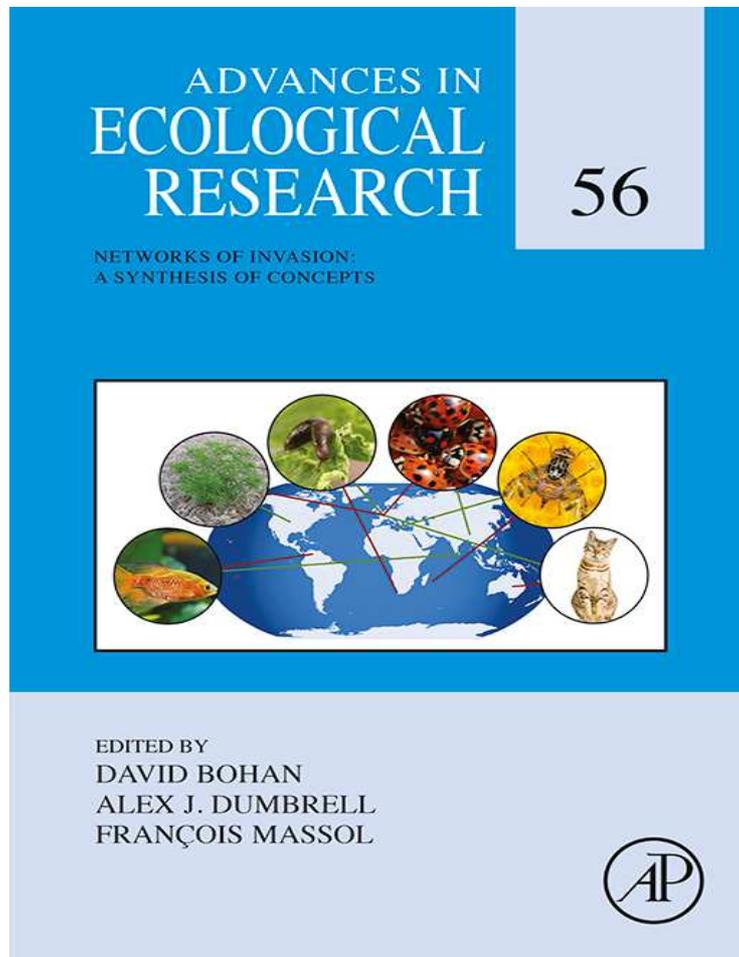


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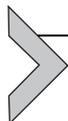
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14 Questions for Invasion in Ecological Networks

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Abstract

Why do some species successfully invade new environments? Which of these invasive species will alter or even reshape their new environment? The answers to these questions are simultaneously critical and complex. They are critical because invasive species can spectacularly alter their new environment, leading to native species extinctions or loss of important ecosystem functions that fundamentally reduce environmental and societal services. They are complex because invasion success in a novel environment is influenced by various attributes embedded in natural landscapes—biogeographical landscape properties, abiotic environmental characteristics, and the relationship between the invasive species and the resident species present in the new environment. We explore whether a condensed record of the relationships among species, in the form of a network, contains the information needed to understand and predict invasive species success and subsequent impacts. Applying network theory to study invasive species is a relatively novel approach. For this reason, much research will be needed to incorporate existing ecological properties into a network framework and to identify which network features hold the information needed to understand and predict whether or not an invasive species is likely to establish or come to dominate a novel environment. This paper asks and begins to answer the 14 most important questions that biologists must address to integrate network analysis into the study of invasive species. Answering these questions can help ecologists produce a practical monitoring scheme to identify invasive species before they substantially alter native environments or to provide solutions to mitigate their harmful impacts.



1. INTRODUCTION

Question 1 What is an Invader from the Perspective of Ecological Networks?

There is no single widely accepted definition of invasive species because the attributes of the invader and the consequences for the invaded habitat often vary. Colautti and MacIsaac (2004) offer a helpful process-based scheme to understand invasions. Their definition of an invasive species depends on which stage—from stage 0 (a resident in a potential donor region), stage I (after uptake into a transport vector, such as human contact), stage II (survived transport and released from vector), stage III (successful reproduction and establishment), stage IV (dispersed from new local habitat or became locally numerically dominant), and stage V (widespread and dominant)—a species is experiencing. In their scheme, any given species can be classified according to the stage they occupy. However, this classification scheme does not clearly define what is unique to the process of invasion. Valéry et al. (2008) provide another definition: ‘A biological invasion consists of a species’ acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population’. Presently, the Global Invasive Species Database (<http://www.iucngisd.org/gisd/>) lists alien species, which are defined as ‘nonnative, nonindigenous, foreign, exotic ... species, subspecies, or lower taxon occurring outside of its natural range (past or present) and dispersal potential (i.e. outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans) and includes any part, gametes or propagule of such species that might survive and subsequently reproduce’, and alien invasive species, which are defined as ‘an alien species which becomes established in natural or seminatural ecosystems or habitat, is an agent of change, and threatens native biological diversity’ (Shine et al., 2000).

Ecological networks are defined as a set of nodes, representing species or trophic groups, connected by edges defining interactions between the nodes, and can be used to describe any type of ecological interaction, including metabolic interactions, trophic interactions, or mutualistic relationships such as pollinator–plant interactions. Studying properties of species interaction networks in general, including food webs, has revealed many important

insights that could not have been gained from considering all pairs of interactions in isolation. Network properties influence the robustness of food webs to extinction. For example, increased interaction nestedness, whereby specialist species are connected only to subsets of the connections of generalist species (e.g. [Bascompte et al., 2003](#)), can buffer against secondary extinctions in mutualistic networks because extinctions of specialists still leave interaction partners for the remaining species ([Memmott et al., 2004](#)). Increased connectance, the number of observed interactions between species divided by the maximum possible number of interactions in the network, can buffer against secondary extinctions after removal of most connected species ([Dunne et al., 2002a](#)). Compartmentalization (or modularity), whereby subsets of species interact frequently with one another but infrequently with species outside the compartment, can minimize the impacts of disturbance in a food web because the disturbance can be contained within a single compartment ([Stouffer and Bascompte, 2011](#)). In contrast, modularity reduces community stability in mutualistic networks ([Thébault and Fontaine, 2010](#)).

The focus of this paper, and of issues 56 and 57 of *Advances in Ecological Research*, is to consider how viewing species in the framework of interaction networks can provide novel insight into the causes and consequences of invasive species. Once an assemblage of species is defined as a network, many different attributes can be studied to determine their impacts on the causes or consequences of invasibility. Here, we draw attention to the most important questions that have emerged from research that views invasive species through the lens of ecological networks, as identified by a diverse group of theoretical and empirical researchers studying species interactions in systems ranging from human microbiomes to agricultural systems. The questions can be divided into four main categories relating to what aspects of network attributes are under consideration—structural, functional, evolutionary, or dynamical properties of networks. One interesting question about the structure of ecological networks and the role these structural attributes may play in the success or impact of invasive species is ([Question 2](#)): [How does empty niche space influence network invasibility?](#) The architecture of connections between species can play an important role in network stability, so it is also interesting to ask ([Question 3](#)): [Are invasive species connected to invaded food webs in particular ways relative to native species?](#) Ecological networks may be defined by different types of interactions, so it is important to compare the impacts of network structure across different network types. We ask

(Question 4): Do distinct types of species interactions influence invasion success in different ways? Additionally, networks of interacting species also perform various ecosystem functions and we seek to better understand (Question 5): How do invaders affect the distribution of biomass in invaded networks? and (Question 6): How do invaders change patterns of ecosystem functioning, particularly nutrient cycling, in invaded networks?

Few ecological systems are evolutionarily static, and this is likely the case for ecological networks as well. Species are dynamically evolving even as they interact with one another and additional evolutionary information associated with nodes and edges, such as phenotypic traits or phylogenetic relatedness, may simultaneously influence and be influenced by network architecture and by the process of invasion. We ask (Question 7): Does the relationship between evolved phenotypic traits of invasive species and invaded networks influence the likelihood of invasions?, (Question 8): How can we use phylogenetic similarity to better understand invasions in networks?, and (Question 9): How do invasive species affect subsequent network evolutionary dynamics? Network dynamics, or how properties of the network change over time, may also be influenced by invasive species, but the fundamental question (Question 10): How do the impacts of invaders on invaded networks change over time and how does network structure influence this? remains to be researched thoroughly. 'Invasion meltdown', whereby nonindigenous species facilitate one another's invasion (Simberloff and Von Holle, 1999), may be influenced by network properties and so it is important to ask (Question 11): Does previous invasion influence the probability of subsequent invasion in ecological networks? Likewise, another attribute of ecological networks, stability, may inform the likelihood of invasion success so we ask (Question 12): How does the [in]stability of the network facilitate or prevent invasions?

Understanding the causes and consequences of species invading ecological networks requires incorporating conceptual and theoretical advances in ecology and evolutionary biology. For example, spatial connectivity among habitats can structure species assemblages, and it will be important to consider how spatial connectivity influences network structure and relate this to the success or impacts of invasive species. We consider this by asking (Question 13): How does spatial connectivity influence ecological networks and what are the implications for the study of invasive species? We also look towards advances in high-throughput sequencing (HTS) to improve data quality and monitoring

of ecological networks by asking (Question 14): [How can we integrate HTS tools to monitor networks before and after invasions?](#)

The questions we introduce here do not have clear answers at the moment. This paper is meant to introduce these questions as novel and promising research directions, discuss the findings of relevant literature, and to highlight which aspects of the questions are strong candidates for future study. Considering species in the context of their relationships with one another increases the chance of understanding and predicting the consequences of alteration in networks due to invasion.



