

Opinion

Deciphering the Interdependence between Ecological and Evolutionary Networks

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Biological systems consist of elements that interact within and across hierarchical levels. For example, interactions among genes determine traits of individuals, competitive and cooperative interactions among individuals influence population dynamics, and interactions among species affect the dynamics of communities and ecosystem processes. Such systems can be represented as hierarchical networks, but can have complex dynamics when interdependencies among levels of the hierarchy occur. We propose integrating ecological and evolutionary processes in hierarchical networks to explore interdependencies in biological systems. We connect gene networks underlying predator–prey trait distributions to food webs. Our approach addresses longstanding questions about how complex traits and intraspecific trait variation affect the interdependencies among biological levels and the stability of meta-ecosystems.

The Stability and Complexity Continuum

The study of interactions, both within and across hierarchical scales, is central to the ongoing synthesis of ecology and evolution in general [1–3], and to debates surrounding the relationship between **complexity** (see [Glossary](#)) and **stability** in particular. Ecologists, for example, have argued for positive [4], negative [5], and non-relationships [6] between the number of **links** and the stability of food webs (i.e., the number of links that is usually defined as the complexity of the food web). This debate is rooted in the mechanisms driving ecological interactions within and among species [5,7–12]. Analogously, evolutionary biologists have puzzled over the relationships between the complexity of gene interactions and the stability of phenotypes [13–16]. Quantitative genetics theory predicts that most genetic variance in populations is additive [17], but accounting for gene interactions can improve predictions about the distribution and evolution of traits [18]. Experiments are also increasingly showing that gene interactions are common, and that additivity can be an emergent property of underlying genetic interaction networks (**gene regulatory circuits**) [19–24].

Although the relationship between complexity and stability has been explored within hierarchical levels, such as individuals, populations, or food webs, the relationship among levels has received less attention [25–27]. Eco-evolutionary theory usually includes interactions in one hierarchical level network, and therefore we do not have a good understanding of how to integrate data and theory to connect complex traits to the stability and complexity of ecological networks. It is possible that small-scale interactions at one hierarchical level might help to explain large-scale patterns at another (**hierarchical networks** in [Figure 1](#), Key Figure). For example, networks of gene interactions could plausibly influence trait-dependent interactions between populations. In such hierarchical systems, what is the relationship between complexity and stability? (see Outstanding Questions).

Highlights

We build on recent studies to show how hierarchical networks can provide a framework for improving the study of the interplay between ecological and evolutionary processes.

In this framework, interaction strength between species depends on ecological and evolutionary processes underlying complex traits and trait distributions, intraspecific niche width, and the interaction with either common or rare phenotypes.

This approach illustrates broad classes of interactions between complex trait distributions and trait change and the complexity and stability of ecological networks.

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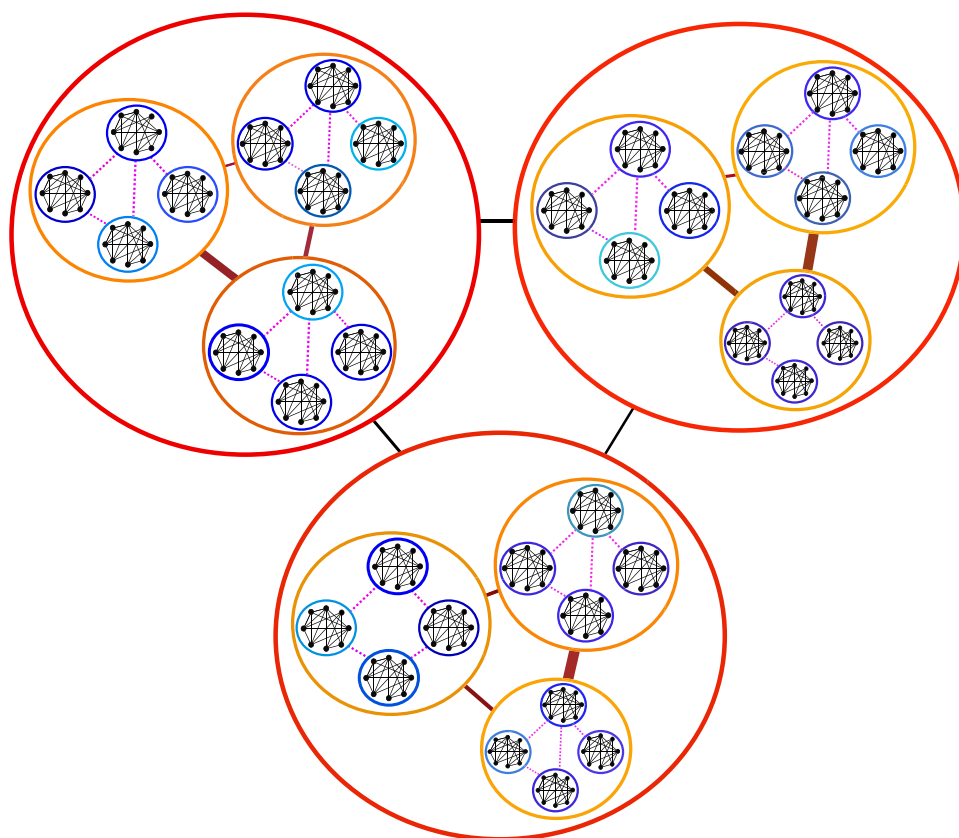
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Key Figure

