Trends in Ecology & Evolution

Review

Using Network Theory to Understand and Predict Biological Invasions

Carol M. Frost,[1,2,*] Warwick J. Allen,[3] Franck Courchamp,[4] Jonathan M. Jeschke,[5,6,7] Wolf-Christian Saul,[5,6,7,8] and David A. Wardle[1,9]

Understanding and predicting biological invasions is challenging because of the complexity of many interacting players. A holistic approach is needed with the potential to simultaneously consider all relevant effects and effectors. Using networks to describe the relevant anthropogenic and ecological factors, from community-level to global scales, promises advances in understanding aspects of invasion from propagule pressure, through establishment, spread, and ecological impact of invaders. These insights could lead to development of new tools for prevention and management of invasions that are based on species' network characteristics and use of networks to predict the ecological effects of invaders. Here, we review the findings from network ecology that show the most promise for invasion biology and identify pressing needs for future research.

Scaling up to a Network Approach in Invasion Biology

Understanding and predicting biological invasions and their impacts is a huge challenge in ecology that will become more important as the homogenization of Earth's biota increases [1]. Invasion biology's ability to predict invasions and their impacts has been limited by the lack of theoretical frameworks that can incorporate and quantify the formidable ecological complexity of direct and indirect species interactions over multiple trophic levels [2]. Ecological networks are a framework for holistic consideration of whole sets of organisms (**nodes**) (see Glossary) (usually species, individuals, higher taxa, or guilds) and their ecological interactions (**links**) that make up natural communities. We are now gaining a burgeoning understanding of how ecological networks relate to the abiotic environment [3], anthropogenic influences [4], ecosystem **stability** [5], and ecosystem functioning [6,7]. Further, ecological network data collection and analytical approaches are developing rapidly, but although many network studies have considered invasive species the findings from network ecology with the greatest potential utility in invasion prevention or management have so far not been incorporated into invasion biology. Here, we aim to help focus future attention on areas likely to advance invasion biology.

Anthropogenic introductions of exotic species span a continuum from unsuccessful, through those that establish and spread, to a subset that inflict significant detrimental impacts on ecosystems, economic activity, and human wellbeing. Several definitions exist for invasive species, but here we consider an invasive species to be one that is introduced by humans outside of its natural distribution and that has since established and spread substantially [8,9]. Interspecific interactions are key to invasion processes, but their complexity renders simple food-chain models inadequate for studying introduced species [10]. Recent research has integrated networks into invasion biology, yet so far, their utility has been more explanatory than predictive. Challenges in understanding species invasions also stem from the complexity of anthropogenic factors, particularly transport patterns of species around the planet [11], and social interactions related to trade and environmental regulation [12]. Here, we focus mainly on how ecological network re-

[1]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Skogsmarksgränd, SE901 83 Umeå, Sweden
[2]Current address: Department of Renewable Resources, University of Alberta, 230D Earth Sciences Building, Edmonton, AB, Canada T6G 2E3
[3]The Bio-Protection Research Centre, Lincoln University, PO Box 84, Lincoln 7647, New Zealand
[4]Ecologie, Systématique, and Evolution, Univ Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, 91400, Orsay, France
[5]Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Müggelseedamm 310, 12587, Berlin, Germany
[6]Freie Universität Berlin, Department of Biology, Chemistry, Pharmacy, Institute of Biology, Königin-Luise-Str. 1-3, 14195 Berlin, Germany
[7]Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), Altensteinstr. 34, 14195 Berlin, Germany
[8]Centre for Invasion Biology (CIB), Department of Botany and Zoology & Department of Mathematical Sciences, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa
[9]Asian School of the Environment, Nanyang Technological University, 50 Nanyang Avenue, Singapore

*Correspondence: cmfrost@ualberta.ca (C.M. Frost).

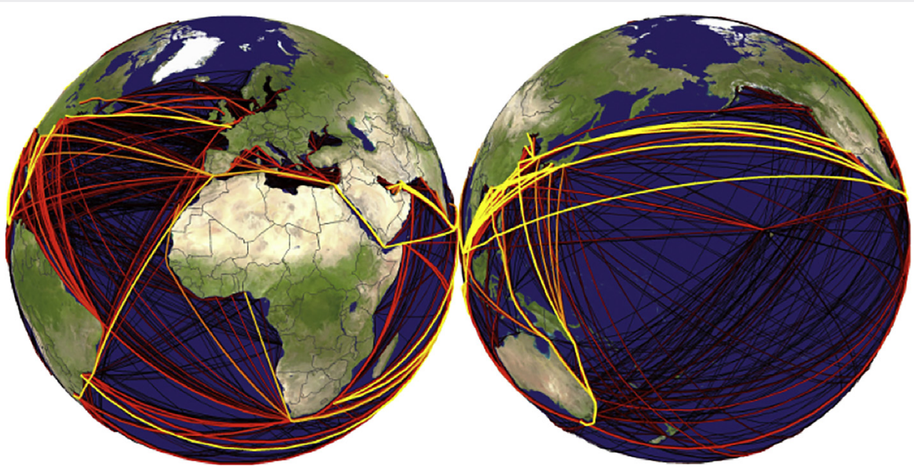
Box 1. The Importance of Anthropogenic Networks for Biological Invasions

Other than ecological networks, two types of network, both linked to anthropogenic activities, are relevant to biological invasions. First, transportation networks refer to a set of locations (nodes), and the connecting transit routes of goods and persons (links; Figure I). They are highly variable, often interlinked and exist from global to local scales (e.g., [94,95]). With the upsurge of global trade and tourism, and the development of various transportation vectors (including facilitating technologies), transportation networks are ever-increasing in size and complexity, and consequently the number of transported species has markedly increased through time [96].

Different transportation networks represent different pathways for biological invasions, and this will impact on which species are introduced [97]. Therefore, they affect: (i) which species with which traits are being moved across the globe, and (ii) which species are then transported more locally. Further, they affect the number of species that are being introduced (i.e., colonization pressure), and the number of introduced individuals and the frequency of introduction events (i.e., propagule pressure), both of which are of demonstrated importance for predicting biological invasions [98,99].

The second type of anthropogenic network includes several types of social network, which are formed by all actors (either individuals or organizations) involved in various aspects of introductions and their management. Adequate consideration of these social networks is key to the success of management programmes, regardless of the invasion stage that they address [12,100]. Network theory is rapidly developing in the social sciences, and is crucial for identifying influential entities, exploring network dynamics, and analysing their effects on output characteristics, such as the success of a conservation programme.

In a nutshell, the way humans transport goods and organisms greatly affects species composition of communities and which organisms interact where, when, and how, while social networks of managers, stakeholders, and decision-makers are key to successful management programmes. The analysis of anthropogenic networks should thus be an important tool in invasion science, especially in combination with ecological networks.



Trends in Ecology & Evolution

Figure I. Shipping Routes Form an Important Global Transportation Network Affecting Biological Invasions. Different colours represent different invasion probabilities (yellow: high; red: intermediate; black: low) based on traffic volume, distance between regions, travel time, and environmental similarity (see [95]; figure kindly provided by H. Seebens).

search can advance invasion biology, but we briefly highlight how network methods can also produce important advances in our understanding of human influences on species invasions (Box 1), and how information from these different network types may be integrated.