2. STRUCTURAL CONSIDERATIONS FOR INVASION IN ECOLOGICAL NETWORKS

Question 2 How does Empty Niche Space Influence Network Invasibility?

Predicting the occurrence and severity of invasions has been at the heart of invasion biology research since its inception (Elton, 1958). Predictive approaches have typically taken one of two directions: either a species-centric focus on traits or attributes that increase or decrease a species' likelihood to become invasive (Kolar and Lodge, 2001; Van Kleunen et al., 2010) or an ecosystem-centric focus on properties of ecosystems or communities that make them more or less resistant to invasions (Lonsdale, 1999; Richardson and Pyšek, 2006). These approaches have been useful starting points but they do not reflect the expectation that invasion is likely to depend more on the match between the potential invasive species and the recipient ecosystem than on the intrinsic properties of either (Facon et al., 2006). A given species is not an ideal invader everywhere. For example, *r*-selected traits such as high growth rate or large numbers of offspring are often thought to promote invasibility (Rejmánek and Richardson, 1996; Sakai et al., 2001), yet many invasions are limited by the presence of competitors in the recipient ecosystem and therefore by the presence of *K*-selected traits such as producing fewer but larger offspring that enhance competitive strength (Duyck et al., 2006). Likewise, a given ecosystem is not identically sensitive to all possible alien species. Perturbed systems may be considered generally susceptible to invasions (Chytrý et al., 2008; Davis et al., 2000), but these environments may only favour invaders with particular characteristics such as the ability to rapidly exploit available resources under low-competition conditions. Low-diversity systems are thought to be susceptible to invasions because fewer species in the ecosystem means

more unexploited niche axes (Levine and D'Antonio, 1999), but more species might also promote invasion because it corresponds to more potential prey or mutualists for invading newcomers. A network-based view of the ecological niche space represented by potential invading species and recipient communities may bridge the gap left by looking only at attributes of both entities alone (Hui et al., 2016).

Using the perspective of ecological networks, the definition of invasion success becomes the ability of the species to establish links within the recipient community and maintain a positive growth rate. The likelihood of invasion success then depends on the number and nature of the potential established links and the degree of energy available for the introduced species to persist. One of the various aspects of food web structure that might influence the likelihood of invasions includes the degree of saturation along niche axes in the recipient community and the invader's position along these niche axes (reviewed by David et al., [this issue](#)). In a network, this might be reflected in the connectance level of the resident community and the links between the resident community and the invasive species (see [Question 3: Are invasive species connected to invaded food webs in particular ways relative to native species?](#)), in the number of species in the same trophic level as the invader, or in the absence of apex predators observed in recently disturbed or historically isolated systems such as islands. Isolating the mechanism of the influence of niche saturation on invasion likelihood in food web networks can prove difficult because these factors can be confounded. Simulating networks with different connectance levels, for example, leads to characteristic values for other structural properties such as nestedness and modularity (Fortunato, 2010; Hui et al., 2016; Staniczenko et al., 2013). Nevertheless, there is evidence that invasion of an ecosystem by a particular species can be predicted using matrices of trait-mediated interactions between species, either quantitative or even simplified to qualitative (+, −, or 0) directions of interactions between species (Hui et al., 2016).

Some limitations remain that must be overcome for a network perspective to appropriately capture the information associated with niche availability. Networks often focus on a single type of interaction—either trophic interactions in food webs or pollination in plant–insect mutualistic networks (see [Question 4: Do distinct types of species interactions influence invasion success in different ways?](#)). Defining network nodes and edges in these ways may mean that some aspects of niche availability are not captured, such as the ability of some species to modify or create new habitat structure

(e.g. ecosystem engineering; Jones et al., 1994). The existence of a vacant niche for an ecosystem engineer is often only realized a posteriori, after they have profoundly modified their invaded habitat. Perhaps, the best-known example of this is the invasive freshwater zebra mussel, *Dreissena polymorpha*, which is capable of filtering large volumes of water, dramatically reducing phytoplankton biomass, and ultimately rechannelling energy pathways from pelagic–profundal to benthic–littoral zones in lakes they have invaded (Higgins and Vander Zanden, 2010; Karatayev et al., 2002). Zebra mussel beds provide substrate for attachment of sessile organisms, biodeposition, and shelter, and these aspects of habitat alteration have facilitated invasion by additional species in the lakes they inhabit (Ricciardi, 2001; Ricciardi and MacIsaac, 2000). Ecosystem engineering and invasion facilitation are difficult to map onto an interaction network framework (but see [Question 11: Does invasion influence the probability of subsequent invasion in ecological networks?](#)), but their incorporation is critically important for understanding the biology of invasions. Invasion facilitation (e.g. ‘invasion meltdown’; Simberloff and Von Holle, 1999) presents an additional complication to the theory that empty niche space promotes invasion because in this scenario, instead of successive invaders gradually contributing to saturate the niche space and therefore decrease the probability of further invasion, the opposite occurs. Invasive species extend, rather than fill, available niche space.

Ecological networks defined in terms of species interactions also lack a potentially helpful predictor of empty niche space, species traits. Syndromes of biological traits are often synthesized into functional groups, and absent functional groups might point towards invasion risk. In this manner, the lack of sessile filter-feeding bivalves attached to hard substrates in various lakes could have indicated a priori their susceptibility to *D. polymorpha* invasion. Traits can indicate additional subtleties of niche complementarity (Hui et al., 2016). For example, Azzurro et al.’s (2014) study about Lessepsian invasions of fish (i.e. invasions of the Mediterranean Sea by taxa from the Red Sea via the Suez Canal) suggests that invasive species that differ morphologically from native species may have a higher likelihood of establishment (see [Question 7: Does the relationship between evolved phenotypic traits of invasive species and invaded networks influence the likelihood of invasions?](#)). Life history traits indicative of competitive hierarchies can inform predictions about the likelihood of invasive species displacing natives (e.g. in Tephritid fruit flies; Duyck et al., 2007). While informative, these trait-based comparative approaches are limited to sets

of species that are similar enough to have homologous traits, typically those occupying the same trophic level.

The data needed to integrate trophic interactions, facilitation interactions such as habitat construction and ecosystem engineering, and species functional traits, as well as other axes of interactions such as competition are rarely observed for a group of species but these multilayered datasets are increasing (i.e. [Melían et al., 2009](#)) and methods to analyse them are being developed (i.e. [Mucha et al., 2010](#)). [Kéfi et al. \(2016\)](#) applied a probabilistic clustering method to a unique dataset of rocky intertidal communities on a stretch of the central Chilean coast ([Kéfi et al., 2015](#)) that encompassed trophic feeding interactions, interference competition for space, and habitat creation by sessile species. They observed that the three-dimensional multiplex network, with 106 species and more than 4600 interaction links, could be described by a small subset of functional groups that could not be identified using any single data layer in isolation. Interaction networks that encompass multi-dimensional interaction types will provide new information about the functional compartments observed in various diverse ecosystems and may suggest potential areas of empty niche space that are vulnerable to invasion in the future.

Some existing theoretical approaches may be ideal to predict invasibility as a function of niche availability. Invasions first require introduction of the alien species into a new environment, so the process is by definition a spatial one. As a null model, a framework based on the theory of island biogeography ([MacArthur and Wilson, 1967](#)) could constitute a baseline to identify factors that operate within this spatial context irrespective of interspecific interactions. These factors include invasive organismal properties such as propagule pressure ([Colautti et al., 2006](#); [Lockwood et al., 2005](#)) and recipient ecosystem properties such as spatial isolation. Deviations from predictions of neutral spatial models (e.g. those based on island area or distance from mainland in the [MacArthur and Wilson, 1967](#) model) can be interpreted as effects of abiotic and biotic filtering processes. The trophic theory of island biogeography ([Gravel et al., 2011](#); also see [Massol et al., this issue](#)) is a promising candidate for an alternative model that considers niche-based processes. In this model, colonization and extinction probabilities depend on the presence of predator and prey species, instead of colonization and extinction events occurring as stochastically independent processes. This dependency thus embodies the concept of available niche space and provides a first attempt to explicitly integrate

both local network properties and landscape characteristics (e.g. distance to mainland and island area) in the prediction of successful invasions.

Question 3 Are Invasive Species Connected to Invaded Food Webs in Particular Ways Relative to Native Species?

Ecological networks have some characteristic signatures for structural properties such as connectance, which is the number of observed interactions between species divided by the total number of potential links between species in the network, and degree distribution, which is the distribution of the number of links for all species in the network. Observed connectance values vary but might be influenced by properties such as temperature (Petchey et al., 2010) and constraints on diet breadth imposed by optimal foraging (Beckerman et al., 2006). Food webs display a range of degree distributions that deviate from the distribution expected if connections assembled at random (i.e. Poisson; Dunne et al., 2002b), suggesting self-organizing properties, and these distributions are related to properties such as network connectance and size (Dunne et al., 2002b). Mutualistic networks often display heavy-tailed distributions of degrees, characterized by a large number of species with low connectivity and a small number of 'super-generalist' species that interact with many other taxa (Jordano et al., 2003).