A Hierarchical Network Represented as a Meta-Ecosystem of Patches (Red), Species (Orange), Individuals (Blue), and Genes (Black)



Trends in Ecology & Evolution

Figure 1. At the intra-organismal level, genes interact to produce a trait (blue). At the inter-organismal level, individuals mate (dotted pink links) to produce the distribution of traits (blue tones). At the population level, trait distribution drives the interaction strength between species (brown links). The meta-ecosystem is pictured as a spatial network (black links) of local interaction networks.

To explore this, we first introduce the connection between gene interaction networks and the distribution of traits. Second, we discuss food webs as interaction networks. We then show in the ‘Merging Evolutionary and Ecological Networks’ section a way to join complex traits and food webs in explicit landscapes. We provide an outline of a meta-ecosystem eco-evolutionary network model to study how interaction strength among species across sites depends on the coupling of gene interaction networks that determine trait distributions of prey and predators (Box 1, and Figures 2 and 3). Such an approach targets the relationship between the stability and complexity continuum in hierarchical networks by explicitly taking into account the interdependence and feedbacks between evolutionary and ecological networks. Although

Glossary

Complexity: usually defined as the number of nodes (i.e., genes, species) and links (i.e., connection between two nodes) in food webs and gene interaction networks.

Epistasis: non-additive phenotypic effects in the face of gene interactions.

Gene regulatory circuits: a set of genes and their regulatory regions that control each other's expression, and thus produce a gene expression or gene activity phenotype.

Hierarchical networks: a collection of networks that interact in a variety of ways at different biological, temporal, and spatial scales. They can be gene interaction networks underlying trait formation, predator–prey interactions, and the dispersal routes connecting many patches (Figure 1).

Interdependent networks: the nodes in two or more networks are connected via interdependent edges. For example, gene interaction networks driving the variance of a trait and the interaction strength between species may affect the stability of a food web (Figures Figure 22 and Figure 33).

Links: connection between two nodes in a network. They could be gene interaction networks that mediate trait interactions among individuals, migration events between two patches, or the effect of one species on another (Figure 1).

Nodes: nodes are the interacting elements of a network. These can be genes, traits, individuals, populations, the whole species, or communities (Figure 1).

Pleiotropy: one genetic change affects more than one trait.

Stability: there are many definitions of stability, and most attempt to characterize changes. Some systems remain constant, oscillate, reach a fixed point, or present another type of behavior that can be described as stable [76]. This multitude of trends can be characterized by different types of ecological (i.e., food webs) or evolutionary (gene interaction networks) stability.

Box 1. Meta-Ecosystem Eco-Evolutionary Network Model

To explore the effect of evolutionary and ecological networks on meta-ecosystem dynamics, we propose a process-based approach that takes into account demography, trait evolution, gene flow, and selection to connect (i) gene interaction networks to a trait distribution (Figures 1 and 2), and (ii) trait distributions to predator–prey interaction strength (Figure 3). The meta-ecosystem contains P patches and S species per patch. Gene interaction networks might range from traits governed by additive genetic variance to different network topologies, and take epistasis and pleiotropy into account to produce a trait distribution with different variance for each species in each patch (Figure 2) [19–21,23,24,29,70].