Networks inherently encompass a wealth of information. Not only the identities of nodes and interactions, but also patterns of ecological network structure are informative for understanding ecosystem stability and function in relation to invasions [5]. In order to give explicit examples of how ecological network research can inform invasion biology, we describe findings relating to

Glossary

Betweenness centrality: the proportion of the shortest paths linking any pair of species in the network that cross through the focal species.
Bipartite network: a network in which nodes fall into two distinct groups, often two trophic levels in the case of ecological networks.
Closeness centrality: the reciprocal of the sum of the shortest path lengths from the focal species to all other species in the network; that is, closeness centrality is a measure of how easily energy or perturbations could theoretically flow from the focal species to all other species in the network. The larger the value, the more central a species is.
Connectance: number of actual links divided by the number of possible links.
Degree: the number of links per node.
Generality: the number of prey taxa per consumer or interaction partners per mutualist.
Interaction asymmetry: in quantitative networks, interaction asymmetry is the difference in strength of the dependence of species *i* on species *j* and the dependence of species *j* on species *i*. The greater this difference, the higher the interaction asymmetry.
(In)vulnerability: the number of consumer taxa per prey.
Keystone species: species for which changes in their abundance have a higher than average effect on abundances of other species within the community.
Link: in ecological networks, links represent interactions between nodes, and may be directional (indicated by arrows).
Modularity: the occurrence of subsets of nodes that interact more frequently and more strongly among themselves than with other nodes in the network, so that the network appears to be composed of relatively distinct 'modules' or 'compartments' of interactions.
Nestedness: a pattern in which specialists interact with species that form well-defined subsets of the species that generalists also interact with, so that there is a core of generalist species interacting among themselves, and a tail of specialists interacting with the most generalist species.
Network hub: a network node with high centrality and high degree.
Network-level metrics: measures of network structure as a whole, that

network structural patterns. Network structure dynamically varies in space and time [13] but is usually measured empirically as a discrete 'snapshot'. Aggregation of these empirical snapshot networks over space and/or time into regional metawebs may allow more general characterization of those network properties that are likely to be important for understanding network invasion [13]. These metawebs can then form the basis of dynamic network models that can project community response to invasion over time. We give an illustrated explanation of the technical terms used in ecological network research in Box 2, and their definitions in the Glossary. Specifically, in this review, we discuss the most promising ways in which network theory can inform us on every key aspect of invasion: where potential invaders may come from, which exotic species are most likely to become invasive, which ecosystems are most invasible, and what an invader's likely ecological impacts will be (Figure 1, Key Figure). We link these separate research areas within a network context and explore the many ways in which an ecological network approach can advance invasion biology.

Invasiveness: Which Species Are Most Likely to Become Invasive?

Two central and intertwined elements of biological invasions are 'invasiveness', which is the ability of a species to invade, and 'invasibility' which is the degree to which a community resists versus facilitates invasion. At a local scale, invasion success should be influenced by an invader's species interactions. More specifically, an invader's success may be determined by its network characteristics, meaning the typical structure (static or dynamic) of its interactions with other species. An important question is whether there exists a set of **species-level network characteristics** that allow a new species to successfully invade across mutualistic and antagonistic networks.

Some commonly measured species-level network characteristics may be useful for predicting invasiveness. For example, invaders may gain an advantage through **interaction asymmetry**, where they interact weakly with interaction partners, but interaction partners interact strongly with the invader (e.g., [14]). Invaders with high **generality** (i.e., many interaction partners) can also experience increased establishment probability, performance, or spread in both mutualistic and antagonistic networks. This is because generalist invaders readily encounter suitable mutualists (generalist host hypothesis [15,16]) or hosts and/or prey (niche breadth invasion success hypothesis [17]), respectively. Likewise, **invulnerability** to higher trophic levels may facilitate invasion (enemy release hypothesis [18,19]), and as trophic cascades, intraguild predation, and other indirect interactions mediate the strength of enemy release [20], a network approach may be indispensable for understanding this mechanism for invasion success.

So far, there have been no direct experimental tests at the network scale of the importance of generality and invulnerability for invasion success. However, several comparative analyses of invaded and uninvaded networks have revealed that invasive mutualists are often highly generalist in both pollination networks ([14,21–24], but see [25]) and seed dispersal networks [26], although this may frequently be related to their high abundance [27,28]. Moreover, Romanuk *et al.* [29] manipulated invader generality and predation vulnerability in simulated dynamic antagonistic networks to show that generalist invaders that were invulnerable to predation were indeed more likely to be successful, a finding since supported by further theoretical studies [30,31]. Empirical evidence is more equivocal, with studies exploring correlations between dietary breadth and invasion success finding mixed results for mammals, birds, and fish [32–34]. Further, while the prediction that fewer connections to consumers (i.e., invulnerability) should benefit invaders is supported by the frequently observed release of invasive species from specialist natural enemies in their introduced range [18,19,35,36], it is inconsistent with invasive plants often suffering strong herbivory from native generalists ([37–39], but see [40]).

cannot describe network roles of individual species (**species-level network characteristics**) but describe the entire structure. Examples include nestedness, modularity, and connectance.
Network size: the number of nodes within a network.
Node: in ecological networks, nodes are points connected by links, and usually represent species, but may alternatively represent individuals, populations, genotypes, groups of functionally similar species, or abiotic resources.
Normalized degree: the number of interactions per species (**degree**) divided by the number of possible interaction partners. Normalization controls for differences in network size when comparing networks.
Path length: the number of links between any pair of nodes.
Peripheral node: a node with low centrality, and often low degree.
Quantitative network: a network in which links are weighted, making interaction strength explicit. For example, flower visitor frequency can be used as a measure of interaction strength in plant-pollinator networks.
Species-level network characteristics: the typical structure of a species' interactions within a network. This can include a species' trophic level, degree, generality, vulnerability, centrality, contribution to nestedness, whether it acts as a network hub or a peripheral species, and whether it acts as a module connector.
Stability: the capacity to resist change or recover from change. Studies relating network structure to ecological stability have used many different measures of stability (Table S1).
Total system throughput (TST): the sum of all flows in an ecosystem, whether calculated as biomass changes or energy flows.
Trophic position: a species' level in the 'food chain'; that is, a species may be a basal autotroph or a primary, secondary, or tertiary (or higher level) consumer.

Box 2. Describing Ecological Interaction Networks

Ecological interaction networks are representations of the interactions that occur among species. They can depict antagonistic (trophic) or mutualistic interactions that occur between species or groups of species and can be used as 'maps' of how energy or resources move through a community. To describe their structure, various metrics can be used (Figure I).