Connectivity patterns can influence invasion success. From an invader's perspective, an increase in generalism (the number of prey species fed on) and in omnivory (calculated as the standard deviation around the weighted average of the trophic levels of an invader's prey species; Williams and Martinez, 2004a) was associated with an increased likelihood of invasion success in theoretical food webs (Romanuk et al., 2009). From the invaded network's perspective, the success of invasive species tended to decrease as the connectance of theoretical food webs increased (Baiser et al., 2010; Romanuk et al., 2009). However, additional factors can interact with connectance to influence the success or failure of invasive species. Vulnerability to predation, i.e., an increase in the number of connections to predator taxa, decreases establishment success of invasive prey (Romanuk et al., 2009), while carnivorous species are actually more successful at invading highly connected food webs (Baiser et al., 2010). These results indicate that the relationship between invasion success and connectance depends on trophic position. Modularity, whereby subsets of species interact frequently with one another but infrequently with species outside the module, may buffer food webs against the consequences of invasion because the disturbance effects may be limited within a single module (Krause et al., 2003).

The type of network considered can also influence the role of connectance for invasion success and subsequent impacts. For example, a comparison of lowly and highly invaded forest and island plant–pollinator networks revealed overall similar connectance levels but a transfer of connections from native to alien generalists in the highly invaded networks (Aizen et al., 2008; but see Bartomeus et al., 2008 for an example where invasive plants facilitate an increase in connectance between native plants and pollinators). Mutualist networks with a few highly connected ‘super-generalist’ species may also facilitate invasions by incorporating novel aliens into the highly connected components of the interaction network (Olesen et al., 2002).

Some important questions on the role of food web connectivity properties for invasion success and susceptibility remain to be addressed. The degree of invaders relative to the degree distribution in the invaded network has not been evaluated systematically in theoretical or empirical studies. It would also be interesting to compare the connectance levels and the degree distributions between an invasive species’ native vs invaded network to determine whether it is possible to predict invasion success based on network (rather than species) properties.

Question 4 Do Distinct Types of Species Interactions Influence Invasion Success in Different Ways?

Interspecific interactions can be antagonistic (beneficial for one partner but detrimental for the other one, as in predator–prey interactions), mutualistic (beneficial for both partners, as in plant–pollinator interactions), or competitive (detrimental to both species). Interactions can also be transitory (e.g. predation events), long-term and sustained (e.g. lifetime mutualistic symbioses), or can lie anywhere along the continuum between these two durations (Fig. 1). Invasive species spanning the entirety of this continuum have successfully integrated into ecological networks in the recipient community (i.e. Eastwood et al., 2007; Traveset and Richardson, 2014). To date, most studies of invasive species focus on a single type of interaction at a time, and the main hypotheses for how species interactions influence the likelihood of invasion success are related to either competition (e.g. the biotic resistance hypothesis), predation and parasitism (e.g. antagonistic interactions, the enemy release hypothesis), or mutualism (e.g. some examples of invasion facilitation, i.e. Green et al., 2011). However, invasion success and associated consequences for communities and ecosystems are likely to result from the joint effect of different types of interspecific interactions (Inderjit and van der Putten, 2010; Mitchell et al., 2006).

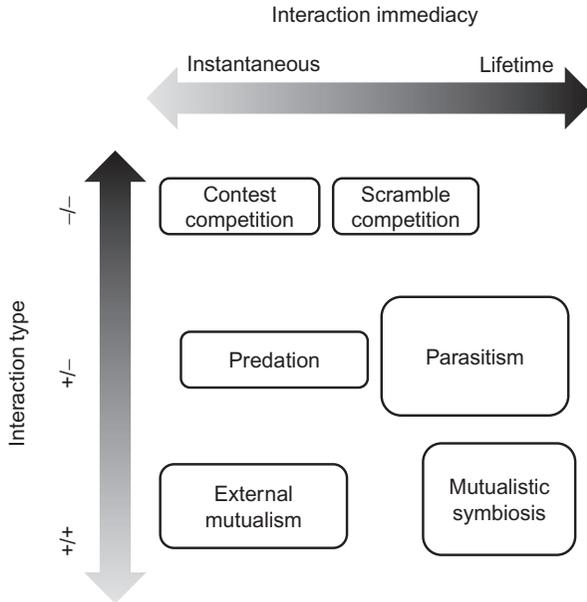


Fig. 1 Type and length of duration of interspecific interactions. The ways in which species interact with one another can vary in the direction and magnitude of their impact for participant species and in the length of time over which the species interact. Both of these axes can influence network properties and the probability of successful species invasions.

Several studies have shown that ecological networks have different structures depending on the type and strength of interaction (Bellay et al., 2015; Chagnon et al., 2016; Fontaine et al., 2011; Thébault and Fontaine, 2010). Interaction type also influences the relationship between network structure and community dynamics—greater connectance and nestedness increase species persistence in mutualistic webs while they decrease persistence in antagonistic networks (Thébault and Fontaine, 2010). It is thus likely that distinct types of interaction networks might respond differently to invasions due to their varying structures and dynamics. The nature of this response is easier to predict for some interaction types than others. Mutualisms have strong impacts on the success of potential invaders and subsequent population dynamics of species in the invaded network (see Amsellem et al., 2017 and Médoc et al., 2017). Invaders that successfully disrupt existing mutualisms may increase their likelihood of establishment in novel habitats and likely create important shifts in ecosystem functioning and effects on native species (Brouwer et al., 2015). Facultative mutualisms may promote

invasions of novel species more easily than obligate mutualisms, which require strong dependencies between partners (Rodríguez-Echeverría and Traveset, 2015; Traveset and Richardson, 2014). On the other hand, the effects of antagonistic relationships for invasion success often vary. Exotic species may spread their parasites in novel ecosystems (Carpentier et al., 2007; Roy et al., 2008, 2011) or acquire novel parasites (Sheath et al., 2015). The enemy release hypothesis posits that alien species will experience increased invasion success in novel habitats that are devoid of the 'natural enemies' found in their original habitats. However, a review of studies of this hypothesis found mixed evidence for this—invasive species did encounter a reduced diversity of enemies in their introduced compared to native range, but the impact of enemies in the invaded community was similar for native and introduced species (Colautti et al., 2004).

Studies of ecological networks will therefore benefit from considering a diversity of trophic and nontrophic interactions (Kéfi et al., 2012), because interaction types are observed to combine in nonrandom ways and to influence community response to perturbation (Fontaine et al., 2011; Kéfi et al., 2012, 2015; Poccock et al., 2012; Sauve et al., 2014, 2016). For example, the effects of species invasions are more likely to propagate in highly connected interaction networks, and this connectedness can arise from either trophic interactions such as low-intimacy mutualisms (Fontaine et al., 2011) or nontrophic interactions such as competition for space or refuge provisioning (Kéfi et al., 2015). In another example, the dominance of superior competitors and exclusion of inferior competitors predicted by traditional resource ratio coexistence theory (León and Tumpson, 1975; Tilman, 1980, 1982) may not be observed if interference competition (and priority effects) is taken into consideration (Gerla et al., 2009).

Using networks to understand interactions between species requires defining edges, and this becomes complicated when multiple interaction types are combined. Kéfi et al. (2012) review modelling approaches to incorporate nontrophic interactions through their modification of trophic functional responses, and even to consider interactions that do not influence feeding. Kéfi et al. (2016) then successfully reduced a complex web of trophic, competitive, and facilitative interactions into a smaller subset of multilayer ecological functional groups. Another solution may be to use phylogenetic distances between species. Mitchell et al. (2006) developed a coherent framework that integrates enemy release, mutualist facilitation, competitive release, and abiotic environmental suitability, and how their relationship to invader success can be viewed via phylogenetic distance

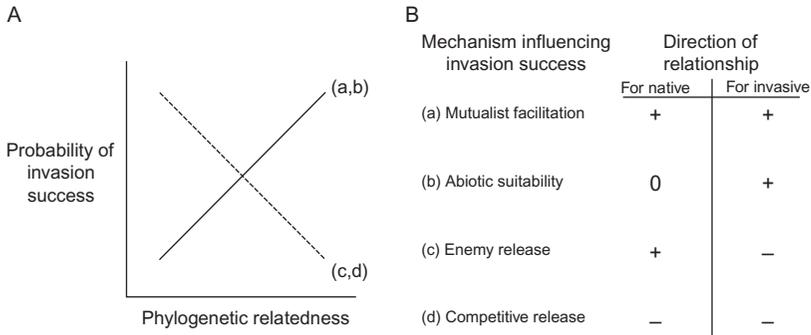
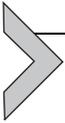


Fig. 2 Dependency of invasion success on phylogenetic relatedness as mediated by species interaction type. (A) Phylogenetic relatedness between an invasive species and species already inhabiting the novel environment can determine whether or not the invasive is likely to succeed in the new environment, but the direction of this relationship depends on (B) whether or not the invasive species receives positive benefits from ecological interactions in the novel environment. If the invasive species (a) has a mutualistic relationship with a species in the novel habitat or (b) benefits from abiotic resources, the invasive species is more likely to succeed in the new habitat if they are closely related to the native species because the invasive species is more likely to share the features that lead to benefits. If the invasive species has (c) enemies or (d) competitors in the novel habitat, the invasive species is less likely to succeed in the new habitat if they are closely related to the native species because the invasive species is more likely to share the features that lead to costs (after Mitchell et al., 2006, Fig. 3).

between invasive and native species (Fig. 2). In this framework, species introduced to communities including close relatives should experience high rates of enemy, mutualist, and competitor accumulation and encounter favourable abiotic conditions. Invasion success would therefore be limited by (the lack of) enemy or competitor release and enhanced by favourable habitat filtering or mutualist facilitation. Species introduced to communities without close relatives could experience successful invasions via enemy or competitor release or unsuccessful invasions via unfavourable habitat filtering or loss of beneficial mutualisms. The mechanistic basis of the direction of some of these relationships between interaction type and phylogenetic distance is better understood than others. Related prey species do tend to share more consumers than related consumers share prey species (Cagnolo et al., 2011; Elias et al., 2013; Naisbit et al., 2012), and related plant species tend to share more herbivores than they share pollinators (Fontaine and Thébaud, 2015), supporting the hypothesized negative relationship between enemy release and phylogenetic relatedness. The mechanism for the negative relationship between phylogenetic relatedness and competitive

release, that more closely related competitors are more likely to be phenotypically similar and thus competitively exclude one another, has mixed support (Jones et al., 2013; see also [Question 7: Does the relationship between evolved phenotypic traits of invasive species and invaded networks influence the likelihood of invasions?](#)). However, phylogenetic relatedness remains a promising explanatory variable of the interactions among different members of a network that may help us understand how distinct types of species interactions influence invasion success (see [Question 8: How can we use phylogenetic similarity to better understand invasions in networks?](#)).



