

Tailoring interaction network types to answer different ecological questions

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Abstract

Ecological interaction networks are an important tool for describing species interactions, but many network approaches are available, each with their strengths and weaknesses. In this Perspective, we describe how interaction networks can be differentiated in two main ways: by the extent of node aggregation (how species are lumped into groups) and by the type of information contained in links (potential versus realized interactions). We discuss the ecological questions that each network type can address, how measurements from different types of network should be interpreted, and their relative advantages. Networks with nodes aggregated to functional groups are suitable when focusing on ecosystem-level processes and ecosystem functions. Species-level networks provide information about the assembly of ecological communities or about how abiotic and biotic drivers influence species persistence. Networks with potential links are particularly useful for understanding ecological redundancy or for long-term or large-scale studies, where all potential interactions are likely to be realized. Networks of realized interactions provide access to finer mechanisms of the interplay between abiotic and biotic factors in determining ecological interactions. Identifying the advantages and limitations of different interaction networks will aid methodological decision making and increase the utility and applicability of ecological networks in biodiversity and conservation research programmes.

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Introduction

In the context of global environmental change, how species interact in natural communities (and how their interactions change over time) influences species' persistence and the stability of ecological communities¹, as well as the functioning of ecosystems and the provision of ecosystem services^{2,3}. Network analyses integrate sets of biotic interactions within and among ecological communities and are a valuable tool for evaluating the responses of communities to global change⁴.

Ecological interaction networks consist of nodes (representing individuals, species or groups of species) connected by links (representing the interactions between nodes). However, the methods and criteria for formulating these nodes and links can vary (Fig. 1). Networks can be constructed with nodes aggregated in different ways; for instance, nodes can be aggregated by different levels of taxonomy or by functional role in the ecosystem^{5,6}. Links can represent different types of interaction (including pollination, consumption and social contact), and these interactions can be determined in different ways. In some cases, interactions are determined through direct observation (typically the case for plant–pollinator and plant–frugivore networks) and links therefore represent realized interactions. In other cases, interactions are inferred from prior knowledge (such as literature

reports of interactions) or from predictive models (for instance, based on species traits)^{7,8}; these links represent potential interactions that might or might not be realized, depending on the environmental context. Therefore, 'ecological interaction network' is an umbrella term for all interaction-based approaches that can refer to very different types of data.

Network approaches have been used in contexts such as biodiversity conservation⁹, biological invasions¹⁰, functional ecology and eco-evolutionary dynamics¹¹. These fields rely on different theoretical assumptions and hypotheses about the information that networks can provide. For example, research in functional ecology often relies on networks with nodes aggregated according to their functional characteristics, assuming that their interactions represent different ecosystem functions. However, to study biological invasions it can be critical to understand how an exotic species will interact with local species and whether it will reshuffle existing ecological interactions, calling for more resolved networks and observed interactions. Given the different goals of these research applications, networks should not always be compiled in the same way, nor should there be a single 'gold standard' method. Rather, researchers should build networks that best reflect the ecological question. In many cases, network construction methods influence the interpretation of the studies. For example, assessing