Trait distributions obtained from additive or non-additive processes are then used to obtain each predator–prey interaction strength, extending previous food web models [40,71,72]. We generalize the function γ_{ixy}^t , represented as a Gaussian function describing the rate with which predator y with trait value z_y^t consumes prey x with trait value z_x^t in patch i at time t , as:

$$\gamma_{ixy}^t = \frac{1}{N_\alpha} \left(\exp \left[- (z_y^t - z_x^t)^2 \right] + 2\alpha \left[\operatorname{sgn} (z_y^t - z_x^t) \right] \left(1 - \exp \left[- (z_y^t - z_x^t)^2 \right] \right) + \operatorname{sgn} (\alpha) \right), \quad \text{[I]}$$

where N_α is a normalization constant, $\operatorname{sgn}(X)$ is the sign function, and α is the prey selection asymmetry. For $\alpha = 0$, -1 , and 1 , predators prefer common prey (Figure 3A, green), rare prey with more distant trait values (Figure 3A, blue), and rare prey with less distant trait values (Figure 3A, red), respectively. The interaction strength, a_{ixy}^t (Figure 3B–D), between prey x for a specific intraspecific niche width ($ianw$) of the predator y in patch i at time t can then be approximated as:

$$a_{ixy}^t = \int_{ianw} \gamma_{ixy}^t D(x)^t D(y)^t dx dy, \quad \text{[II]}$$

where $D(x)$ and $D(y)$ are the density of the prey and predator, respectively.

The community matrix containing the interaction coefficients between species x and y in patch i at time t and the connectivity obtained from the species interspecific niche width ($ienw$) [71,72] is given by $A = [a_{ixy}^t]$. The phenotypes after interaction selection for each prey selection asymmetry scenario and before reproduction can be used to calculate fitness using a fitness gradient approach in the additive scenario [73], or without having to assume a particular fitness function in the non-additive scenario [74]. Fitness will then determine the ecological dynamics that is represented as a spatial network of local interaction networks.

The model can be run for many generations, with each iteration containing interaction selection, mating, and migration to compute the community matrix and the Jacobian matrix for a gradient of dispersal values, following dispersal between patches i and j , using the dispersal matrix, $D = [d_{ij}]$. The Jacobian matrix can be used following the S-map or other stability methods to study the effect of gene interaction networks, prey selection asymmetry, intra- and interspecific niche width, and dispersal dynamics on the stability of local food webs and the meta-ecosystem [12,75].

we focus on specific mechanisms in an eco-evolutionary context, such as traits associated with prey defenses and prey preference, we show that for some eco-evolutionary questions it might be important to account for the genetic architecture of traits to advance cross-field synthesis aimed at understanding the interdependencies between ecological and evolutionary networks (**interdependent networks**).

Gene Interaction Networks and the Distribution of Traits

Many empirical and theoretical studies have shown the effects of gene interactions on trait formation and the distribution of traits [18,24,28,29] (Figure 2). Genes regulate each other's expression, thereby producing genetically encoded phenotypic traits and impacting the distribution of traits in a population. Interactions between genes can be represented as a network [28] (Figure 2A). In such networks, some genotypic changes do not affect a phenotype, which is evidence for a characteristic robustness [16,30]. Robustness can increase phenotypic variance if those phenotypes are maintained by negative frequency-dependent selection (i.e., the advantage of rare phenotypes), but it will decrease the variance if there is strong selection for a single optimal phenotype [16]. In addition, the gene-to-phenotype relation is best understood as a network with **epistasis** and **pleiotropy** [17,18,22,30–34].