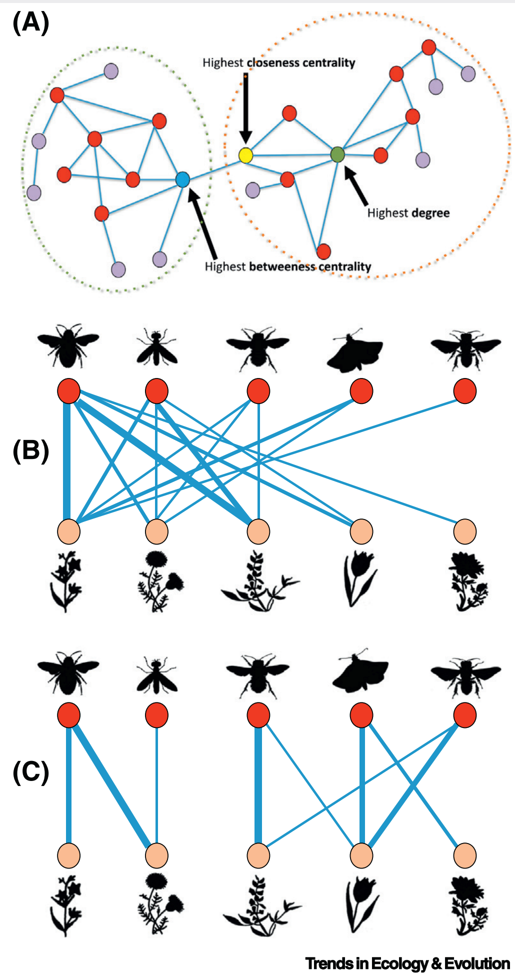


Figure I. Ecological Networks Can Be Visually Depicted In Various Ways, Which Can Give Insight Into Species Importance Within The Network and Network Stability And Function. (A) In this network, coloured circles (nodes) represent species, and lines connecting two species (links) represent ecological interactions between those species. Species in networks may be **peripheral** (purple circles), meaning that they are not connected to many species, and a disturbance within the network would take a long time to reach them. Other species may be central and act as 'network hubs' (blue, yellow, and green circles) that are connected to many species and are likely to be impacted by any network disturbance due to their proximity in **path length** to most other species. Several different 'species-level network characteristics' can be described relating to centrality and connectedness. In this network the yellow species has the highest 'closeness centrality' (reciprocal of the sum of the shortest path lengths from the focal species to all other species in the network). The blue species has the highest 'betweenness centrality' (proportion of the shortest paths linking any pair of species that cross through a focal species). The green species has the highest **degree** (number of interaction partners). **Network-level metrics** can describe whole-network architectural features. This network exhibits high 'modularity', such that the interactions circled by the green dotted line form a separate module from the interactions circled by the orange dotted line. That is, the species within each dotted circle interact much more with each other than with species in the other circle. (B,C) These panels depict **bipartite networks**, in this case networks that consist of two trophic levels, with peach circles representing plant species, and red circles representing pollinator species. These are **quantitative networks** (unlike in A), because interaction strength is made explicit by differing line width of links. The network in (B) exhibits 'nestedness' (specialists interact with species that form well-defined subsets of the species that generalists also interact with) but not modularity, while the network in (C) exhibits modularity but not nestedness (though networks can be both modular and nested). The network in (B) also has higher 'connectance' than that in (C).

Key Figure

A Network Framework Can Be Used for Predicting and Informing on Different Aspects of Biological Invasions at Each of the Various Stages of Invasion, from Anthropogenic Transportation and Introduction of Propagules, through Propagule Establishment, and to Spread and Ultimately Impact

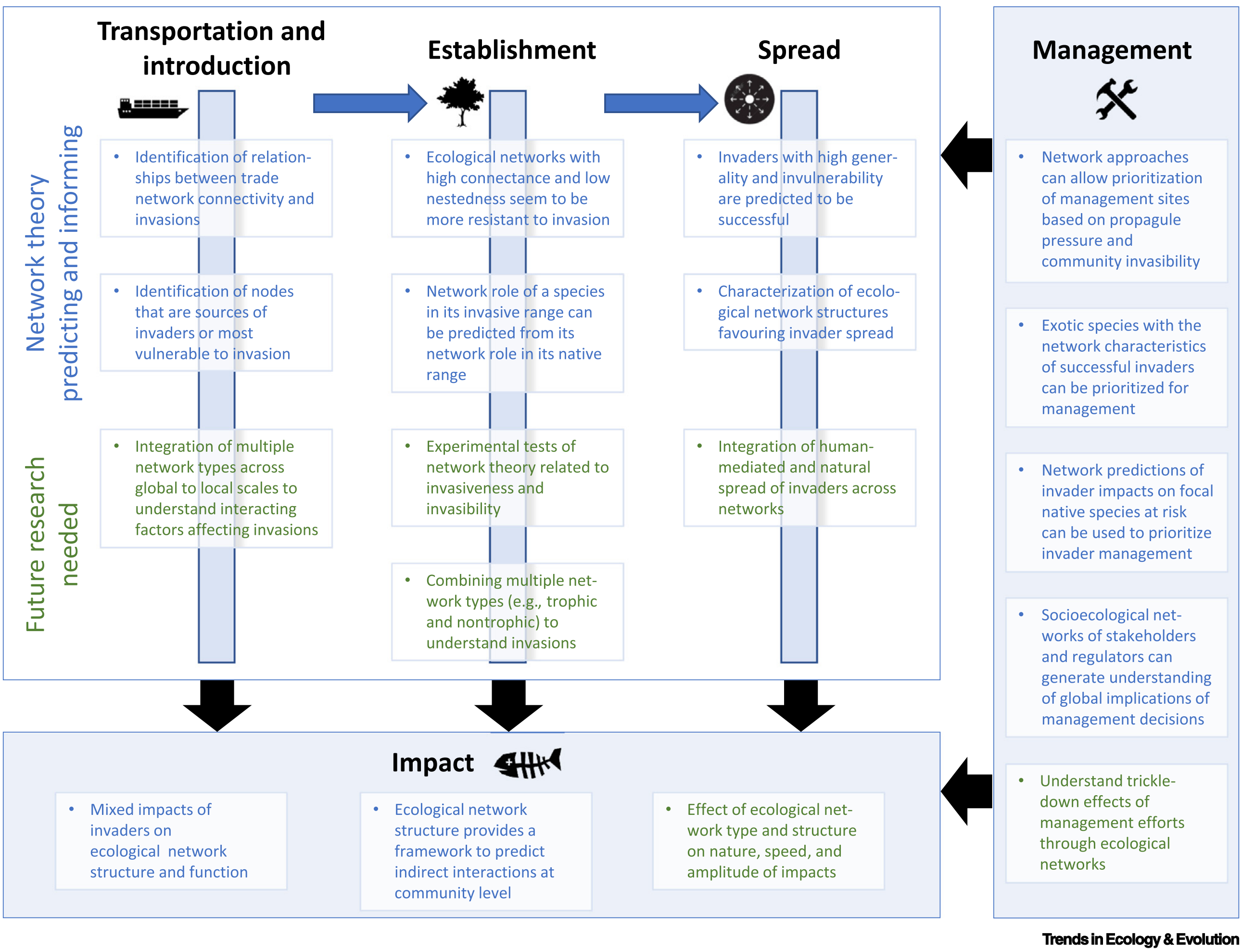


Figure 1. Network approaches can also inform predictions about ecological impact and management approaches at all stages. Blue text describes ways that networks can be used to understand and predict invasions. Green text describes future research necessary in each area.