3. FUNCTIONAL CONSIDERATIONS FOR INVASION IN ECOLOGICAL NETWORKS

Question 5 How do Invaders Affect the Distribution of Biomass in Invaded Networks?

The consequences of biological invasions for recipient communities are often considered in terms of events such as extinctions and decreases in species richness (i.e. [Gurevitch and Padilla, 2004](#); [Ricciardi, 2004](#); [Wilsey et al., 2009](#)). However, shifts in the relative abundances and biomass distribution of the community may be substantial and are important to consider as well ([Ehrensfield, 2010](#)). Abundance shifts typically precede extinction events and may therefore provide early signals of biodiversity loss in an invaded system, and altered biomass distributions should produce a consequent redistribution of energy fluxes in the ecosystem. In order to truly understand the novel functioning and services of the invaded ecosystem, it is therefore crucial to understand the changes in abundance and biomass that result after alien species have invaded ([Walsh et al., 2016](#)). Here, we consider the shifts in species abundances and biomass distributions expected after invasion of novel species from a trophic network perspective, including shifts in the same functional group as the invaded species, in lower trophic levels (e.g. top-down effects), and in higher trophic levels (e.g. bottom-up effects).

Species abundance distributions in communities generally indicate the coexistence of a few dominant and many rare species (e.g. 'hollow curve' species abundance distributions; [McGill et al., 2007](#)). This pattern, observed across different types of ecological systems regardless of the proportion of native and invasive species it holds, appears to be one of the few general laws in ecology ([McGill et al., 2007](#)). Because the general shapes of abundance distributions are unchanged by invasion and because invasive species tend

to become one of the dominant species in the system (e.g. in order to be noticed and labelled as an invasive species), it follows that invasive species vastly decrease the abundance of and replace at least one dominant native species. This is consistent with empirical observations. A multihabitat study in the Bruce Peninsula National Park in Canada found that invasive plant species represented the majority of the standing biomass, particularly when total abundance in the sampled location was low (de Gruchy et al., 2005). A review of 64 grasslands in 13 countries also indicated invasive replacement of dominant species: exotic plant species were six times more likely than native species to be dominant in the observed system (Seabloom et al., 2015). If invasive species act as super-competitors that assume one of the positions of numerical dominance in the invaded system, they may in turn lead to either a null (if they simply acquire resources at the expense of competitors) or positive (if they extract additional resources not available to native species) effect on total biomass and a negative effect on the evenness of biomass distributions. The above-ground biomass in experimental grassland communities containing all exotic species was significantly higher than those containing all native species in one study (Wilsey et al., 2009). Another study compared vegetation of environmentally similar sites with either invasive-dominant or uninvaded plant communities and observed reduced evenness in the percent cover of species in the invaded plots (Hejda et al., 2009).

Invasive species that become abundant are potential energy sources for other species and may create bottom-up effects within trophic networks, but they may also consume more resources and thus create important top-down effects as well. The direction and magnitude of effects for the abundances of existing species in the network greatly depend on the trophic level of the invasive species. Lower trophic levels are strongly constrained by bottom-up effects (Loeuille and Loreau, 2004; Strong, 1992; White, 2005), so exotic plant or herbivore species may substantially increase abundances in higher trophic levels by relaxing key energy constraints. An exception might occur when, for example, an invading plant is so highly defended that its biomass is mostly unavailable for the rest of the food web (Loeuille and Leibold, 2008; Loeuille and Loreau, 2004; Strong, 1992). Top-down effects are more likely when invasive species occupy higher trophic levels, and numerous studies have observed decreasing prey abundances and increasing extinctions following invasions by exotic predators (David et al., *this issue*; Dorcas et al., 2012; Rodda et al., 1997). This idea is so widely accepted that trophic manipulation, via adding exotic predators to control biomass at

lower trophic levels, is a commonly applied biocontrol technique (Demelo et al., 1992). We therefore hypothesize that in most instances, the addition of invasive species at lower trophic levels will increase abundances at higher trophic levels by increasing resource availability (Correia, 2001; Pintor and Byers, 2015), while invasive species introduced at higher trophic levels will create trophic cascades by decreasing biomass of the trophic level below and thus increasing biomass two trophic levels below (see David et al., this issue).

Additional complexities to determine how invasive species influence biomass distribution in ecological networks remain to be addressed. Invasive species can have indirect effects on recipient communities as well, such as niche construction or facilitation, that influence the distribution of biomass and functioning of the network (Ehrenfeld, 2010). These indirect effects may interact with the previously described bottom-up and top-down effects in complex ways. In one particularly striking example, the presence or absence of introduced arctic foxes on the Aleutian Islands determined whether or not the landscape remained a grassland or was transformed into a tundra system. In this instance, arctic foxes preying on seabird populations (a top-down effect) led to reduced nutrient transport from ocean to land and reduced soil fertility, promoting transformation from a grassland into a system dominated by shrubs and forbs (Croll et al., 2005). Until these indirect effects, especially those with large magnitude, are integrated into ecological network perspectives (see Question 11: Does invasion influence the probability of subsequent invasion in ecological networks?), it may be difficult to predict the range of effects that invasive species have on abundance and biomass distributions. One promising direction includes reconceptualizing existing metaecosystem models (Gounand et al., 2014; Gravel et al., 2010; Loreau et al., 2003) in the context of invasive species to consider their effects on nutrient cycling processes and consequent biomass distributions. In addition to these conceptual advances, improved empirical and experimental data to understand the importance of niche construction relative to direct top-down and bottom-up effects are greatly needed.

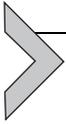
Question 6 How do Invaders Change Patterns of Ecosystem Functioning, Particularly Nutrient Cycling, in Invaded Networks?

Invaders affect the functioning of invaded ecosystems in a variety of ways. A primary mechanism of influence is via effects on primary production and

nutrient cycling (Strayer, 2012), but other notable effects include shifts in fire regimes after invasion by fire-adapted plants (Brooks et al., 2004), changes in soil or marine substrate structure (Simberloff, 2011), and ecosystem engineering (Ehrenfeld, 2010). Invasions can trigger further invasions (see Question 11: Does previous invasion influence the probability of subsequent invasion in ecological networks?), and the mechanism for this in some instances is through shifts in ecosystem functioning, for example, after invasion by nitrogen-fixing plant species (Simberloff, 2011). Even after their removal, the impact of these ecosystem shifts can continue to linger and promote the persistence of other exotic species. This was observed in the instance of Australian bridal creeper, where decomposition of its phosphorus-enriched leaves increased local soil fertility and led to effects that persisted and promoted enhanced cover of some exotic species after the creeper was experimentally removed (Turner and Virtue, 2006; Turner et al., 2008; see Grove et al., 2015 for another example). Microbial ecosystems within a host's body can also be affected by foreign species. Consequences include perturbations or disruptions of the host's immune functioning (Khosravi and Mazmanian, 2013), release of toxins that influence other microbiota (Hecht et al., 2016; Wexler et al., 2016), and even manipulation of the host's metabolism (Brown et al., 2008; Martin et al., 2008), which can subsequently alter or 'ecosystem engineer' environmental conditions such as the host's diet (Ezenwa et al., 2012). The interesting case of invasions in microbiomes is discussed further in Murall et al. (this issue).

A comprehensive meta-analysis by Vilà et al. (2011) provides substantial insight into the consequences of invasive plants for nutrient cycling. Invasive species tend to increase carbon, nitrogen, and phosphorus pools in most invaded ecosystems, but on average, they decrease litter decomposition (though variation among studies is considerable). Examples of the mechanisms for alteration of nutrient cycling include significant increases in nitrogen pools after invasion of nitrogen-fixing plants (Grove et al., 2015), altered stream nutrient storage and remineralization rates after invasion of phosphorus-rich freshwater fish (Capps and Flecker, 2013), and disruption of native plant-fungi mutualistic interactions by invasive plants leading to decreased seedling growth of native plants (Stinson et al., 2006). These alterations of nutrient regimes may have substantial impacts across large spatial scales, spanning multiple trophic levels. For example, the invasion of a nitrogen-fixing tree, *Myrica faya*, in Hawaii led to vast changes in the stoichiometry not only of the forest but also of associated freshwater ecosystems (Asner and Vitousek, 2005). The sensitivity of ecosystem nutrient cycling to

invasive species could be evaluated by applying network stability analysis to food webs with edges determined by nutrient transfer and weighted by transfer efficiency (Moe et al., 2005). Incorporation of ecological stoichiometric information into trophic networks (Lee et al., 2011) may provide the link between the consequences of invasive species for nutrient cycling (González et al., 2010).



4. EVOLUTIONARY CONSIDERATIONS FOR INVASION IN ECOLOGICAL NETWORKS

Question 7 Does the Relationship Between Evolved Phenotypic Traits of Invasive Species and Invaded Networks Influence the Likelihood of Invasions?