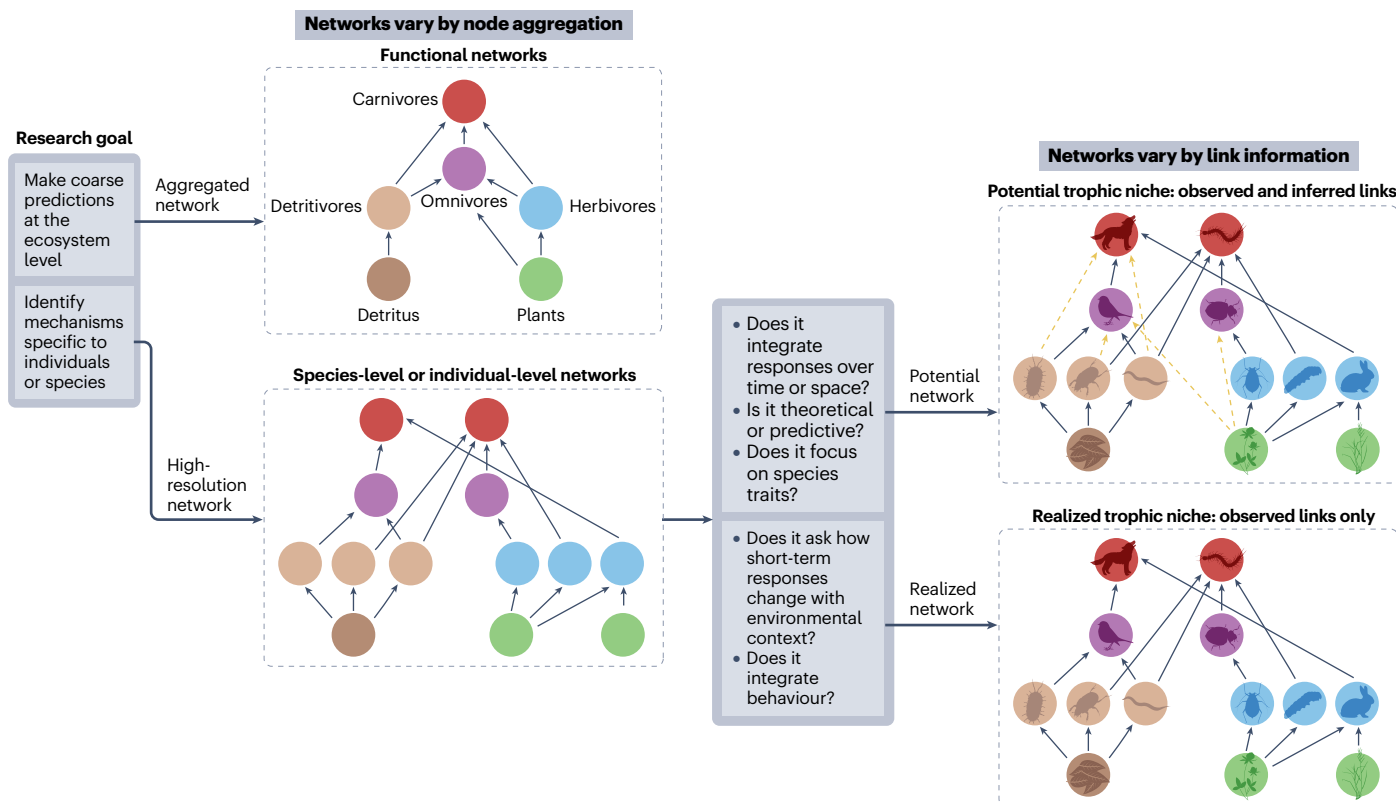


Fig. 1 | Flowchart representing the methodological choices underlying the decision to use a specific network type. The general research goals envisioned for a specific research question might influence the level of resolution needed to produce sound answers. If highly resolved networks are needed, a subsequent question relates to the information contained in links. A more precise set of questions related to each category can be found in Box 1 (node aggregation) and Box 2 (link information). For highly resolved networks, black links represent observed interactions, and yellow dashed links represent inferred interactions

that do not occur when observing the community because of specific local environmental conditions (for instance, because of processes related to optimal foraging theory). For example, when resources are plentiful, foxes would focus on more rewarding prey, such as birds and rabbits, and ignore less rewarding ones, such as worms and isopods. The notion of inferred versus observed links is unlikely to be relevant at low node resolution, because the group definition itself is determined by the link information (herbivores consume plants, detritivores consume detritus).

how network structure changes along environmental gradients can be biased when using different levels of resolution¹².

In this Perspective, we argue that for ecological network research to progress, the different methods of network construction must be distinguished according to node aggregation and link estimations. We discuss the extent to which particular network types and analyses are (or are not) well suited to addressing specific ecological questions. We also argue that comparisons among published networks will be more meaningful if the comparisons account for the ecological processes represented by the methods used for compiling nodes and links.

Aggregated versus high-resolution networks

Questions about the level of taxonomic resolution needed in ecological networks have spanned decades of research¹³. Concerns have been raised that aggregation of species into groups alters network structure in a way that prevents theoretical exploration of key concepts such as community stability¹⁴. However, aggregated networks require less effort in identifying taxonomy and links between species compared to species-level networks. In this section, we argue that decisions about the extent of node aggregation should be guided by the specific research question rather than solely by methodological convenience (Box 1).