Other species-level invader network characteristics may also be important in predicting invasion success, but little is currently known about their role in understanding invasion success. For example, the high **betweenness centrality** and **closeness centrality** observed for some network invaders suggests that invasive species often act as **network hubs** by mediating a large proportion of connections within and between network compartments [9,15,16,41]. One study that compared 40 paired invaded and uninvaded plant-pollinator networks showed that invasive plants attracted new generalists to the network and increased **connectance** both within and between network modules [42]. Moreover, because generalist species may be more attractive to newly introduced mutualists in some networks [43], invasive species that act as network hubs could even promote invasional meltdown (i.e., mutual facilitation of multiple invasive species; [19]) via increased network connectivity.

Importantly, a species' abundance can influence its network characteristics, with more abundant species often being more generalist, and with changes in abundance shifting the strength of a species' interactions with other species. That is, abundant species interact more, and with more species, simply because they encounter more species [28]. This has important implications for the invasion of ecological networks, because it means that invader network characteristics will be dynamic over the course of invasion. For example, an invader entering a community will begin at low abundance and interact with few species, even if it has the potential to interact with many. As its abundance increases, it will interact with an increasing number of species, thus becoming more general and central from a network perspective [14]. Combining findings from research on typical network characteristics of invaders (as assessed from empirical metawebs) with research on how network characteristics shift with species abundance (which could be assessed empirically using 'snapshot' networks sampled over the course of an invasion) is a promising avenue for understanding how non-native species become 'invasive', and how intrinsic species interaction characteristics combine with neutral processes to determine invasion success.

Invasibility: Which Communities Have the Greatest Invasion Resistance?

Given that ecological interaction networks vary greatly among ecosystems, habitats, or communities [44,45], understanding how network structure is related to niche space available for invasion, and ultimately invasibility, may allow us to identify communities that are resistant or vulnerable. For antagonistic networks, the prediction that high connectance should simultaneously confer stronger biotic resistance to higher trophic levels and provide fewer available niches for invaders has mixed support from theoretical studies [29–31,46,47]. These varying results suggest that the relationship between network connectance and invasibility is complex and may vary with other factors, such as species richness (diversity-invasibility hypothesis, [19,31]), the trophic level being invaded [29,44,48], and the relative strength of interspecific interactions and intraspecific density dependence [49].

Meanwhile, few theoretical studies have examined the role of network **nestedness** and **modularity** in resisting or promoting invasions. Food web models suggest that highly nested antagonistic networks are more susceptible to invasion, possibly due to high interaction asymmetry [47]. That is, extreme generalists should interact weakly with many specialists, whereas extreme specialists should depend strongly on generalists. This interaction asymmetry may lead to opportunities for specialist invaders that are more efficient than generalist native species at exploiting resident specialists [47]. In contrast, food web models applied to mutualistic networks have found a weak negative relationship of invasibility with nestedness [46]. Finally, both mutualistic and antagonistic networks with higher modularity are predicted to be highly susceptible to invasions ([46,47], but see [31]), particularly by species with high plasticity or complex life cycles that can invade across more than one network compartment in space or time.

One possible conclusion from these mixed results is that context dependency is rife and satisfactory prediction lacking. A recent study has argued that, to overcome this, future approaches seeking to investigate invasibility should move past static and dynamic networks to adopt complex adaptive networks [50]. More specifically, the authors proposed a theoretical framework based on community stability theory [51] with which to assess the invasibility and biotic resistance of a recipient network. This theoretical model represents exciting progress in developing an explicit theoretical framework with which to test hypotheses around invasions into ecological networks. However, empirical tests of network invasion hypotheses are scarce, particularly manipulative experiments.

In one of the few empirical studies to test whether higher antagonistic network connectance provides stronger biotic resistance, no effect of host–parasitoid network structure was found on attack rates of the experimentally introduced firethorn leaf miner (*Phyllonorycter leucographella*) on farms in England [52]. Meanwhile, Smith-Ramesh *et al*. [44] used a synthetic global approach that combined connectance values of published antagonistic networks with corresponding estimates of invasive species richness to show that greater connectance was associated with lower invasive species richness and higher biotic resistance. However, higher connectance could be due to effects of highly generalist invasive species on network structure rather than a driver of their invasion, which highlights the need for manipulative experiments to confirm causation. To date, the only study to experimentally test how network structure influences invasion success revealed that the pathogen *Ralstonia solanacearum* was best able to invade bacterial resource competition networks with high nestedness and low connectance [53], in line with theoretical model predictions [29,30,46–48].

How Will an Invasive Species Interact with Native Species?

Recent ecological network studies suggest that certain species-level network characteristics of invasive species may be predictable in their new ranges. For example, Emer *et al*. [54] found for 17 nonnative species (12 plants and five pollinators) for which plant-pollinator network data were available from both their native and invasive ranges, that two metrics describing a species' network characteristics (i.e., its **normalized degree** and closeness centrality) significantly predicted its invasive range value. This means that a plant that interacts with many pollinators in its native range will also do so in its invasive range, and a plant that is central in a network in its native range will also be central in its invasive range [54]. If a species is central in a network, then it interacts with other highly connected species, and thus any direct effects of this invasion on other species (like drastic abundance changes) will spread rapidly throughout the network. Although it is likely that the extent to which an invader has attained its maximum degree, and centrality in its invasive or native range is proportional to its relative abundance within its trophic level [28], the results of this study suggest that species-level network characteristics are inherent to a species, rather than its resident network. Thus, we may expect species' network characteristics to be conserved in any part of the world, should it achieve high enough local abundance.

As a second example, recent work by Kéfi *et al.* [55] suggests that nontrophic species interactions, which may be more than twice as abundant as trophic interactions, have somewhat predictable relationships with species traits and trophic level. If these relationships were relatively invariant across systems (which is presently unknown), then knowing only a potential invader's **trophic position** and vagility would sufficiently inform us on two issues. First, it would enable insights about whether the invader will primarily engage in trophic or nontrophic interactions (which could be positive or negative). Specifically, sessile (usually basal) species could be involved in nontrophic interactions (e.g., competition for space, environmental modifications) that are stronger than their trophic interactions. Conversely, vagile species may be involved in more and stronger trophic interactions [55]. Second, knowing an invader's vagility would enable prediction about whether the invader's nontrophic interactions are most likely to be positive or negative. Again, sessile species would mostly be subjected to negative nontrophic effects from other sessile species (e.g., resource competition), and vagile species would receive mostly positive nontrophic effects from basal species (e.g., habitat provisioning) [55]. Although research on these topics is currently limited, further

Table 1. Empirical Evidence for Effects of Invasive Species on Different Structural Properties, Persistence, and Function of Ecological Networks[a]