The notion that phenotypic traits of organisms may influence the success, failure, or subsequent impact after establishment of invasive species has been thoroughly explored. Researchers have made efforts to retrospectively analyze properties associated with harmful invasive species such as likelihood of human transport or ecological range tolerance (i.e. Marchetti et al., 2004; Nyberg and Wallentinus, 2005; Van Kleunen et al., 2010). The biological invasion process itself plays a role in favouring some phenotypic attributes. For example, species that interact commensally with humans or are associated with human recreational activities are more likely to have invasion opportunities (Jeschke and Strayer, 2006). Attributes such as small body size or propagule dormancy are also associated with movement and thus may play a role in invasion propensity (King and Buckney, 2001; Kolar and Lodge, 2001; Wainwright and Cleland, 2013; but see Blackburn et al., 2009). Phenotypic traits can also play an important role in structuring communities and food webs (Brose et al., 2006; Loeuille and Loreau, 2010; Rezende et al., 2009), and these phenotypic attributes of the recipient communities also influence their likelihood of being invaded (Thuiller et al., 2006).

However, the relationship between a species' invasion success or a recipient community's invasion susceptibility may not be fixed but instead may depend on the difference between the traits possessed by the invader and the recipient community. The mechanisms of this matching between the invader and the invaded community may be either that: (i) limiting similarity prevents niche overlap between the invader and the invaded community, and therefore, invasive species are more successful if they bring some novel

phenotype or function to the recipient community (e.g. discrete trait invaders that add a new function to the invaded ecosystem or continuous trait invaders that differ substantially from natives in traits that are continuously distributed among species in the recipient community; [Dukes and Mooney, 2004](#)), or (ii) invaders are better able to succeed in novel environments if they share traits with natives that serve as preadaptations in the new environmental conditions ([Duncan and Williams, 2002](#); mechanisms described in more detail in [Strauss et al., 2006a](#)). Some studies have found that the same phenotype in one species can lead to differential impacts on the rest of the species in the community depending on the phenotypic properties of that community. For example, plant species in the North American range of the invasive knapweed, *Centaurea diffusa*, were more susceptible to *C. diffusa* allelotoxin than plant species in the native Eurasian habitat ([Vivanco et al., 2004](#)).

Few studies have explicitly tested the influence of phenotypic matching between invasive species and recipient communities. [Fargione et al. \(2003\)](#) experimentally added plant species from different functional guilds to prairie-grassland plots with varying composition and found that introduced species were less successful when functionally similar species were present and abundant. Competitive inhibition of similar species, via resource consumption or soil nitrate reduction, was the primary mechanism of this exclusion. More studies used phylogenetic relatedness or presence of species in the same taxonomic group as a proxy for similarity in ecological niche use (discussed in more detail in [Question 8: How can we use phylogenetic similarity to better understand invasions in networks?](#)). From a network perspective, many traits are implicitly encoded by setting species as nodes in a food web, and many of these traits are correlated with body size (reviewed in [Woodward et al., 2005](#)). For example, dietary overlap is an important structural component of trophic networks ([Williams and Martinez, 2000](#)), and this is often determined by body size ([Woodward and Hildrew, 2002](#)). It may thus be possible to use body size to visualize empty niche space that suggests potential vulnerability to invasive species (see [Question 2: How does empty niche space influence network invasibility?](#)). Increased phenotypic matching that results from coevolution of interaction partners can influence the structure of mutualistic networks and increase their connectance ([Nuismer et al., 2013](#)), and connectance can influence the susceptibility of networks to invasion (see [Question 3: Are invasive species connected to invaded food webs in particular ways relative to native species?](#)).

It is important to note that phenotypes of invading species and recipient communities can evolve and change following invasion (Strauss et al., 2006b; see also [Question 9: How do invasive species impact subsequent network evolutionary dynamics?](#)). This can alter the information needed to compare invasive and native phenotypic distributions, and it may be important to take evolutionary potential into account when constructing Invasive Species Predictive Schemes (ISPS; Whitney and Gabler, 2008). Organisms of course also possess numerous traits, many of which may either contribute to fitness in a novel environment or may be correlated with other traits that are selected upon. For example, Strauss et al. (2006b) discuss instances where sexually selected traits such as mate signalling may face distinct selection pressures in novel environments when new predators or competitors are encountered. As with any study using trait-based approximations for niche use, caution must be exercised when choosing the phenotypes to be used as predictors.

Question 8 How can we Use Phylogenetic Similarity to Better Understand Invasions in Networks?

The evolutionary relationships between species in a food web can have an important, often under-appreciated role in determining the structure of that food web. For example, herbivores often consume a phylogenetically constrained set of hosts (Ødegaard et al., 2005; Weiblen et al., 2006). This constraint is observed for invasive species as well. Invasive European plants, which have not coevolved with native European butterfly and moth herbivores, were constrained to interact with particular phylogenetic groups of the Lepidopteran herbivores, and these invasive plant species were more likely to be consumed by native herbivores if they had a confamilial native plant already present in the system (Pearse and Altermatt, 2013). For this reason, phylogenetic similarity may be used to forecast likely interaction linkages when new species invade landscapes (Ives and Godfray, 2006; see also Kamenova et al., [this issue](#)).

While predicting interactions between novel invasive and native species is a relatively new direction of study, using evolutionary similarity to determine the likelihood of invasion success has a longer history. Darwin (1859) suggested that the relatedness of an exotic species to the native community could both: (i) confer an advantage to the exotic species by increasing the likelihood that the invasive species' traits match the novel environment, and (ii) lead to a disadvantage because the invasive species would be more likely to encounter direct competitors or shared enemies with the native

species. Empirical evidence has yielded evidence for both directions of effect as well as no effect (reviewed in [Diez et al., 2008](#)). [Mitchell et al. \(2006\)](#) provide a useful framework that takes into account the different types of interactions between an exotic species and the new ecosystem that are important for determining invasion success ([Fig. 2](#)). Enemies, mutualists, competitors, and abiotic niche use all constrain invasion success and can be evaluated using measures of phylogenetic relatedness (see [Question 4: Do distinct types of species interactions influence invasion success in different ways?](#)). [T.N. Romanuk et al. \(personal communication\)](#) uncovered an intriguing new mechanism that may explain increased success when invaders are more similar to native species. In their series of simulated invasions into trophic food webs, invasive species that were more closely related to species in the novel food web experienced increased invasion success and displayed more links with both predator and prey species in the novel food web compared with invasive species that were less closely related. They hypothesize that more closely related species increased trophic overlap and may thus serve to stabilize novel food webs and increase their complexity and persistence. Their results support observations that invasive species with no close relatives in the novel habitat and with extremely novel niche use are associated with substantial alterations and simplifications of local trophic networks (i.e. invasion of the brown tree snake in Guam, [Wiles et al., 2003](#); invasion of Burmese pythons in the Everglades, [Dorcas et al., 2012](#)). Their results also support the dichotomy between ‘discrete trait invaders’ (that add a novel niche or function to the invaded system) and ‘continuous trait invaders’ (that vary along a niche or function already present and continuously distributed among species in the invaded system; [Dukes and Mooney, 2004](#)) and, subject to further testing, these results would seem to indicate that discrete invaders may be rarer but have larger impacts than continuous invaders.

Some studies used phylogenetic relatedness or presence of species in the same taxonomic group as a proxy for similarity in ecological niche use. [Ricciardi and Atkinson \(2004\)](#) found that high-impact invaders in a diverse array of aquatic ecosystems are more likely to belong to genera that were not already present in the invaded location, while [Strauss et al. \(2006a\)](#) found that highly invasive California grass species were significantly less related to native grasses than introduced but noninvasive (i.e. nonpest) grass species were. However, an extensive survey of New Zealand plant species ([Duncan and Williams, 2002](#)) revealed the opposite pattern, i.e., that introduced and naturalized plant species were more likely to belong to genera that also

contained native species. However, it is important to note that phylogenetic and taxonomic relatedness is only a proxy for trait similarity, and the assumption that the traits most relevant for niche use are phylogenetically conserved is not always borne out by observation (Gerhold et al., 2015; Gianuca et al., 2016).

Question 9 How do Invasive Species Affect Subsequent Network Evolutionary Dynamics?

Establishment of invasive species in a novel habitat requires, at a minimum, available resources for that species, which means that invasive species must insert themselves into interaction networks in the invaded habitat. This insertion can create an altered selective landscape for the invasive species and for the organisms the invasive species interacts with. In some instances, invasive species experience genetic alteration subsequent to their invasion (Bossdorf et al., 2005; Dlugosch and Parker, 2008). This alteration results from numerous mechanisms, such as bottlenecks, hybridization, polyploidy, and stress-induced modification of the genome (Lee, 2002; Prentis et al., 2008). While these mechanisms may promote rapid adaptation in invasive species, it is also important to consider that evolutionary change in invasive species may not necessarily be adaptive (Keller and Taylor, 2008).

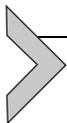
The ways in which invasive species influence the evolution of natives is complex. Multiple species may interact with an invasive and show differential responses to the novel selection pressure (e.g. Mealar and Hild, 2007). Species in the recipient community may differ in plasticity, in the degree of preexisting adaptations, or the genetic architecture underlying traits under selection, which can all influence whether or not they experience evolutionary responses to invasive species. Species may not experience evolutionary change, due to natives already possessing preadapted traits (exaptations) that enhance coexistence with the invader (examples reviewed in Strauss et al., 2006b) or due to an 'evolutionary trap', where the traits or behavioural decision-making rules of a species are in mismatch with the new postinvasion selective environment and thus lead to reduced survival or reproduction (Schlaepfer et al., 2005). These varying degrees of adaptive ability in the invasive or in the recipient community may actually determine the ultimate impact of the invasive species.