Aggregated networks

We define aggregated networks as those that depict interactions between groups of species, usually trophic guilds (such as detritivores), life modes (such as plankton), or even large community assemblages (such as microorganisms). Aggregation can be based on information contained in nodes (for example, grouping species with similar traits, such as body mass or phylogenetic proximity) or information contained in links (for example, grouping species with similar types of interaction, such as herbivores or detritivores).

Node-based aggregation is usually preferred over link-based aggregation in studies aiming to better understand the biomass dynamics of the different groups^{15,16} or more complex indirect effects, such as trophic cascades^{17,18}. An important advantage of aggregated networks is that they simplify complexity to enhance tractability while preserving essential network information, such as the functional roles of species^{19,20}. Although aggregated networks leave within-group interactions unresolved, they provide a practical compromise for tracking the dynamics of individual nodes over time. By focusing on large groups, analyses of aggregated networks can indicate the shape of biomass pyramids (bottom-heavy when most of the biomass is located in groups at the base of the food webs or top-heavy when a higher amount of biomass is located in groups at the top of the food webs) or predict trophic cascades in a given community^{15,21}. In such cases, the use of aggregated networks can reveal the mechanistic underpinnings of the consequences of interactions by identifying potential indirect effects occurring between groups, leading, for instance, to long cascading effects throughout the communities^{21,22}.

Link-based aggregation is often used to represent ecological functions related to interactions, such as detritivory, pollination or pest control². This approach aggregates species with similar functional roles (for example, herbivores, detritivores, and secondary consumers in food webs²³) or traits (for example, short versus long mouthparts in plant–pollinator networks²⁴). As a consequence, links can be merged across very large taxonomic categories. For example, elephants and locusts could be lumped together in a functional group associated with the herbivory function. By summarizing entire functions related to the fluxes of energy transitioning through interactions, networks with

Box 1 | Examples of ecological questions associated with different levels of node aggregation

Aggregated networks

- Trophic group dynamics: what determines the distribution of biomass amongst trophic levels? Is the network top-down or bottom-up controlled?
- Functional ecology: how does functional diversity affect ecosystem processes or dynamics? How do functional groups affect each other?
- Elemental and energetic fluxes: how does an element cycle or flow through an ecosystem?

High-resolution networks

- Species diversity responses and effects: how does environmental change affect multitrophic biodiversity? How does multitrophic biodiversity affect ecosystem functioning?
- Species roles in networks: which species are most important for network structure, function and coexistence? Which species are positionally similar or unique regarding specific functions?
- Population dynamic mechanisms: what drives network stability and allows for species persistence? How does dispersal affect network persistence?
- Evolutionary mechanisms: how do interaction strengths change through evolutionary time? How do interaction networks affect the evolution of new traits or species?

aggregated links make it easier to integrate community-level effects on ecosystem functions, such as the relative importance of predator control and resource availability for herbivory or predation²³. Such an approach is therefore very useful for relating the response of multiple ecosystem functions or services to different environmental gradients or perturbations^{25,26}. For example, aggregated networks have been used to document how the transformation of rainforest into oil palm plantations reduces herbivory and predation in canopies²⁷.

High-resolution networks

Highly resolved interaction networks (in other words, networks in which nodes are individual species, subspecies or individuals) can provide insights about the assembly of ecological communities²⁸, the evolutionary mechanisms driving network structure^{29,30}, and how abiotic and biotic drivers influence species persistence^{31,32}. Networks with nodes resolved to sub-species levels (individuals^{33,34}, ontogenetic stages or size groups³⁵) can be used to examine within-species trait variation in response to energetic constraints^{34,36} or foraging behaviour and animal personality³⁷. This level of resolution allows comprehensive integration of population trait structures, such as body mass, sex or ontogenetic stage shifts, into the understanding of ecosystem functions^{33,38} and their response to ecological gradients^{39,40}.

Indices of network structure (including measures of connectance, average degree or trophic level) can describe how interactions within complex communities are structured⁴¹. Network structure reflects the constraints imposed by the environment on communities, which cannot be fully captured by information on species composition alone. For instance, the amount of resource available limits the number of trophic

levels because of the low energetic efficiency of food consumption⁴², or high food-web connectivity might lead to instability, making highly connected networks unlikely to occur in natural environments⁴³.