Network structural property	Change in network structural property caused by invasive species		
	Increase	Decrease	No change
Connectance	Plant-pollinator [22] Plant-frugivore [7][b] Galler-inquiline[c] [82] Marine food web [6]	Plant-frugivore [7][b]	Plant-pollinator [14] Plant-pollinator [23] Plant-pollinator [83] Plant-pollinator [84] Plant-pollinator[d] [85] Plant-seed disperser [86] Plant-galler[c] [82] Galler-parasitoid[c][82] Host-parasitoid [87][e]
Link density			Plant-pollinator [83]
Modularity	Plant-pollinator [84]	Plant-fungal [88]	
Nestedness	Plant-pollinator [21] Plant-pollinator [89] Plant-frugivore [7][b]	Plant-pollinator [84]	Plant-pollinator [24] Plant-pollinator [83] Plant-seed disperser [86] Plant-ant [90] Plant-galler[c] [82] Galler-inquiline[c] [82] Galler-parasitoid[c] [82] Soil food web [91] Plant-beetle [92]
Interaction strength asymmetry	Plant-pollinator [14]		
Mean shortest path length		Marine food web [6]	Plant-pollinator [83]
Interaction evenness	Galler-inquiline[c] [82] Marine food web [6]	Plant-pollinator [89]	Plant-pollinator[d] [85] Plant-seed disperser [86] Plant-galler[c] [82] Galler-parasitoid[c] [82] Host-parasitoid [87][e]
Network stability			
Robustness	Plant-frugivore [7][b]		Plant-pollinator [84] Plant-seed disperser [86]
Network function			
Fruit set	Plant-pollinator[d] [85]		Plant-pollinator[d] [85]
Frugivory or seed dispersal	Plant-frugivore [7][b]		
Total system throughput (TST; see Glossary)	Marine food web [6]	Lake food web [93]	
Ecosystem flow organization (AMI)	Lake food web [93]		Marine food web [6]
Trophic efficiency		Marine food web [6] Lake food web [93]	

[a]The number of invasive plants or pollinator species considered in each network vary from one to many. Underlining denotes the functional group of the invasive species in the study. If no functional group is underlined, the invasive species was present in the system but not within one of the functional groups that described the food web.
[b]Connectance varied quadratically with proportion of interactions accounted for by exotic birds [7].
[c]Galler-inquiline, plant-galler, and galler-parasitoid interaction evenness were tested along a gradient of plant invasion by one highly invasive species, *Acacia longifolia* (though other invasive plants also occurred at the sites).
[d]Networks included both invasive plants and pollinators, but responding variables were only tested in relation to plant invasion.
[e]Networks included both invasive hosts and parasitoids, but response variables were only tested in relation to invasion history of one host species, that is, the gypsy moth (*Lymantria dispar*).

work on predicting species-level network characteristics and nontrophic interactions has the potential to increase predictive accuracy to a level meaningful for applied invasive species management.

Box 3. How Do Invaders Affect Ecological Networks?

Invasive species may affect network structure [22,88], stability [7], or functioning [6,93] directly, through interactions with co-occurring species. For example, the invasive ice plant *Capobrotus affine acinaciformis* incorporates into and reduces the modularity of a shrubland plant-pollinator network in Cap de Creus, Spain (Figure I; [24]). This likely increases the rate at which effects of perturbation (e.g., an introduced pathogen) travel through the network, but also makes the network more resilient against secondary extinctions [24]. Invaders may also indirectly affect ecological network structure and functioning by causing environmental modifications. That is, the invader does not interact directly with species in the affected module, but the interaction structure of that module changes after invasion as a consequence of the changed environment. For example, invasion of New Zealand offshore islands by rats, and their predation on seabirds, has reduced seabird nesting on invaded islands, thus changing soil nitrogen levels, which has, in turn, indirectly impacted soil arthropod food webs (Figure II; [91]).

However, while many examples exist of invaders significantly changing ecological network structure and function, is this the usual case? To date, studies have mainly considered plant-pollinator networks, and few have investigated invader impacts on network function (Table 1). However, these studies suggest that, although invaders in some cases dramatically alter ecological network structure (e.g., Figure I), in most cases they do not. To date, too few studies have looked at the effects of invaders on network function to tell if general or recurrent patterns exist.

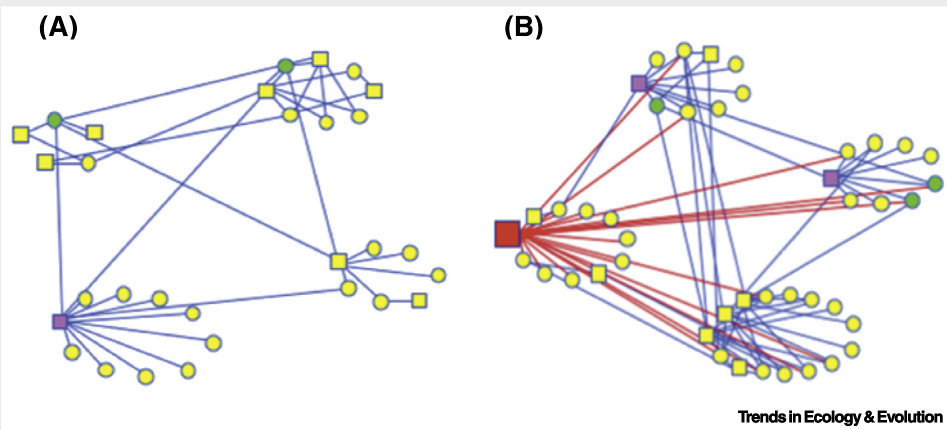


Figure I. Plant-Pollinator Networks Showing Modular Structure Representing Mediterranean Shrubland Communities from Two Locations in Cap de Creus, Spain. Plants represented by squares and pollinators by circles. (A) Uninvaded. (B) Invaded by an alien plant species (*Carpobrotus affine acinaciformis*, red box) which becomes a central hub in the network connecting the disparate compartments through the interactions that it forms (red lines). Figure reproduced, with permission, from [24].

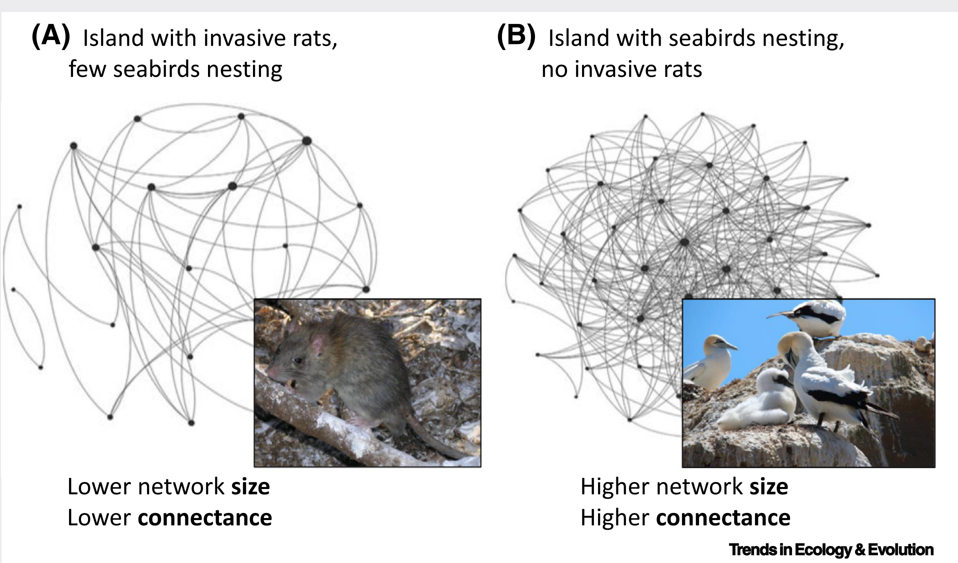


Figure II. Predation of Seabirds by Invasive Rats on New Zealand Offshore Islands. (A) Predation of seabirds by invasive rats on New Zealand offshore islands has severely reduced seabird nesting which has, in turn, drastically reduced leaf litter invertebrate **network size** (number of species) and connectance (number of the possible links between nodes that are realised), when compared with (B) uninvaded islands that still have high densities of nesting seabirds [91]. (Figure reproduced, with permission, from [91]).