An ecological network perspective may be necessary to understand evolutionary responses to invasive species because it has been increasingly shown that evolution in native and invasive species can depend on variation

in ecological interactions with other species (i.e. Thompson, 2005). For example, *Alliaria petiolata*, a Eurasian understory plant that has invaded North American forests, has a patchy distribution in the invaded habitat and differentially invests in an allelochemical that slows the growth of competitors. This spatial variation in competitive strength has in turn led to coevolution in the degree of tolerance of understory competitors in the invaded communities (Lankau, 2012). Another plant species native to California grasslands, *Lotus wrangelianus*, demonstrated adaptive responses to compete with invasive *Medicago polymorpha*, but this adaptive response was only observed in communities that did not have the exotic insect herbivore *Hypera brunneipennis* present (Lau, 2006). Increasing trophic complexity—for example, the presence of alternate host plants for invasive parsnip webworms that attack native wild parsnips—can decrease the selective impact of the invasive species (Berenbaum and Zangerl, 2006). These studies indicate that the interaction network—the presence and magnitude of connections between invasive and invaded species—sets a context for the degree of evolution and coevolution in an invaded system. Researchers have even posited that in addition to escape from enemies (Enemy release hypothesis; Keane and Crawley, 2002) and escape from the costs of defence (evolution of increased competitive ability; Blossey and Notzold, 1995), an introduced species' escape from community complexity in their native habitat and consequent decrease in interactions with fitness-impacting species may be an additional type of 'release' in the novel habitat (Müller-Schärer et al., 2004; Strauss, 2014).

The complexity of experimental and survey designs will necessarily increase in order to separate adaptive from nonadaptive evolution (i.e. Keller and Taylor, 2008) and to take into account the effects of interactions in a trophic network. However, there are many interesting hypotheses to test. The likelihood of evolutionary rescue, where evolution rescues a declining population from extinction after an environmental change (Gomulkiewicz and Holt, 1995), may be influenced not only by the degree of maladaptation and the speed of adaptive evolution but also by interactions with other species in a community context. Theoretical studies (de Mazancourt et al., 2008) and empirical tests in experimental adaptive radiations of the bacteria *Pseudomonas fluorescens* (Fukami et al., 2007; Gómez and Buckling, 2013) have demonstrated that biodiversity can restrict evolutionary opportunities in groups of competitors. It may be that the number of links connecting resident to invasive species or the per-capita influence of the invasive species on interacting natives, via direct or indirect

effects, mitigates the selection pressure exerted on species in the native habitat after an invasion. Evolutionary rescue or rapid evolution in native species can reduce the impact of invasive species. Evolution of feeding morphology in the Australian soapberry bug *Leptocoris tagalicus* occurred on a relatively rapid time scale following the spread of an invasive vine, leading to an almost doubled attack rate of the herbivore on the seeds of the invasive species (Carroll et al., 2005). Eco-evolutionary dynamics—where ecological and evolutionary processes influence one another and may lead to dynamic feedback loops where evolution alters an ecological process that in turn drives further evolutionary change (Fussmann et al., 2007)—may also be important to understand the consequences of invasive species. Shifts in community composition and diversity caused by phenotypic differentiation in a focal species may be almost as substantial as those caused by the addition of the species to the system (Bassar et al., 2010; Walsh et al., 2012), and local adaptation to environmental conditions may affect community structure as strongly as the presence or absence of those environmental conditions (Pantel et al., 2015). It is currently unknown whether the evolutionary changes that occur following invasions in ecological networks have the effect either of mitigating the ecological and functional consequences of invasion or of leading to further such ecological impacts. To understand how evolution is likely to propagate across food web networks after invasion, future studies might explore comparisons between ecological networks based on trophic interactions and evolutionary networks of fitness impacts or selection strengths.



5. DYNAMICAL CONSIDERATIONS FOR INVASION IN ECOLOGICAL NETWORKS

Question 10 How do the Impacts of Invaders on Invaded Networks Change Over Time and How does Network Structure Influence This?

Though the consequences of invasive species for ecosystem composition, structure, and function can be profound, much less attention has been paid to understanding how these consequences manifest over time. In a 2006 study, Strayer et al. (2006) reviewed 185 papers spanning a 5-year period (2001–05) that studied the effects of an invading species and found that 40% of the studies did not record the time since the invasion occurred and very few included multiple time points in the study. Given the variety and complexity of effects invasive species may have on a system—influencing abundance and biomass

distributions, species interactions, ecosystem functioning, and evolution—it is important to implement the additional dimension of understanding temporal dynamics in these effects. [Strayer et al. \(2006\)](#) emphasize considering not only the ‘acute’ phase of invasions, immediately after the new species has arrived, but also the ‘chronic’ phase of invasions, when ecological and evolutionary processes have reacted to the incorporation of the new species. They also suggest a combination of mathematical modelling, microcosm experiments, and chronosequences (surveys that include site variation in the time since the invasion event has occurred) to better elucidate how invaded systems have changed with time.

Some attention has been paid to the existence of lags between a new species arrival and when it begins to affect the new ecosystem. The presence of such lags, whether in population growth or in range expansion, can vary because the match between the invasive species and the abiotic and biotic features of the novel habitat will vary for all invaders and invaded systems. The timing of the lag will thus depend on the timing over which a mismatch between the invasive species and the novel environment shifts to become more favourable to the invasive species. This can occur if the environment shifts to become more favourable to the alien species or if the alien species experiences genetic shifts to become better adapted to the novel landscape ([Crooks and Soulé, 1999](#); see also [Question 9: How do invasive species affect subsequent network evolutionary dynamics?](#)). Delays in the effects of invasive species may also arise if these effects are density-dependent (i.e. an invasive canopy tree shading understory growth) or dependent on the ontogeny of the invading species (i.e. a long-lived invasive with stage-dependent impacts on other species; [Simberloff et al., 2013](#)). Two potential evolutionary mechanisms for sudden changes in impacts of invasive species in their novel habitats include: (i) hybridization of invasive with native species, leading to evolutionary changes that alter the way the invasive species participates in the ecosystem it inhabits ([Hastings et al., 2005](#); [Lee, 2002](#)), and (ii) evolution of host shifts, for example, when parasites arrive together with their hosts and later adapt to infect resident host species ([Dunn, 2009](#)). Even if the invaded pathogens and parasites do not evolve, these species could contribute to decreasing the impact of an invasive host species on the novel ecosystem over time if they display a lag in the start of epidemics that serve to decrease any temporary (acute) abundance accumulations experienced by the invasive species ([Amsellem et al., 2017](#); [Médoc et al., 2017](#)). The influence of network structure on the dynamics of invasive species effects through time remains an unexploited and novel area of research.

Question 11 Does Invasion Influence the Probability of Subsequent Invasion in Ecological Networks?

The North American Great Lakes are now home to approximately 180 invasive species introduced since the era of European exploration and colonization. Though one of the most important vectors of such nonnative taxa has been ballast water transport, the rate of invasion increased sharply even after the implementation of ballast water controls in 1989 (Holeck et al., 2004). Examples of this acceleration in the rate of successful invasions over time are referred to as 'invasional meltdown' (Cohen and Carlton, 1998; Simberloff and von Holle, 1999). Potential mechanisms for invasional meltdowns that are well known include the replacement of invasion-resistant native herbivores with exotic herbivores (Parker et al., 2006), habitat alteration, and introduction of the entirety of species needed to complete parasitic life cycles (Ricciardi, 2001; Ricciardi and MacIsaac, 2000). However, the invasion acceleration observed in the Great Lakes in the 1990s coincided with a profound shift in the region of origin of nonnative species, where 70% of species invading since 1985 are native to the fresh and brackish waters of the Ponto-Caspian region (Ricciardi and MacIsaac, 2000). This suggests that previously shared habitat may be another driver of invasional meltdown.

We simulated sequential species invasions to evaluate the role of shared history on establishment success. The simulations were constructed similarly to those described in Romanuk et al. (in press): briefly, we constructed food webs at each of three connectance levels ($C=0.05, 0.15,$ and 0.25) using the niche model (Williams and Martinez, 2000), computed the dynamics of the food webs for 2000 time steps using the structure-dynamical integrated model (Brose et al., 2005, 2006; Williams and Martinez, 2004b; Yodzis and Innes, 1992) to generate dynamically persistent webs, then randomly selected 50 webs from each connectance level (10 webs each with species richness $S=26, 27, 28, 29,$ and 30) to serve as native webs to be invaded. We then generated two types of invaders to serve as sources, copersistent and random invaders. For copersistent invaders, we constructed food webs with $C=0.15$ using the niche model, computed the dynamics of the food webs for 2000 time steps using the structure-dynamical integrated model to generate dynamically persistent webs, then randomly selected webs with $S=26, 27, 28, 29,$ or 30 (150 webs total). For random invaders, instead of constructing webs, we simply assembled a list of species using niche properties (n_i, r_i, c_i ; Williams and Martinez, 2000) associated with $C=0.15$ then randomly selected 150 sets of 30 species from this list. By not constructing webs from

these species, there were thus no interactions or associated biomass shifts as there were for copersistent invaders. We thus generated sets of species to be used as sources for invaders that either did or did not have a shared history prior to their arrival in the new food web. To simulate invasions, for each of the 150 native webs, we randomly chose either one of the 150 copersistent invader webs or one of the 150 random invader species groups, without replacement. We then randomly assigned the invasive species an order of introduction and sequentially added these invasive species to the native web every 200 time steps, beginning at time step 2000. The simulation ended 200 time steps after the last addition of an invasive species. Biomass of introduced species ranged between 10^{-9} and 10^{-2} and invasive and native species were eliminated from the web if their abundance decreased below an extinction threshold of 10^{-10} . Parameterization of the dynamical model and functional responses follows the methods described in Romanuk et al. (2009). Invasion success was calculated as the proportion of species added to a native web that persisted until 200 time steps following the last invasion.