Network analyses can also examine the implications of network structure for ecosystem function and stability. The impact of network structure on ecosystems can be evaluated by examining how various network descriptors relate to ecosystem processes, such as species coexistence and stability⁴³ or functions⁴⁴. For example, the productivity of basal species is increased by the number of trophic levels⁴⁵, and network connectivity would decrease stability in food webs while increasing persistence in mutualistic networks⁴³. Finally, assessing the importance of network structure on the biodiversity–ecosystem functional relationship, by definition, relies on networks resolved at the species level to represent the varying levels of species diversity across local communities.

Network structure can be viewed both as a response parameter to environmental conditions, reflecting the capacity of the community to cope with perturbations^{43,46}, and as an effect parameter that influences the functioning of ecosystems⁴⁴. The responses of network structure to environmental conditions are typically assessed using correlative approaches based on data compilation⁴⁷, field observations^{48,49} or the experimental manipulation of environmental gradients^{50–52}. Less often, they rely on comparisons to null models²⁸. Therefore, the selected descriptors of network structure should have established connections to the ecological processes associated with the hypotheses or questions being addressed^{53,54}. For instance, a study using network structure to examine the consequences of nutrient enrichment would ideally first define its goals (which consequences it aims to infer) and then select descriptors according to their established capacity to derive relevant information in this context.

Interaction networks can also be used to infer how an individual species contributes to the ecosystem^{19,55} or to ecosystem services⁵⁶. For example, the metrics of species (node) importance⁵⁷ or centrality⁵⁸ can determine the importance of a species to the energetic integrity of the network and the likelihood that a secondary extinction will occur if the focal species is removed through extinction. The position of a species within the network either buffers against or propagates perturbations throughout the community; for example, in plant pollinator networks, highly generalist species such as honeybees are more likely to transmit pathogens⁵⁹. However, it remains unclear how network position would affect the spread of other types of perturbation, for instance those related to changes in biomass. Substantial variation in node properties can also occur within a species. For instance, trophic level⁶⁰, level of specialization⁶¹, and even interaction type can change with individual body size or across developmental stages within a species.

Properties of nodes and networks are not independent of each other. Even species that are not connected directly can be connected through multiple indirect paths, and the propagation of effects across the network depends on how these paths are organized⁶². How a perturbation (often defined as the removal of a species) percolates throughout networks depends not only on the structure of the network (for instance, modularity tends to reduce secondary extinctions⁶³), but also on species-level properties (for instance, central species are more likely to trigger secondary extinctions⁵⁸). Some ecological applications, such as predicting the likelihood of an exotic species becoming established in a community, should consider both node and network properties. Networks with certain structures (for example, highly connected and species-rich) tend to be resistant to invasions^{10,64,65}, and individual species with certain interaction patterns (for example, generalists

with central positions in the network) are more likely to successfully invade new habitats^{65,66}.

When high resolution is needed

The effect of node resolution on the usefulness of network approaches to convey a meaningful ecological message has been thoroughly explored using case-specific analyses^{67–69}. Their aim was to show how the aggregation process alters the structural properties of networks^{69,70}, or to understand whether, despite these differences across levels of resolution, differences in structure observed at the species level hold for aggregated networks¹². Yet, how and when the use of aggregated networks leads to erroneous or valid interpretations of observations remains poorly understood. This understanding would depend on whether the effects of ecological factors differ across levels of biological organization. Specifically, comparing results obtained at different levels of network aggregation could test whether variations in environmental conditions affect specific levels of organization differently.

Consequently, aggregated networks are a suitable tool when aiming to derive predictions on coarse-level variables, such as ecosystem functions associated with multiple different species (like detritivores for the detritivory function). When focusing on the response of network structure to environmental gradients, in the absence of a general framework to determine which level of resolution should or should not be used, the approach should be to use highly resolved networks, unless there is a well established link between the effects that the gradient being considered has on individuals and the aggregation criteria. For instance, aggregation of species to family level could be acceptable if the gradient considered is affecting specific taxonomic families. Evaluating how networks associated with levels of biological organization interconnect (for example, how social networks often resolved at the individual levels connect to food webs, often resolved at the species level) is a first step to understanding how different processes percolate through different levels of biological organization^{71,72}. For instance, social interactions or information flow occurring at the individual level can influence interactions realized at the species level^{73,74}.

Finally, the network view of interactions occurring in a community helps to identify key nodes for preserving biodiversity and ecosystem functions. Targeting conservation efforts toward key species or nodes that rely on multiple network pathways could be more effective (in terms of maintaining multiple components of ecosystem function) than protecting a flagship or umbrella species alone^{75,76}.

