Meester, L. (2009) Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proc. R. Soc. B Biol. Sci.* 276, 4129–4138
75. Toju, H. *et al.* (2017) Species-rich networks and eco-evolutionary synthesis at the metacommunity level. *Nat. Ecol. Evol.* 1, 0024
76. Toju, H. and Sota, T. (2006) Imbalance of predator and prey armament: geographic clines in phenotypic interface and natural selection. *Am. Nat.* 167, 105–117
77. Kagiya, S. *et al.* (2018) Does genomic variation in a foundation species predict arthropod community structure in a riparian forest? *Mol. Ecol.* 27, 1284–1295
78. Hart, S.P. *et al.* (2016) How variation between individuals affects species coexistence. *Ecol. Lett.* 19, 825–838
79. Fortuna, M.A. *et al.* (2013) Evolving digital ecological networks. *PLoS Comput. Biol.* 9, e1002928
80. Barbour, M.A. *et al.* (2016) Genetic specificity of a plant–insect food web: implications for linking genetic variation to network complexity. *Proc. Natl. Acad. Sci. U. S. A.* 113, 2128–2133
81. Melián, C.J. *et al.* (2018) Deciphering the interdependence between ecological and evolutionary networks. *Trends Ecol. Evol.* 33, 504–512
82. Timóteo, S. *et al.* (2018) Multilayer networks reveal the spatial structure of seed-dispersal interactions across the Great Rift landscapes. *Nat. Commun.* 9, 140
83. García-Callejas, D. *et al.* (2018) Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos* 127, 5–22
84. Pilosof, S. *et al.* (2017) The multilayer nature of ecological networks. *Nat. Ecol. Evol.* 1, 0101
85. Hackett, T.D. *et al.* (2019) Reshaping our understanding of species' roles in landscape-scale networks. *Ecol. Lett.* 22, 1367–1377
86. Nuismer, S.L. *et al.* (1999) Gene flow and geographically structured coevolution. *Proc. R. Soc. B Biol. Sci.* 266, 605
87. Post, D.M. and Palkovacs, E.P. (2009) Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Philos. Trans. R. Soc. B* 364, 1629–1640
88. Agosta, S.J. (2006) On ecological fitting, plant–insect associations, herbivore host shifts, and host plant selection. *Oikos* 114, 556–565
89. Pigliucci, M. (2006) Phenotypic plasticity and evolution by genetic assimilation. *J. Exp. Biol.* 209, 2362–2367
90. Brännström, Å. *et al.* (2012) Modelling the ecology and evolution of communities: a review of past achievements, current efforts, and future promises. *Evol. Ecol. Res.* 14, 601–625
91. Poisot, T. *et al.* (2012) The dissimilarity of species interaction networks. *Ecol. Lett.* 15, 1353–1361
92. Urban, M.C. and Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary perspective on metacommunities. *Ecology* 87, 1616–1626
93. Tylianakis, J.M. *et al.* (2008) Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363
94. Kiers, T.E. *et al.* (2010) Mutualisms in a changing world: an evolutionary perspective. *Ecol. Lett.* 13, 1459–1474
95. Dunne, J.A. and Williams, R.J. (2009) Cascading extinctions and community collapse in model food webs. *Philos. Trans. R. Soc. B* 364, 1711–1723
96. Veron, S. *et al.* (2018) Predicting the impacts of co-extinctions on phylogenetic diversity in mutualistic networks. *Biol. Conserv.* 219, 161–171
97. Reiss, J. *et al.* (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505–514
98. Laughlin, D.C. and Messier, J. (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends Ecol. Evol.* 30, 487–496
99. Agrawal, A.A. (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294, 321–326
100. Franks, S.J. *et al.* (2014) Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evol. Appl.* 7, 123–139