What Are the Impacts of Invasive Species?

Ecological network theory currently provides the tools for helping to predict invasive species' ecological impacts on three levels: the invader's impact on individual native species success (i.e., biomass production, fitness, and population size), network stability, and ecosystem functioning.

When invasive species arrive in new locations, it is common to already have some information about their potential direct trophic interactions (e.g., from species traits data [56], their interactions in their native range [54,57], their invasions elsewhere, or interactions of related species [58]). Their indirect interactions, including resource competition [59], apparent competition [60], and trophic cascades [20], are often much harder to predict but can play an important role in the invasion process [61]. Quantitative ecological networks can be thought of as diagrams of all the likely indirect interactions between the species in the network. As such, they have considerable potential for predicting how an invader might change all or part of the indirect effects that species exert on one another.

The extent to which predictions of indirect interactions based on quantitative food-web data are actually realised at the community level has been best tested for apparent competition and demonstrated to be substantial [62–64]. For example, a large-scale field experiment showed that for host-parasitoid networks of forest lepidopteran larvae, 31% of the variation in host abundance could be predicted based on apparent competitive relationships calculated from quantitative food-web data at a previous time step [63]. Thus, for a system in which an exotic herbivore has recently arrived, quantitative food-web data could allow predictions about how populations for all other herbivores would change based on shared enemies if its population size began to increase. Pairwise calculations of the potential for density-mediated indirect effects between species have also been made for quantitative mutualistic networks [65], but the extent to which these effects are realised at the community level in real systems remains to be tested. Further testing of to what extent predicted indirect effects actually do occur across several main indirect interaction types would be important for improving predictive ability.

The impact of invasive species on stability of an entire community (i.e., broadly defined as its capacity to resist change or recover from change) would also be very desirable to predict. A large body of theoretical work has sought to link network structure to community stability [5,22, 66–76] (see also Tables S1 and S2 in the supplemental information online). Interestingly, this work has found that network properties often have opposing effects on the stability of antagonistic and mutualistic networks [74,77]. For example, higher modularity stabilizes antagonistic networks but destabilizes mutualistic networks, whereas higher nestedness stabilizes mutualistic networks but destabilizes antagonistic networks [77]. Moreover, many studies have sought to predict the effects of invasive species on network structure (Table 1), which, when combined with information on how the structural properties relate to community stability, could provide insights into potential impacts of the invader on stability. Although some studies have found that invasive species have increased or decreased network structural properties that link to community stability (Box 3), the majority have not (Table 1).

To date ecological networks have increased our understanding of ecosystem functioning through explicit mapping of functional redundancies and complementarities between species in terms of their interactions [78]. Such studies have shown in which situations species loss is most likely to lead to secondary extinctions, and thus changes in ecosystem functioning, for functions such as pollination [79] and seed dispersal [7]. The same framework could be used to predict the effects of invasions on ecosystem functioning.

In considering ecosystem functions that rely on species abundance, such as primary productivity or natural enemy control of pests, network methods can inform us of likely functional changes following invasion, based on how invader effects on other species' abundances transmit throughout the network. For example, network methods can be used to predict which '**keystone**' species in a community are of particular importance for network function or stability [80,81]. Although these methods need empirical verification, they potentially allow analysis of network structure to determine how influential an invader has become in a network. This would be useful in predicting impacts of management efforts aimed at removing the invader on the rest of the community.

Concluding Remarks and Future Directions

Invasion biology is a complex field due to the many context dependencies among a multitude of factors that affect all aspects of the invasion process from invader propagule pressure, through establishment, population growth, spread, and ecological impact. As we show here, findings to date have suggested that invasive species often do not greatly alter ecological network structure or stability (Table 1, Table S1). However, invasive species still operate as important players within ecological networks, through taking up central, highly connected positions once they have reached high abundance within an invaded system. This finding suggests that invasion biology is likely to be advanced through more focus on species-level network characteristics rather than specifically on **network-level metrics** (see Outstanding Questions). In particular, there is a need for future research that systematically investigates which species-level network characteristics are inherent species traits, which confer invasiveness, and how change in a species' abundance predicts change in its network characteristics. A further promising avenue would involve the use of ecological networks to predict the indirect effects of invaders. The potential of this approach to be predictive in complex communities has been shown for apparent competition, though further work is required to test the extent to which this is repeatable, or applicable to other indirect interaction types or effects. Network methods of predicting impacts of invaders on other species could also be more broadly applied to predicting the success and ecological effects of controlled releases of exotic species (e.g., biological control agents, managed pollinators, substituted taxa), reintroduction of native species into their previous ranges, or even de-extinction.

Finally, just as an ecological network approach is a framework for bringing together a large amount of ecological information, multilayer networks could be used in the future to organize and synthesize information from the many types of networks relevant to understanding biological invasions. For example, within a vision of future invasion prevention, spatial transport networks could feed information on propagule pressure (for example, differing realistic initial abundances of invaders) into ecological network models that contain an algorithm predicting whether the propagules will establish, based on their species-level network characteristics. Those invaders that establish will increase in abundance at a certain rate, which will, in turn, change their network characteristics, and thereby alter their predicted effects on the abundances of other species, as well as on functions such as total primary productivity, herbivory, and pest regulation. At the highest level of the model, human regulatory networks (spatial or political) could be overlaid to test the effects of proposed management actions, and the extent to which this would, in turn, ripple through all stages of invasion and ecological impact.

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Outstanding Questions

How do species-level and network-level network characteristics interact with other factors, such as species richness, phylogenetic and functional traits, interaction type, and demography to influence the outcome of invasions? This could be addressed by manipulating empirical networks and systematically testing their resistance and response to diverse invaders, using a range of network metrics.

How do invader species-level network characteristics change throughout the course of invasion, and is this related to the invader's change in abundance? This could be studied by analysing patterns from empirical networks measured along an invasion gradient or resampled over the course of invasion, or by performing simulations of changes in invader abundance in theoretical networks.

Do an invader's species-level network characteristics in its native range typically remain unchanged in its invasive range? This could be studied by sampling invasive species' interaction networks in their native and invasive ranges.

Can network data be used to generate accurate predictions of future species abundance for all species within a community following food-web invasion, or following invader changes in abundance? A generalized food-web model could be used. For more accurate system-specific predictions, indices of potential for indirect effects based on network structure could be tested empirically.