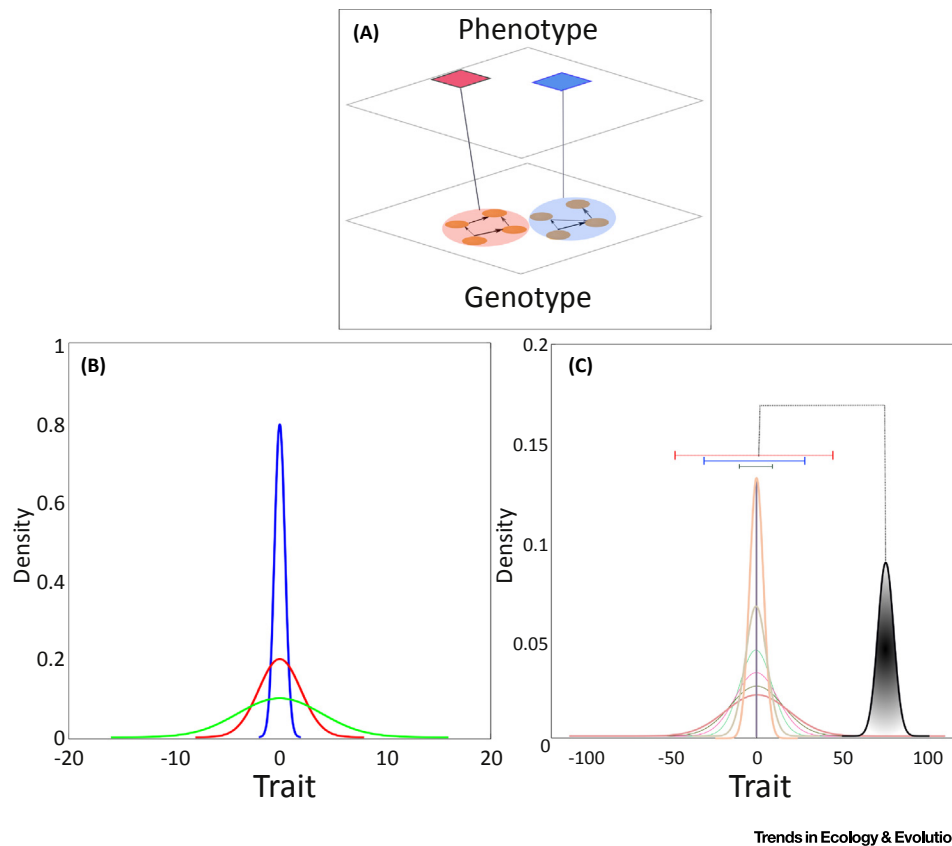


Figure 2. Effects of Gene Interactions on Trait Formation and the Distribution of Traits. (A) The effect of gene interaction networks on a single trait. Two genotypes are shown, each representing **nodes** as genes and links as interactions between genes. Each gene interaction network produces a trait* (blue or red). (B) The x and y axes represent trait value and the density of prey or predator at each trait value, respectively. Red, blue, and green represent the distribution of a trait under different gene interaction networks. (C) A predator (grey) may have narrow (black), medium (blue), or broad (red) intraspecific niche width, meaning it can attack only the most common, common and intermediate, or most prey phenotypes, respectively.

There is evidence of how gene interactions of a complex trait may help to predict the observed phenotypic variance. In a model system for studying the genomics of adaptation, the three-spined stickleback, large phenotypic effects due to changes in pleiotropy in the Ectodysplasin locus (*Eda*) on body growth and armor differed between marine and freshwater environments [35]. In freshwater, only fish with the low *Eda* allele reduced armor and achieved large body size, whereas in the marine environment this trade-off was absent, allowing fully armored fish with the high allele to reach a large body size. Thus, *Eda* affects size and armor in freshwater environments, but only armor in marine environments. A recent experiment in yeast has shown how gene interactions largely influence the variance observed in the population. Specifically, accounting for epistasis increased accuracy in the prediction of observed rare phenotypes, suggesting that genetic interactions should be considered when it is important to identify phenotypes that are likely to lead to extreme phenotypes [18]. Many experiments have also revealed that trait variance driven by epistasis is common in other model organisms including *Drosophila melanogaster*, mice, *Arabidopsis thaliana*, and maize [22].

These studies show that the phenotypes produced by gene interactions, be they plastic or not, can be important in understanding the evolution of trait variance in traits that play a key role in