Our simulations revealed that invasion success increased over time for both the copersistent and random invaders, but the slope of this increase was steeper for invaders with shared history (Fig. 3A), indicating that shared history increased invasion success. The magnitude of these differences were similar across low, medium, and high connectance webs. However, invasion success for both random and copersistent invaders decreased with increasing connectance. As invaders from basal trophic levels were almost always successful, differences in invasion success were driven primarily by consumer invaders (Fig. 3B).

The benefit of shared history that we observed matches similar advantages noted in 'invasion cartels' of species invading, for example, the Great Lakes where prior invasion of Eurasian zebra mussels, *D. polymorpha*, and amphipods, *Echinogammarus ischnus*, provided established prey to facilitate the invasion of the round goby, *Neogobius melanostomus*, and lakes in Spain where invasive North American populations of the northern pike, *Esox lucius*, are sustained by previously invasive populations of the American crayfish, *Procambarus clarkii* (Ricciardi, 2005). Our results, combined with additional recent evidence that nonnative species are accumulating at an accelerating rate in some freshwater (Reid and Orlova, 2002; Ricciardi, 2001), marine (Cohen and Carlton, 1998), and terrestrial (Parker et al., 2006) systems, suggest that hypotheses to explain the likelihood of invasion success must incorporate the facilitative mechanisms known to promote invasional meltdown. Future studies will also benefit from assessing the importance of invader facilitation relative to native biotic resistance.

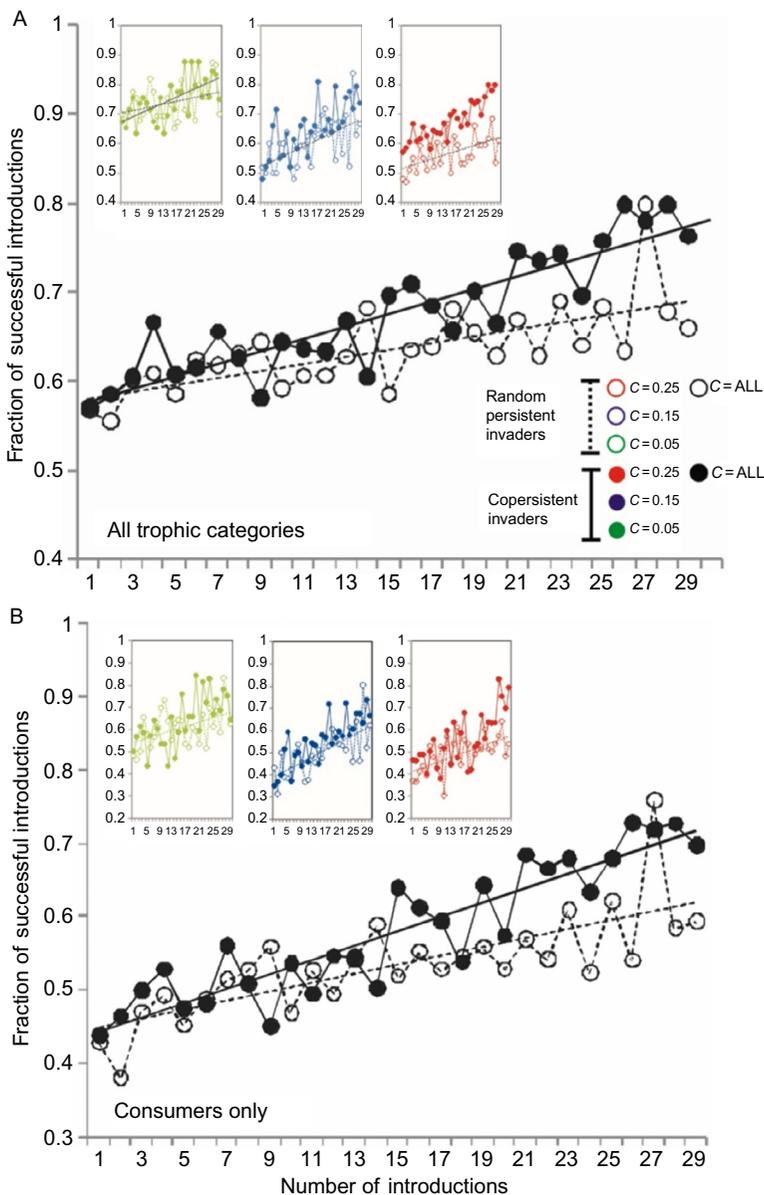


Fig. 3 Invasion success over time. The y axis is the fraction of invasions that were successful (e.g. the proportion of species added to a native web that persisted until 200 time steps following the last invasion), and the x axis shows how this changes across each sequential species invasion attempt. *Solid lines and filled symbols* are for copersistent invaders, with a shared history, and *dashed lines and unfilled symbols* are for random invaders, without a shared history. The main panels show invasion success
(Continued)

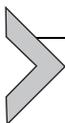
Question 12 How does the [In]Stability of the Network Facilitate or Prevent Invasions?

The stability of a system is defined as its ability to return to an equilibrium state after a disturbance. Unstable systems may therefore by definition enhance the likelihood of invasion success, since invasions represent a perturbation to the system and unstable systems enhance or propagate perturbations. However, this broad theoretical perspective has not been tested specifically for the perturbation of invasion. Some recent studies have used ecological stability concepts to understand evolutionary systems (Débarre et al., 2014; Svardal et al., 2014) and vice versa (Borrelli et al., 2015), and this cross-use of stability concepts may provide more concrete evidence that a perturbation of any type may promote a perturbation of any other type. Instead of stability inherently favouring or disfavouring invasion, unstable ecosystems may be adverse for species that have evolved in stable systems. In addition to selection for r and K strategists, c strategies may be observed in species well adapted to life in unstable, chaotic environments (Doebeli, 1995). For example, the theoretical study of Demetrius (2000) found that demographic stability of a population was positively correlated with a

Fig. 3—Cont'd across all levels of connectance (C) for (a) all trophic categories and (b) consumer invaders only. The inset panels show invasion success within low ($C=0.05$, green), medium ($C=0.10$, blue), and high ($C=0.25$, red) connectance webs. For analyses conducted on invaders at all trophic levels (A), the regression equation for copersistent invaders across all C (black solid line) is $y=0.007x+0.5721$ ($r^2=0.802$, $P<0.001$), for random invaders across all C (black dashed line) is $y=0.004x+0.577$ ($r^2=0.496$, $P<0.001$), for copersistent invaders at low C (green solid line) is $y=0.005x+0.669$ ($r^2=0.398$, $P<0.001$), for random invaders at low C (green dashed line) is $y=0.003x+0.702$ ($r^2=0.137$, $P=0.048$), for copersistent invaders at medium C (blue solid line) is $y=0.008x+0.536$ ($r^2=0.535$, $P<0.001$), for random invaders at medium C (blue dashed line) is $y=0.006x+0.518$ ($r^2=0.327$, $P=0.001$), for copersistent invaders at high C (red solid line) is $y=0.007x+0.571$ ($r^2=0.791$, $P<0.001$), and for random invaders at high C (red dashed line) is $y=0.004x+0.512$ ($r^2=0.319$, $P<0.001$). For analyses conducted for consumer invaders only (B), the regression equation for copersistent invaders across all C (black solid line) is $y=0.010x+0.435$ ($r^2=0.828$, $P<0.001$), for random invaders across all C (black dashed line) is $y=0.006x+0.443$ ($r^2=0.575$, $P<0.001$), for copersistent invaders at low C (green solid line) is $y=0.009x+0.505$ ($r^2=0.442$, $P<0.001$), for random invaders at low C (green dashed line) is $y=0.00x+0.536$ ($r^2=0.225$, $P=0.009$), for copersistent invaders at medium C (blue solid line) is $y=0.010x+0.397$ ($r^2=0.670$, $P<0.001$), for random invaders at medium C (blue dashed line) is $y=0.008x+0.384$ ($r^2=0.460$, $P<0.001$), for copersistent invaders at high C (red solid line) is $y=0.010x+0.403$ ($r^2=0.526$, $P<0.001$), and for random invaders at high C (red dashed line) is $y=0.006x+0.408$ ($r^2=0.357$, $P<0.001$).

measure of the variability in the age of reproducing individuals in the populations. Therefore, instability may introduce an environmental context that favours species adapted to this instability and disfavours invasion by species from more stable habitats.