Link information

The second method of differentiating ecological networks is according to the information that the links depict: potential versus realized interactions. The potential and realization of an interaction between two co-occurring species result from both neutral processes and niche processes that can sometimes interact in complex ways^{77,78}. Neutral processes, which are typically related to species' relative abundances, affect the likelihood of a consumer encountering its resource⁷⁸. By contrast, niche processes influence both the probability of encounter (through exploratory movement speed or specific habitat structures) and the feasibility of interactions (for example, whether the traits of the consumer and resource are compatible for an interaction). Realized links (those that are determined directly from visual observations during foraging or from remnants of prey in stomach or pollen deposition) arise from a combination of neutral and niche processes. By contrast, potential links typically reflect only the subset of niche

processes related to species traits that determine interaction feasibility and so do not account for whether species actually encounter and interact in local communities.

The methods used to determine interactions can differentiate between niche and neutral processes, thereby influencing the information content of the networks being considered, and the types of question that can be addressed (Box 2). An analogy can be drawn with fundamental versus realized niches: networks based on potential interactions depict the interactions that can occur (similar to the fundamental trophic niche), whereas realized interaction networks reflect the links that actually occur at a specific point in time and space (similar to the realized niche). The concept of ‘realization’ underscores the importance of defining realized networks within a specific temporal and spatial context. Compiling realized interactions across large spatial or temporal scales – such as aggregating data or using methods such as gut-content analysis to infer links in different contexts – or combining various methods^{79,80} effectively shifts the analysis away from depicting the realized trophic niche towards depicting the fundamental trophic niche. Conversely, trait-matching models have frequently been used to generate networks of potential interactions. Traditionally, they only reflect niche processes because they identify functional trait combinations that allow interactions to occur^{81,82}; however, newer implementations of the models have incorporated encounter probabilities^{78,83} and abiotic conditions⁸, bringing them closer to representing realized interactions.

Because they integrate the most information about the determinants of interactions, networks based on realized interactions could be seen as the gold standard. Conversely, those based on potential interactions have been criticized as being unrealistic or unverified because it remains unclear whether they reflect *in situ* communities. In this section, we discuss how both approaches can be advantageous depending on the ecological question.

Networks of potential interactions

An important application of network ecology is to identify the drivers of ecological interactions. In ecosystems governed by a few environmental and trait dimensions^{82,84,85}, different ecological interactions and resulting network properties can be predicted from the estimated functional trait distribution and environmental characteristics^{86–88}. When we determine the set of traits that allows an interaction to occur between two species we are asking who can interact with whom (potential interactions), rather than who does interact with whom (realized interactions, specific to a unique community context). Indeed, neutral processes would alter the realization of an interaction because of stochastic processes related to the probability of encounter between two interactors or because of a specific community context. Datasets of networks of potential interactions rest on the assumption that two species that can interact because of their traits will interact, which excludes this stochasticity and community context in interactions. For instance, in such networks, a link is drawn between two species if there is any evidence for an interaction at a different point in time and space (Table 1). As a consequence, it is assumed that similar communities will always have comparable interaction networks, independently of relative species abundances or abiotic conditions. Therefore, these networks are relevant for validating models predicting interactions from traits and, thus, direct hypothesis testing. This approach can, for example, be used to assess the importance of the body mass or feeding mode of a species⁸⁹, or ecosystem dimensionality⁸⁴ for trophic interactions, or pollinator mouthpart and flower corolla shape⁹⁰ for plant–pollinator

Box 2 | Examples of ecological questions associated with different levels of link information

Potential interactions

- Spatio-temporal integration: how many species will be affected by a particular extinction? How would spatial processes such as dispersal propagate perturbations or maintain diversity? What are the long-term effects of a stressor on an interaction network?
- Novel interactions: how could an infectious disease move through a wildlife community? How might a species introduction affect an ecosystem?
- Theoretical network models: does diversity result in stability? Do weak interactions stabilize networks? How do eco-evolutionary processes shape interaction networks?