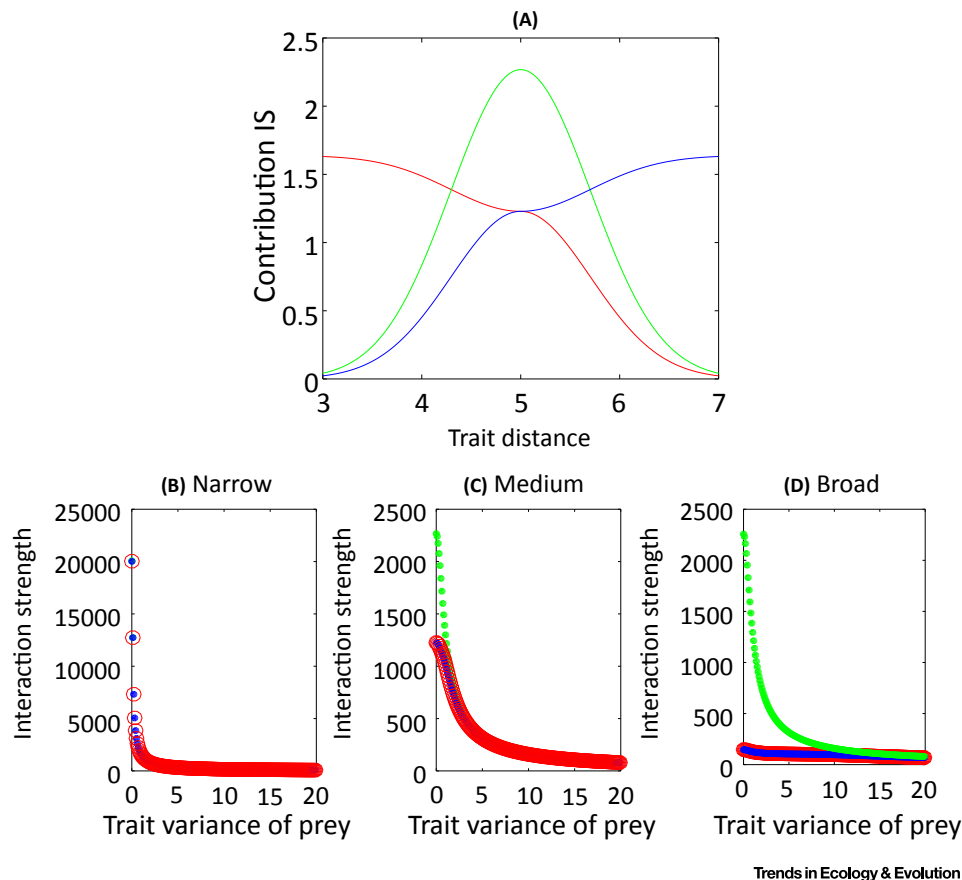


Figure 3. Geographic Variation in Interaction Strength and Trait Variance. (A) The contribution to interaction strength (IS, y axis; Eq. (I) in Box 1) as a function of the trait distance between a predator and a prey (x Axis). Green, blue, and red represent, according to Eq. (I) in Box 1, mean preference (i.e., common prey contribute more to interaction strength, $\alpha = 0$), mismatching trait preference (i.e., more distant prey contribute more to interaction strength, $\alpha = 1$), and matching trait preference (i.e., less distant prey contribute more to interaction strength, $\alpha = -1$), respectively. (B–D) Interaction strength (Eq. (I) in Box 1) for each of the scenarios in panel (A) as a function of the trait variance of prey (x axis) for a narrow (B), medium (C), and broad (D) niche width. Red and blue fully overlap because we have explored the symmetric case shown in panel (A).

ecological interactions. To date, however, we are lacking (i) a framework that connects complex traits (i.e., defense and attack traits) to interaction strength between species, and (ii) a mechanistic understanding of how the gain or loss of genetic and phenotypic variation will affect the complexity of ecological and evolutionary networks in species-rich meta-ecosystems. Eco-evolutionary network models accounting for a gradient of epistasis and pleiotropy in explicit landscapes can be outlined to generate distributions of interaction traits with different variances for preys and predators (Box 1 and Figure 2) [17,18,22,28,29]. In such a framework gene networks are connected to traits, traits to food webs, and food webs to meta-ecosystems.

Food Webs as Interaction Networks

Most network-related research in ecology has focused on trophic interactions among species, particularly in the context of food webs or mutualistic networks [9,11,12]. Many studies have shown empirical evidence that populations are a collection of specialized individuals [36–38],

and that intraspecific trait variation has a major role in understanding coexistence in ecological communities [39–42]. Nevertheless, only a few studies have documented how intraspecific trait variation influences the connectivity and the number of trophic levels within food webs [43,44]. One might expect that the larger the phenotypic variance within a species, the larger the number of direct and indirect interactions in which the species may be involved, potentially increasing its contribution to shape the species interaction network. However, unexpected outcomes can occur when taking into account variation of phenotypes, niche width, and prey preferences. Figures 2C and 3 illustrate this example. A predator with a given trait variance can have many intraspecific niche widths (Figure 2C) and prey preferences (Figure 3A), suggesting that we can have many distinct interaction strengths and stability properties in a food web for a given trait variance (Figure 3B–D and Box 1). Therefore, combining gene interaction networks with trait variance and ecological networks might provide a fruitful approach to unifying patterns and processes across networks. The following section aims to integrate ecological and evolutionary networks into hierarchical networks to understand the forces behind interaction strength and the complexity–stability relationship across scales.