How does invasion of a network change functional complementarity and redundancy within the network? Does this depend on the network's structural properties, such as nestedness and modularity, and what are the consequences for ecosystem functioning? This could be addressed using simulation models that change invader abundance and network levels of nestedness, modularity, or other metrics. It could be tested empirically by resampling interaction networks over the course of an invasion and comparing invader abundance, network structure, and ecosystem function at several time steps.

Supplemental Information

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References

1. Ricciardi, A. *et al.* (2017) Invasion science: a horizon scan of emerging challenges and opportunities. *Trends Ecol. Evol.* 32, 464–474
2. Courchamp, F. *et al.* (2017) Invasion biology: specific problems and possible solutions. *Trends Ecol. Evol.* 32, 13–22
3. Tylianakis, J.M. and Morris, R.J. (2017) Ecological networks across environmental gradients. *Annu. Rev. Ecol. Evol. Syst.* 48, 25–48
4. Peralta, G. *et al.* (2017) Non-random food-web assembly at habitat edges increases connectivity and functional redundancy. *Ecology* 98, 995–1005
5. Bastolla, U. *et al.* (2009) The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458, 1018–1020
6. Baird, D. *et al.* (2012) Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. *Mar. Ecol. Prog. Ser.* 462, 143–162
7. García, D. *et al.* (2014) Exotic birds increase generalization and compensate for native bird decline in plant – frugivore assemblages. *J. Anim. Ecol.* 83, 1441–1450
8. Blackburn, T.M. *et al.* (2011) A proposed unified framework for biological invasions. *Trends Ecol. Evol.* 26, 333–339
9. Richardson, D.M. *et al.* (2008) Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6, 93–107
10. Strong, D.R. (1997) Fear no weevil? *Science* 277, 1058–1059
11. Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *J. Appl. Ecol.* 46, 10–18
12. Lubell, M. *et al.* (2017) Network governance for invasive species management. *Conserv. Lett.* 10, 699–707
13. Poisot, T. *et al.* (2012) The dissimilarity of species interaction networks. *Ecol. Lett.* 15, 1353–1361
14. Aizen, M.A. *et al.* (2008) Invasive mutualists erode native pollination webs. *PLoS Biol.* 6, e31
15. Birnbaum, C. *et al.* (2012) Mutualisms are not constraining cross-continental invasion success of *Acacia* species within Australia. *Divers. Distrib.* 18, 962–976
16. Klock, M.M. *et al.* (2015) Host promiscuity in symbiont associations can influence exotic legume establishment and colonization of novel ranges. *Divers. Distrib.* 21, 1193–1203
17. Vasquez, D.P. (2006) Exploring the relationship between niche breadth and invasion success. In *Conceptual Ecology and Invasion Biology: Reciprocal Approaches to Nature* (Cadotte, M., *et al.*, eds), pp. 317–332, Springer
18. Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17, 164–170
19. Jeschke, J.M. and Heger, T. (2018) *Invasion Biology: Hypotheses and Evidence*, CABI
20. Allen, W.J. *et al.* (2015) Multitrophic enemy escape of invasive *Phragmites australis* and its introduced herbivores in North America. *Biol. Invasions* 17, 3419–3432
21. Bartomeus, I. *et al.* (2008) Contrasting effects of invasive plants in plant-pollinator networks. *Oecologia* 155, 761–770
22. Valdovinos, F.S. *et al.* (2009) Structure and dynamics of pollination networks: the role of alien plants. *Oikos* 118, 1190–1200
23. Vilà, M. *et al.* (2009) Invasive plant integration into native plant-pollinator networks across Europe. *Proc. R. Soc. B* 276, 3887–3893
24. Albrecht, M. *et al.* (2014) Consequences of plant invasions on compartmentalization and species' roles in plant – pollinator networks. *Proc. R. Soc. B* 281, 20140773
25. Stouffer, D.B. *et al.* (2014) How exotic plants integrate into pollination networks. *J. Ecol.* 102, 1442–1450
26. Heleno, R.H. *et al.* (2013) Integration of exotic seeds into an Azorean seed dispersal network. *Biol. Invasions* 15, 1143–1154
27. Dormann, C.F. *et al.* (2017) Identifying causes of patterns in ecological networks: opportunities and limitations. *Annu. Rev. Ecol. Syst.* 48, 559–584
28. Fort, H. *et al.* (2016) Abundance and generalisation in mutualistic networks: solving the chicken-and-egg dilemma. *Ecol. Lett.* 19, 4–11
29. Romanuk, T.N. *et al.* (2009) Predicting invasion success in complex ecological networks. *Philos. Trans. R. Soc. B Biol. Sci.* 364, 1743–1754
30. Galiana, N. *et al.* (2014) Invasions cause biodiversity loss and community simplification in vertebrate food webs. *Oikos* 123, 721–728
31. Lurgi, M. *et al.* (2014) Network complexity and species traits mediate the effects of biological invasions on dynamic food webs. *Front. Ecol. Evol.* 2, 1–11
32. Cassey, P. *et al.* (2004) Global patterns of introduction effort and establishment success in birds. *Proc. R. Soc. B Biol. Sci.* 271, 405–408
33. Jeschke, J.M. and Strayer, D.L. (2006) Determinants of vertebrate invasion success in Europe and North America. *Glob. Chang. Biol.* 12, 1608–1619
34. Comte, L. *et al.* (2017) Global test of Eltonian niche conservatism of nonnative freshwater fish species between their native and introduced ranges. *Ecography* 40, 384–392
35. Colautti, R.I. *et al.* (2004) Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.* 7, 721–733
36. Liu, H. and Stiling, P. (2006) Testing the enemy release hypothesis: a review and meta-analysis. *Biol. Invasions* 8, 1535–1545
37. Levine, J.M. *et al.* (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* 7, 975–989
38. Parker, J.D. and Hay, M.E. (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecol. Lett.* 8, 959–967
39. Agrawal, A.A. and Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol. Lett.* 6, 712–715
40. Agrawal, A.A. *et al.* (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology* 86, 2979–2989
41. Hoffmann, B.D. and Courchamp, F. (2016) Biological invasions and natural colonisations are different – the need for invasion science. *NeoBiota* 29, 1–14
42. Richardson, D.M. *et al.* (2011) A compendium of essential concepts and terminology in invasion ecology. In *Fifty Years of Invasion Ecology: The Legacy of Charles Elton* (Richardson, D.M., ed.), pp. 409–420, Blackwell Publishing Ltd
43. Olesen, J.M. *et al.* (2008) Temporal dynamics in a pollination network. *Ecology* 89, 1573–1582
44. Smith-Ramesh, L.M. *et al.* (2017) Global synthesis suggests that food web connectance correlates to invasion resistance. *Glob. Chang. Biol.* 23, 465–473
45. Fabian, Y. *et al.* (2013) The importance of landscape and spatial structure for hymenopteran-based food webs in an agro-ecosystem. *J. Anim. Ecol.* 82, 1203–1214
46. Minoarivelo, H.O. and Hui, C. (2016) Invading a mutualistic network: to be or not to be similar. *Ecol. Evol.* 6, 4981–4996
47. Hui, C. *et al.* (2016) Defining invasiveness and invasibility in ecological networks. *Biol. Invasions* 18, 971–983
48. Baiser, B. *et al.* (2010) Connectance determines invasion success via trophic interactions in model food webs. *Oikos* 119, 1970–1976
49. Barabás, G. *et al.* (2017) Self-regulation and the stability of large ecological networks. *Nat. Ecol. Evol.* 1, 1870–1875
50. Hui, C. and Richardson, D.M. (2018) How to invade an ecological network. *Trends Ecol. Evol.* 34, 121–131
51. May, R.M. (2001) *Stability and Complexity in Model Ecosystems*, Princeton University Press