Realized interactions

- Network context-dependency of interactions: how do the interactions between species change with environmental, spatial or temporal context?
- Species context-dependency of interactions: how does a species’ fear of predation affect its interactions? How do higher-order interactions drive community dynamics?
- Plasticity or evolution of interactions: do networks rewire after species loss? What novel interactions arise following species introductions?
- How stable will networks be after global change (rewiring potential, behavioural and intraspecific flexibility/variability)?

networks. Ultimately, networks of potential interactions can be used to develop a mechanistic understanding of biophysical factors that facilitates or hinders interactions⁸⁸, as well as to identify the key traits necessary for these interactions to occur⁸⁵. These methods are steps towards prediction of ecological networks in general contexts without the need to observe or sample every interaction, thus complementing networks with potential missed interactions. As such, they can help to reconstruct palaeo-communities⁹¹ or project networks for future ecosystems.

Several approaches have been used to predict potential interactions. Models that generate synthetic networks^{92,93} have been instrumental in identifying the ecological mechanisms that drive species’ coexistence and their responses to perturbations^{64,94}. However, earlier models relied on a single trait axis representing either an abstract niche dimension⁹² or species body mass⁹⁵ to predict interactions and ignored the effect of abiotic conditions. These choices limited the utility of the models in assessing the interplay between trait diversity, variation in local abiotic factors and consequences for ecological processes and biodiversity³¹. Artificial intelligence (AI)-based models^{96–98} have the potential to circumvent these issues at the cost of losing an explicit mechanistic construction of interactions. Nevertheless, networks based on potential interactions still provide a valuable foundation for theoretical approaches, such as models predicting population dynamics or community assembly²⁸. Finally, analysing networks over large spatial (macro-ecology) or temporal (future projections) dimensions makes it increasingly unlikely that stochastic processes would completely prevent any interaction from occurring at least once.

Table 1 | Methods used to infer potential interactions

Method	Description	Strengths	Weaknesses	Interaction type	Level of node resolution ^a
Literature ¹¹⁹	For each node, check whether an interaction was already recorded in the literature	Large amount of information available; non-invasive; helps to characterize interactions of rare species; helps to fill gaps due to undersampling	Reduced quality control (relying on consistency and integrity of methods in other studies); difficult to identify ‘forbidden links’ or quantitative information	All	All
Feeding trial ¹²⁰	Experiment (usually in microcosms) to force an encounter between a consumer and a resource	Identification of ‘forbidden links’; provides information on the frequency of occurrence; allows inferences about interaction strength	Outcomes of trials can be biased because of the artificial setting (not observed in situ, and therefore used only to infer links); ethical concerns for larger animals	Trophic, parasitism, potentially pollination	Individual
Trait matching ^{8,95}	Mathematical models defining the combination of one or several traits allowing an interaction to occur	Uses objective rules; multiple available models can be compared; abiotic factors can be integrated into predictions	Potentially returns false positives or negatives; performance depends on the input data quality; usually restricted to a small number of traits	All	Individual or species only; trait information for large taxonomic groups is highly variable
Expert knowledge ¹²¹	An expert on an ecosystem or a group of organisms decides the presence or absence of links	Fixes the issue of undersampling of diets; useful for rare species with very little information in the literature	Not evidence-based; subject to biases of the expert	All	All
AI ^{86,96–98}	Classification algorithms deriving predictions by identifying patterns from a training dataset	Can process a large amount of available data; multiple co-variables can be considered	No explicit mechanisms	All	All

^aHigher levels of resolution are often used to determine interactions at lower levels of resolution (for instance, individual information to determine interaction between species or groups). AI, artificial intelligence.

At these large scales, we expect that networks of potential interactions will accurately represent all the realized interactions.

Networks based on realized interactions

Realized interactions can be compiled in numerous ways, with different advantages and disadvantages (Table 2). The main difference, compared to potential interactions, is that working with realized interactions relaxes the assumption that similar communities always have comparable interaction networks. By documenting how interactions between two species can change depending on the local context, realized interaction networks enable the investigation of mechanisms beyond interaction traits, such as the relative importance of local biotic and abiotic conditions. For example, the local presence of predators (fear effect⁹⁹), resource availability¹⁰⁰, or temperature¹⁰¹ can influence whether a potential interaction is realized. Such local variations in species interaction patterns can be documented only when information on realized links is available.