Merging Evolutionary and Ecological Networks

In our previous example with the three-spined stickleback, pleiotropy in the *Eda* locus affects size and armor in freshwater environments, but only armor in marine environments. This causes the interaction strength between the three-spined stickleback and their predators in marine environments to be weakened because the fully armored phenotype is more common (Box 1). The phenotypes with less armor may be preferentially consumed by predators, thereby driving those phenotypes to be rare in marine environments. In this scenario, selection is then rather weak, and, assuming any cost, defense traits can become counterselected, closing the feedback loop [45]. Therefore, at the landscape level, variation in environmental selection [46] and changes in the architecture of gene interaction networks across locations might alter the stability of the three-spined stickleback and predator populations.

There is also evidence that the outcome of trait interactions between species in host–parasite and mutualistic interactions depends of epistasis and the number of underlying loci [47,48]. We might expect that specific architectures of gene interaction networks containing different degrees of epistasis and numbers of loci produce large phenotypic variance. Estimating the architecture of gene interaction networks affecting the evolution of trait variance and the interaction strength between species is an exciting avenue to integrate evolutionary and ecological networks (see Outstanding Questions). This can be achieved using hierarchical networks [11,12,49] (Figure 1). Many gene interactions and mutations in multiple loci, at different locations in the genome, determine variation in morphological traits (Box 1 and Figure 2) [19–21,23,24]. However, traits accounting for niche width and prey selection also play a role in inferring the interaction strength between species [50] (Figure 3). Classically, common phenotypes contribute more to interaction strength (Figure 3A). However, if the common prey phenotype has higher defense traits than the rare types, then predators can selectively avoid this phenotype. In the three-spined stickleback these processes shape phenotypes ranging from full to low armor defenses. In such scenarios predator preference can be biased towards rare prey driving geographic variation of interaction strength and altering the stability of food webs (Figure 3A).

Therefore, the interaction strength can be a function of the gene interaction network underlying the distribution of a trait with a given variance, niche width, and the strength with which predators prefer rare or common prey, i.e., prey selection asymmetry (Figure 3B–D and Box 1). Accounting for asymmetry in prey selection weakens interaction strength for a broad gradient of

niche width and trait variance of the prey (Figure 3B–D). Because interaction strength is one of the key processes governing the dynamics of ecological networks [9,12,51], trait-based approaches combining gene interaction networks and prey selection asymmetry as drivers of the fluctuations of interaction strength might lead to a promising avenue to unify the stability of evolutionary and ecological networks.

A Roadmap for Studying the Stability and Complexity Continuum

Theoretical and empirical studies have shown that intraspecific genetic and phenotypic variation alter the complexity and the structure of ecological networks [43,44]. Nevertheless, process-based approaches connecting complex traits to intraspecific variation and the strength of ecological interactions as drivers of meta-ecosystems remain at a very incipient stage [52]. We have provided here an approach to merging evolutionary and ecological networks in meta-ecosystems (Figure 1 and Box 1). Large intraspecific genetic and phenotypic variation may increase the complexity of an ecological network by reducing overall interaction strength (Figure 3B–D). However, population heterogeneity in prey selection can also play a role in predicting the complexity of an ecological network. Preferentially selecting rare prey weakens interaction strength in comparison to selecting common prey for a broad range of trait variance of prey and intraspecific niche width (Figure 3C,D). Preferentially selecting common prey, on the other hand, might produce strong interactions between common prey and predators, but rapid trait changes can have stabilizing effects on population dynamics and abundances [53,54]. In this regard, the genes and phenotypes of one organism can strongly modify the phenotype of another (i.e., the ‘extended phenotype’ [55]), such as host behavioral modification by parasites or plant structural modifications by galling insects.