Moving from theoretical to applied instances of system instability, managed agricultural ecosystems are highly perturbed by anthropogenic interventions such as regular modifications of the cultivated plant and associated other species, the mechanical alteration of soil, nutrient input, and pesticide use and therefore present an excellent case study to understand the effects of instability for invasion success. Invasive species in agroecosystems may follow dynamics similar to the reinvasion of pests that have been previously excluded via pesticide application or host suppression. Less perturbed agricultural networks—in this instance organic farms that maintain a higher evenness of natural enemies than conventional farms—clearly demonstrated an increased resistance to pest outbreak (Crowder et al., 2010). The mechanism for this resistance to invasion may be increased connectance observed in the organic networks, a property that is often associated with decreased success of invasive species (Baiser et al., 2010). Less intensively managed agricultural systems that are less perturbed should also, in accordance with the intermediate disturbance hypothesis, experience increased diversity and system stability and decreased likelihood of invasion success (Catford et al., 2012; Connell, 1978). This prediction is consistent with agroforestry systems, which are not intensively managed and experience increased stability associated with the presence of perennial plants, and in turn demonstrate a diverse array of species interactions that allow increased control of pests (Liere et al., 2012; Morris et al., 2015). The management of associated plants—plants that grow inside the agricultural system but are not the targets of cultivation—can have important impacts on stability and consequent control of pest reestablishment as well. Increasing the diversity of cover crops can help stabilize the food web (Djigal et al., 2012) and enhance predation on invasive pests (Mollot et al., 2012). Decreasing the frequency of mowing cover crops can increase system stability and pest control (Tixier et al., 2013) via an increase in generalist-feeding species (Dassou and Tixier, 2016; Letourneau et al., 2011) and enhanced complexity of interspecific interactions (e.g. enhanced intraguild predation or trophic coherence, which is a measure of food webs associated with species that feed on species in a variety of trophic levels; Johnson et al., 2014).



6. FUTURE DIRECTIONS FOR RESEARCH IN INVASION NETWORKS

Question 13 How does Spatial Connectivity Influence Ecological Networks and What are the Implications for the Study of Invasive Species?

Invasions span multiple stages—introduction, establishment, dispersal to new sites, and subsequent spread—and any of these stages may be sensitive to properties of the landscape where the invasion occurs. For example, the potential for introduction of alien species can depend on the degree of spatial or dispersal connectivity between the native and introduced habitat. This connectivity can be modelled in a variety of ways, such as considering a very strong spatial connection where all species invade on a similar timescale (consistent with the sudden appearance of bridges connecting previously isolated habitats) or considering sequential invasion attempts by individual species at varying rates (as in the Trophic Theory of Island Biogeography, [Massol et al., this issue](#), or in metacommunity models related to food web dynamics, [Calcagno et al., 2011](#); [Pillai et al., 2011](#)). Establishment of invasive species can be influenced by the spatial distribution of resources, of other species, and of habitat availability and quality ([Hastings et al., 2005](#); [With, 2002](#)). Diversity ([Fridley et al., 2007](#); [Shea and Chesson, 2002](#)) and competitive strength of the recipient community ([Hart and Gardner, 1997](#)) influence invasibility and these factors vary widely in a landscape as well.

Spatial properties such as patch size, shape, and connectivity also influence the spread of invasive species ([Harrison et al., 2001](#); [Maheu-Giroux and de Blois, 2007](#)). Spatial models of the spread of invasive species ([Ellner et al., 1998](#); [Fisher, 1937](#); [Shigesada and Kawasaki, 1997](#)) can be used to determine how invasive species might occupy a novel landscape and to determine practices to slow their spread ([Sharov and Liebhold, 1998](#)). This approach has been further developed to consider potential evolution of invading species along the advancing invasion front. Evolution of dispersal in invasive species can be important to understand their spread ([Burton et al., 2010](#); [Phillips et al., 2008](#)) and was observed in the invasive Australian cane toad ([Phillips et al., 2006](#)). Trade-offs among life history traits have also led to the evolution of deleterious traits in advancing invasive species. In the case of the invasive Australian cane toad, evolution of increased dispersal was associated with decreased reproductive rates ([Hudson et al., 2015](#)).

Spatial locations can also be described as networks, where edges represent distance or connectivity and nodes represent a geographic location (Dale and Fortin, 2010). This network perspective was used to identify inland lakes in Ontario, Canada that served as major hubs of transport for the invasive spiny waterflea *Bythotrephes longimanus* and thus were the most promising targets for management efforts to reduce boat traffic (Muirhead and MacIsaac, 2005). Properties of the spatial networks underlying food webs in a landscape are likely to have important effects for the stability and structure of resident populations and food webs. For example, species persistence is strongly influenced by spatial network spatial configuration (Adler and Nuernberger, 1994) and topology (Gilarranz and Bascompte, 2012). Bellmore et al. (2015) used an incremental aggregation of fish and aquatic invertebrate food webs from different locations in a river floodplain into increasingly complex metafood webs to show that increasing spatial complexity led to reduced strength of consumer–resource interactions, which is an important driver of food web stability. Much work remains to incorporate the full complexity of spatial networks into ecological network dynamics and this task is not simple (see Gravel et al., 2016; Mougi and Kondoh, 2016). It is currently unknown what spatial properties of food webs in a landscape render them more or less susceptible to invasion. It is also unclear whether these properties would depend on the trophic level or other attributes of the invasive species in the ecological network. Future research may identify geographic nodes that contribute most strongly to the spread of invasive species (e.g. Muirhead and MacIsaac, 2005) and try to identify properties of those nodes that promote invasion. Controlled invasion experiments (e.g. Morel-Journel et al., 2015) and theoretical modelling will be important tools to facilitate such analyses.

Question 14 How can we Integrate HTS Tools to Monitor Networks Before and After Invasions?

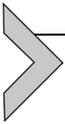
Monitoring multispecies interactions as well their response to various alterations such as biological invasions is resource-demanding and methodologically challenging. However, predicting the success of management actions requires the explicit and detailed quantification of direct and indirect ecological interactions within an invaded ecosystem (Bull and Courchamp, 2009). Emerging molecular techniques based on HTS such as metabarcoding or metagenomics have the potential to alleviate current methodological hurdles in network ecology (Kamenova et al., this issue; Vacher et al., 2016). HTS

techniques allow the detailed reconstruction of past and present biodiversity even from minute amounts of environmental DNA (eDNA) (Cannon et al., 2016; Hajibabaei et al., 2011; Willerslev et al., 2014; Yoccoz et al., 2012; Zaiko et al., 2015; Zhou et al., 2013). HTS methods can quantify complex trophic interactions without extensive a priori knowledge or taxonomic expertise (Bohmann et al., 2011; Boyer et al., 2013; Deagle et al., 2009; Mollot et al., 2014; Valentini et al., 2009). Finally, genomic HTS data can be used to derive direct quantitative estimates of species relative abundances or biomass (Andersen et al., 2012; Evans et al., 2016; Willerslev et al., 2014). Such quantitative biodiversity and trophic interaction data could therefore be used to quickly and inexpensively monitor weighted interaction networks across gradients of invasion or after management actions.

HTS-based food webs are scarce in the literature and studies that use this approach for understanding biological invasions have not been conducted yet. However, the application of HTS to other ecological questions can illuminate how this approach might benefit studies of invasion of networks of interacting species. HTS has been used to estimate prey attack rates at the level of complete interacting communities (Mollot et al., 2014; Vacher et al., 2016) and could similarly be used to estimate parasitism or pollination rates. Such data could be readily used to quantify the top-down impact of an invasive species or to assess the degree to which a potential biocontrol species affects an invader. HTS-based assessments of diet preference and the degree of trophic plasticity could be used to predict competition between native and invasive species or to forecast undesired cascading effects in feeding behaviours following management actions such as addition of biocontrol species or removal of target nuisance species. The simultaneous characterization of multiple types of species interactions is possible using HTS techniques (i.e. trophic or parasitic; Tiede et al., 2016), and such data could be used to simulate realistic species management scenarios and anticipate the impact of unexpected synergies or antagonisms that might increase invasion success.

Despite its vast potential, integrating HTS tools to monitor biological invasions will present technical and conceptual challenges as well. Technical challenges are inherent in setting up a universal HTS methodological framework to identify multiple types of species interactions in any type of habitat and organism in the field. Developing universal primers that amplify across a range of organisms spanning entire food webs will be challenging, and developing a bioinformatics pipeline to manage the massive amounts of data generated by HTS will require substantial time as well.

Conceptually, the use of HTS data does not provide the answer to questions that researchers must decide. Which network metrics are most suitable for efficient monitoring of invasions in natural systems? Which food web alterations are caused by the invasion in progress as opposed to other potential drivers of change in the system? One potentially interesting forward direction might be to use HTS to estimate and manage the functional role of invasive species, facilitated by techniques in the fast growing field of functional metagenomics (Chistoserdova, 2009). Invasive species monitoring could then focus on the profiles of gene or protein expression or functional activity, rather than on taxonomic identity per se. This approach could be useful to identify key genes influencing invader success and impact (Dlugosch et al., 2013; Scully et al., 2013) or to implement management strategies that seek to optimize an invasive species' integration in invaded ecosystems and minimize its impact on ecosystem functioning, rather than removal of the species.



7. CONCLUSION

Considering groups of interacting species as a network—where the links between the species represent interactions of competition, predation, parasitism, and mutualism—is a framework that may improve our understanding of and our ability to predict the dynamics of invasive species. Network properties such as connectance and modularity, which emerge only when arrays of ecosystem residents are considered, are indicative of system stability and provide important information about the system's susceptibility to invasion. Our goal here has been to address the information gaps and highlight exciting future directions of research needed to implement a network perspective in the study of invasive species. Some of the questions raised will contribute to advancing the field of ecology from a theoretical and conceptual perspective (e.g. Questions 2, 3, 5, 8, 10, and 12), while others are directly relevant to assist system management decisions (e.g. Questions 13 and 14). We end by emphasizing that it is important to consider not just the invasive organism and its strongest interaction partners but instead to identify the role the novel species plays in the context of the broader set of existing connections between resident species. Only then can researchers identify emergent signals that can be used to monitor the establishment and growth of invasive species and to manage them in ways that mitigate their harmful impacts for ecosystems.

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