Given that understanding species interactions is crucial for predicting the future of communities, it is essential to evaluate the importance of these local processes – insights often missed when relying solely on potential interactions – and to determine whether they are necessary for making accurate ecological predictions. For example, some species can shift their interactions^{102–104}, leading to networks being ‘rewired’ with different structural properties. Such plasticity depends on the occurrence or abundance of interacting species as well as on the generality of the consumer, with generalist and omnivore species being more likely to change their realized interactions³². This foraging plasticity can be essential in governing network stability¹⁰³, community response to perturbations¹⁰⁴, or to temperature increases⁵². However, whether the outcome of rewiring is associated with higher resistance to species loss is still unclear, with

contrasting results observed so far: some studies suggest a positive effect of rewiring on coexistence^{105,106} and others a negative effect^{36,107}. The absence of clear consensus could arise from the effectiveness of the interaction choices made by species¹⁰⁸, stressing the limitations of current models that are missing an empirical mechanistic basis. Although the environmental factors leading to rewiring have been documented for both plant–pollinator networks^{109,110} and food webs¹¹¹, the interplay between environmental conditions and the characteristics of the predator and the prey that determine whether and how rewiring occurs remain untested. This knowledge gap limits effective forecasting of the effects of restoration actions such as rewilding¹¹² and, more generally, the integration of network and restoration ecology⁷⁵.

When realized interactions are needed

Because they describe all the interactions that can be realized, potential interaction networks are relevant tools with which to explore questions related to the fundamental niche of species (for instance, questioning species traits underlying interactions) or to address questions at large spatial and temporal scales. However, shifting predictions from potential to realized interactions will be an important step towards understanding how multiple interacting environmental factors influence networks, with consequences for biodiversity and ecosystem functions, a crucial challenge in the context of a multifaceted global change. Although they are informed and validated by networks of both potential and realized interactions, generative models^{92,113} generate predictions of potential interactions because they do not consider the potential influence of ignoring possible modifications by the biotic (species relative abundances) and abiotic (local conditions, such as temperature) context on the realization of links. Predicting realized ecological interactions might be easier for plant–pollinator networks than for food webs, because published plant–pollinator data are usually based on observations,

whereas published food-web data are more often based on potential interactions (Tables 1 and 2). The scarcity of empirical descriptions of realized trophic interactions forces generative food-web models to rely on hypotheses and concepts to predict which links are realized under changing abiotic and biotic conditions. In this vein, optimal foraging theory is a very promising avenue of research because it enables us to determine the subset of potential links that are realized by assuming that consumers select their resources to optimize their energy intake^{114,115}.

An example of network selection

To describe how researchers can select among network types depending on specific questions, we provide an example related to the general topic of how temperature influences ecological systems. When exploring how temperature affects biomass pyramids, aggregated networks are suitable because these networks simplify ecological complexity into broader categories, making it easier to discern changes in biomass distribution across trophic levels as temperatures increase. If the goal

is to understand how trophic interactions change with temperature – such as when sampling networks at different elevations on a mountain, using space-for-time substitution – then species networks based on realized interactions should be used. These detailed networks integrate how traits and the behavioural response of individuals or species respond to changes in temperature to form new assemblages of links, and lead to modification of network structures. If the aim is to model how temperature will affect the temporal dynamics of species and their coexistence, high-resolution networks based on potential interactions should be used to inform the set of interactions that can be realized. Because dynamic models integrate large timescales, all potential interactions are likely to be realized at some point, and their strength will be governed by the biomass dynamics.

Outlook

Here, we have argued that two key properties differentiating most ecological interaction networks are the level of node aggregation and the