There is currently a wealth of data spanning many branches of ecology and evolution that could be used to understand the interaction strength between species and the connections across levels of biological organization [56–59]. Many libraries are also rapidly emerging to integrate, analyze, and visualize patterns across networks ([56,58,60] and www.plexmath.eu/?page_id=327). Recent analysis of six different levels of biological organization depicting gene interactions, complex phenotypes, animal societies, metapopulations, food webs, and vertebrate communities has shown invariant patterns of nestedness that are independent of interaction type or biological scale [61]. In a nested network, interactions are organized such that specialists (for example predators that eat only a few prey) interact with a subset of the species with whom generalist, for example, predators that attack many preys, interact. Nestedness has received significant attention because it has been suggested that a nested pattern of interactions may lead to greater or lower biodiversity in ecological networks [62,63]. Regardless of whether nestedness increases or decreases the number of species in ecological networks, it is an open question how many of these networks are necessary to represent these multilevel systems (see Outstanding Questions). A method was recently introduced [64] to reduce the numbers of layers to a minimum while maximizing the distinguishability between each pair of networks. They found that protein–genetic interactions, social, economic, and transportation systems can be reduced by up to 75% without losing their structural properties.

Evolutionary and ecological networks could be analyzed using only a small number of layers in which the correlations driven by the interdependencies and feedbacks might be strong. An example of reducing complexity in evolutionary networks may be that the expression of single genes rather than the gene interaction network *per se* influences the interaction strength between species. In this case, the gene interaction network can be redundant and the links associated to the gene network can be removed. In this regard, we need approaches combining pattern-detection metrics in evolutionary and ecological networks with process-based approaches so as to capture

how the interdependency between hierarchical levels and spatial fluxes across locations might drive the stability of species and communities in meta-ecosystems [65].

The field of eco-evolutionary dynamics has recognized the overlap of timescales between ecological and evolutionary processes [66], and many studies have shown that evolution alters the trajectory of ecological processes if the heritable phenotypic change occurs sufficiently quickly [67]. It also has made many contributions to disentangling the evolutionary and ecological processes affecting population dynamics and the feedbacks between ecology and evolution [68,69]. However, the connection between complex traits, trait distributions, and interaction strengths in ecological and evolutionary networks remains poorly integrated. In our example, the components of the system at one scale, for example the interaction between the individuals of two species, are linked to specific changes in another scale, for example genetic networks, and the strength of the interdependencies between these two scales can be addressed. We introduce a meta-ecosystem eco-evolutionary network model to account for the interdependencies and feedbacks between gene interaction networks, ecological networks, and spatial networks. These systems might contain many layers that cannot be reduced because each level potentially has many independent processes that drive its dynamics. In this regard, many open questions remain in connecting evolutionary to ecological and spatial networks by combining the empirical patterns obtained from analyzing gene, population, and ecological networks to the processes governing biological hierarchical networks.

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Outstanding Questions

How do evolutionary networks affect population dynamics and food webs, and ultimately the stability of large meta-ecosystems? How does the genetic architecture underlying complex traits affect interaction strength between species? How do ecological networks and food webs feed back into gene networks to alter interaction strength? For example, does assuming a simple gene network, in quantitative genetics style, versus incorporating the network perspective with epistasis and pleiotropy, matter for predicting the interaction strength between species? Do food webs increase in complexity, stability, and diversity when considering simple gene networks? Do the complexity and diversity of food webs feed back into single gene networks? Likewise, if we make the ecological part simple, but the gene network complex, then do food webs increase or decrease in complexity and diversity? To what extent does the complexity of gene interaction networks drive intraspecific trait variance and the complexity of ecological networks? Gene interaction networks containing pleiotropic and epistatic interactions have been identified in interaction traits that could drive interaction strength between species and the stability of meta-ecosystems. However, genetic and trait data are mostly available for a few model organisms, and more data on a wider range of species interactions, environmental contexts, and traits will be necessary to compare model predictions with empirical patterns.

How does the interaction between the genetic architecture of defense and attack traits influence the stability of meta-ecosystems? What is the role of phenotypic plasticity in this regard? How strong is the interdependence among the genetic architecture underlying interaction traits, local community dynamics, and spatial connectivity?

Hierarchical networks might facilitate the integration of interacting genes within genomes, individuals within populations, and subpopulations with communities in the same framework. Nevertheless, further studies considering process-based approaches will be necessary to understand the strength of the interdependence between trait

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distributions of interacting species, and how such interdependence may vary geographically. Hierarchical networks might also allow feedbacks between ecological and evolutionary networks to be explored. For example, how do interactions between evolutionary and ecological networks with feedbacks differ in their behavior from networks without feedbacks?

Finally, merging patterns and processes into hierarchical networks is at a very incipient stage. What are the main eco-evolutionary network patterns within and across biological scales? Which evolutionary and ecological network processes reproduce such patterns? Are interdependencies and feedbacks among evolutionary and ecological networks necessary to reproduce the empirical patterns?