52. MacFadyen, S. *et al.* (2009) Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecol. Lett.* 12, 229–238
53. Wei, Z. *et al.* (2015) Trophic network architecture of root-associated bacterial communities determines pathogen invasion and plant health. *Nat. Commun.* 6, 8413
54. Emer, C. *et al.* (2016) Species roles in plant-pollinator communities are conserved across native and alien ranges. *Divers. Distrib.* 22, 841–852
55. Kéfi, S. *et al.* (2015) Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* 96, 291–303
56. Bartomeus, I. *et al.* (2016) A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.* 30, 1894–1903
57. Penk, M. *et al.* (2017) A trophic interaction framework for identifying the invasive capacity of novel organisms. *Methods Ecol. Evol.* 8, 1786–1794
58. Stouffer, D.B. *et al.* (2012) Evolutionary conservation of species' roles in food webs. *Science* 335, 1489–1492
59. Gioria, M. and Osborne, B.A. (2014) Resource competition in plant invasions: emerging patterns and research needs. *Front. Plant Sci.* 5, 1–21
60. Bhattarai, G.P. *et al.* (2017) Geographic variation in apparent competition between native and invasive *Phragmites australis*. *Ecology* 98, 349–358
61. White, E.M. *et al.* (2006) Biotic indirect effects: a neglected concept in invasion biology. *Divers. Distrib.* 12, 443–455
62. Morris, R.J. *et al.* (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature* 428, 310–313
63. Frost, C.M. *et al.* (2016) Apparent competition drives community-wide parasitism rates and changes in host abundance across ecosystem boundaries. *Nat. Commun.* 7, 12644
64. Carvalheiro, L.G. *et al.* (2008) Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecol. Lett.* 11, 690–700
65. Carvalheiro, L.G. *et al.* (2014) The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness. *Ecol. Lett.* 17, 1389–1399
66. Okuyama, T. and Holland, J.N. (2008) Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.* 11, 208–216
67. Burgos, E. *et al.* (2007) Why nestedness in mutualistic networks? *J. Theor. Biol.* 249, 307–313
68. Bascompte, J. *et al.* (2006) Asymetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433
69. Dunne, J.A. *et al.* (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567
70. Dunne, J.A. *et al.* (2004) Network structure and robustness of marine food webs. *Mar. Ecol. Prog. Ser.* 273, 291–302
71. McCann, K. *et al.* (1998) Weak trophic interactions and the balance of nature. *Nature* 395, 794–798
72. Berlow, E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334
73. de Ruiter, P.C. *et al.* (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269, 1257–1260
74. Tan, J.P.L. (2016) Symmetric and asymmetric tendencies in stable complex systems. *Sci. Rep.* 6, 31762
75. Allesina, S. and Pascual, M. (2008) Network structure, predator–prey modules, and stability in large food webs. *Theor. Ecol.* 1, 55–64
76. James, A. *et al.* (2012) Disentangling nestedness from models of ecological complexity. *Nature* 487, 227–230
77. Thébault, E. and Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329, 853–856
78. Schleuning, M. *et al.* (2015) Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. *Ecography* 38, 380–392
79. Kaiser-Bunbury, C.N. *et al.* (2017) Ecosystem restoration strengthens pollination network resilience and function. *Nature* 542, 223–227
80. Cagua, E.F. *et al.* (2019) Keystoneness, centrality, and the structural controllability of ecological networks. *J. Ecol.* https://doi.org/10.1111/1365-2745.13147
81. Harvey, E. *et al.* (2017) Bridging ecology and conservation: from ecological networks to ecosystem function. *J. Appl. Ecol.* 54, 371–379
82. López-Núñez, F.A. *et al.* (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. *Ecology* 98, 782–293
83. Padrón, B. *et al.* (2009) Impact of alien plant invaders on pollination networks in two archipelagos. *PLoS One* 4, e6275
84. Santos, G.M. de M. *et al.* (2012) Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biol. Invasions* 14, 2369–2378
85. Kaiser-Bunbury, C.N. *et al.* (2011) The tolerance of island plant-pollinator networks to alien plants. *J. Ecol.* 99, 202–213
86. Heleno, R.H. *et al.* (2013) Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. *Proc. R. Soc. B* 280, 20122112
87. Timms, L.L. *et al.* (2012) Establishment and dominance of an introduced herbivore has limited impact on native host–parasitoid food webs. *Biol. Invasions* 14, 229–244
88. Dickie, I.A. *et al.* (2016) Loss of functional diversity and network modularity in introduced plant-fungal symbioses. *AoB Plants* 9, plw084
89. Traveset, A. *et al.* (2013) Invaders of pollination networks in the Galapagos Islands: emergence of novel communities. *Proc. R. Soc. B Biol. Sci.* 280, 1758
90. Falcão, J.C.F. *et al.* (2017) Assessing the impacts of tramp and invasive species on the structure and dynamic of ant–plant interaction networks. *Biol. Conserv.* 209, 517–523
91. Thoresen, J.J. *et al.* (2017) Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecol. Appl.* 27, 1190–1198
92. Sugiura, S. *et al.* (2008) Biological invasion into the nested assemblage of tree-beetle associations on the oceanic Ogasawara Islands. *Biol. Invasions* 10, 1061–1071
93. Miehls, A.L.J. *et al.* (2009) Invasive species impacts on ecosystem structure and function: a comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. *Ecol. Model.* 220, 3194–3209
94. Tatem, A.J. (2009) The worldwide airline network and the dispersal of exotic species: 2007–2010. *Ecography* 32, 94–102
95. Seebens, H. *et al.* (2013) The risk of marine bioinvasion caused by global shipping. *Ecol. Lett.* 16, 782–790
96. Seebens, H. *et al.* (2017) No saturation in the accumulation of alien species worldwide. *Nat. Commun.* 8, 14435
97. Saul, W.-C. *et al.* (2017) Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *J. Appl. Ecol.* 54, 657–669
98. Lockwood, J.L. *et al.* (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Divers. Distrib.* 15, 904–910
99. Jeschke, J.M. and Starzer, J. (2018) Propagule pressure hypothesis. In *Invasion Biology: Hypotheses and Evidence* (Jeschke, J.M. and Heger, T., eds), pp. 147–153, CABI
100. Abrahams, B. *et al.* (2019) Exploring the dynamics of research collaborations by mapping social networks in invasion science. *J. Environ. Manag.* 229, 27–37