Table 2 | Methods used to identify realized interactions

Method	Description	Strength	Weaknesses	Interaction type	Level of node resolution ^a
Field observation ²⁴	Direct observation of events occurring in the study system	Non-invasive; consideration of environmental conditions; can provide quantitative feeding information; could use video technology	Labour-intensive; observer can bias interactions; under-sampling can be an issue for accurately characterizing diet; limited taxonomic resolution	All, but mostly used for pollination	Variable, mostly depending on environmental conditions and species
Adhesion ¹²²	Use of sticky traps that will attract pollinators	Could stay a long time in the field; can capture a wide taxonomic diversity of pollinators; can give access to pollen transportation	Invasive; labour-intensive	Pollination	Individual
Net trapping ¹¹⁹	Capture and identification of interacting taxa	High level of taxonomic resolution	Invasive	Pollination	Individual
Pollen transport ¹²⁰	Transportation of pollen by pollinators	Effective interactions; high level of taxonomic resolution	Labour-intensive, invasive	Pollination	Individual
Microscopy ¹²³	Identification and documentation of interacting taxa using microscopy	Direct observation of interaction	Invasive; labour-intensive	Mycorrhiza, lichens	Aggregated groups (can be improved by DNA sequencing)
Faecal analysis ¹²⁴	Analysis of faeces content, based either on visual identification or on meta-barcoding	Direct observation, less invasive than gut contents (useful for large or protected animals)	Labour-intensive	Seed dispersal, trophic	Variable
Stable isotopes, fatty acids ¹²⁵	Estimate interactions based on element composition in the consumer	Assimilated 'effective' food; integrates consumption over longer periods; less sensitive to abiotic conditions	Quality depends on the number of tracers and on how distinct the signatures (origin of resources) are	Trophic, parasitism	Aggregated groups
Gut content ¹²⁶	Identification of prey (or remains of prey) directly in the stomachs of consumers	Ensures that an interaction occurs at the study location under certain environmental conditions; provides quantitative feeding information	Labour-intensive; high level of expertise; digestion complicates identification of resource species; biased towards hard-bodied organisms	Trophic	Variable
Meta-barcoding ¹²⁷	DNA identification of species involved in the interaction	Multiple types of observation (such as guts, excrement and pollen) provide a large amount of data	Selection of primers; potentially over-estimates the importance of accidental feedings (species swallowed with the target prey or the prey of the prey)	All	Species, conditioned to primer used

^aHigher levels of resolution are often used to determine interactions at lower levels of resolution (for instance, individual information to determine interaction between species or groups).

establishment of the links between them¹¹⁶. The relevance of a network type depends on the question addressed, and the type of node and link to be used are associated with different opportunities and limitations (Boxes 1 and 2). Different levels of node aggregation are usually associated with different fields of ecology: aggregated networks often rely on functional groups and are, therefore, related to functional ecology, whereas highly resolved networks are relevant to address questions related to community structure and their response to ecological drivers. Networks of potential interactions (representing the fundamental interaction niche) are particularly useful for understanding potential ecological redundancy or for long-term or large-scale studies, in which all potential interactions are likely to become realized at some point. Networks of realized interactions (representing the realized interaction niche) provide access to finer mechanisms to better understand the interplay between abiotic and biotic factors in determining ecological interactions.

Although resolved networks of realized interactions can be seen as finer representations of interactions occurring in communities, we do not call for their systematic use. Rather, we argue that the different levels of node aggregation and link information can all be valid depending on the question addressed. Understanding the differences between network approaches, along with their respective strengths and weaknesses, can enhance decisions about network methodology. A clear definition of the hypotheses underlying network construction – as well as the potential descriptors derived from it and how they link to tested hypotheses – would clarify the connection between data and questions. By defining the assumptions and advantages of different network types, and discussing which questions are best suited to which networks, we hope that this paper will facilitate progress on key issues in ecology.

Network comparisons are useful for drawing generalities about interaction structure across ecological systems. If networks were compiled in similar ways, these network comparisons would be straightforward. However, compiling networks derived using different approaches can be problematic because structural properties of networks can differ substantially depending on the method used to construct them¹¹⁷. We have argued here that a diverse range of network construction methods are valid, and we also appreciate efforts to compile and compare published networks. However, we recommend that network comparison efforts compare networks of similar node resolution and link information^{12,69}. Standardizing for network resolution would require using the most aggregated level common to all networks at the cost of a loss of information, whereas standardizing for link information can be done in either direction because models exist either to prune non-realized interactions from networks of potential interactions¹¹⁵ or to complement networks of realized interactions with potential non-realized interactions¹¹⁸.

Published online: 13 June 2025

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Acknowledgements

The authors are supported by the German Centre for Integrative Biodiversity Research (iDiv) and its synthesis centre (sDiv) Halle-Jena-Leipzig, funded by the German Research Foundation grant FZT 118.

Author contributions

All authors participated in the conceptualization of this study. B.G. wrote the first draft of the manuscript (with substantial contributions from J.H.). L.T. drew the figure. All authors contributed to the review and editing process.

Competing interests

The authors declare no competing interests.

Additional information

Peer review information *Nature Reviews Biodiversity* thanks Fredric Windsor and the other, anonymous, reviewers for their contribution to the peer review of this work.

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