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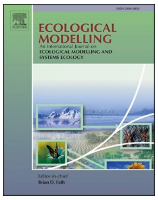

Metacommunity robustness to invasion in mutualistic and antagonistic networks

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ABSTRACT

One of the most significant threats to biodiversity is alien species invasion, and consequently understanding and predicting biological invasions has become an important issue in ecology. While numerous studies have explored the effect of community diversity and structure on invasion success, a systematic comparative analysis on system robustness to invasion between antagonistic and mutualistic networks from a metacommunity perspective is still lacking. Here we seek to address this gap using patch-dynamic models, which integrate local communities into the landscape metacommunity. We find that both mutualistic and antagonistic metacommunities displayed qualitatively similar responses to species invasion, except for animal invasion in antagonistic networks. Specifically, increasing network size and connectance generally promoted metacommunity persistence, while nestedness (negative) and modularity (positive) had contrasting effects on metacommunity robustness to invasion. However, these structural effects were strongly dependent on the generalization levels of both invader and the resident species it displaces. Overall, this study provides new and more general insights into how alien species are well integrated into native networks and how they affect metacommunity persistence.

1. Introduction

The disruption of established communities by invasive species is one of the most significant threats to biodiversity worldwide (Drake et al., 1989; Cronin and Haynes, 2004; Ricciardi et al., 2017; Frost et al., 2019; Hui and Richardson, 2019). Consequently, understanding and predicting biological invasions has become an important issue in ecology. As we know, natural communities are complex assemblages of species (or functional groups) which interact through a variety of trophic and non-trophic processes, for example, antagonistic and mutualistic networks (Cronin and Haynes, 2004; Baiser et al., 2010). Thus, whether and how the architecture of interaction networks can influence community invasibility has recently become a hot topic in invasion ecology, and significant progress has been made in our understanding of the architecture-invasibility relationship (Aizen et al., 2008; Hui et al., 2016; Valdovinos et al., 2018; Frost et al., 2019; Hui and Richardson, 2019; Häussler et al., 2021).

Despite these advances, field observations have actually found that invasive species can be well integrated into native communities (Olesen et al., 2002; Lopezaraiza-Mikel et al., 2007; Aizen et al., 2008; Romanuk et al., 2009; Albrecht et al., 2014; Frost et al., 2019). For example, absolute failure of invaders to integrate into native pollination webs seems unlikely, as many plant-pollinator interactions are rather unspecific and diversified, and alien mutualists have a high chance of interacting with native generalists (Memmott and Waser, 2002; Lopezaraiza-Mikel et al., 2007; Aizen et al., 2008; Albrecht et al., 2014). In addition, alien species associated with high invasiveness (due to high dispersal ability and reproduction rate; Sakai et al., 2001; Kolar and Lodge, 2001; van Kleunen et al., 2010), can quickly establish in a novel environment by displacing native competitors and therefore disrupting species interactions (Richardson et al., 2000; Traveset and Richasrdson, 2006; Aizen et al., 2008; Montero-Castaño and Vilà, 2012; Morales et al., 2013). As such, while invasion may result in a viable community, there is no guarantee that all resident species will survive (Larson et al., 2006; Bartomenus et al., 2008) or that the original community structure will be preserved (e.g. nestedness and modularity; Lopezaraiza-Mikel et al., 2007; Albrecht et al., 2014). In turn, interaction structure within resident communities has also been observed to play an important role in resisting invasion (Shea and Chesson, 2002; Fridley et al., 2007; Romanuk et al., 2009; Baiser et al., 2010; Frost et al., 2019).

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Furthermore, local communities even can benefit from the invader, for example, invasive plants can act as the resources for local predators in antagonistic communities, while invasive pollinators can effectively pollinate native plants and therefore increase their reproduction in mutualistic communities (Junker et al., 2010; Sanguinetti and Singer, 2014; Valdovinos et al., 2018). Therefore, the complexity of factors involved in determining the outcomes of invasion presents a significant modeling challenge which has yet to be systematically addressed (Valdovinos et al., 2018).

Besides, many natural communities on the landscape scale are typically spatially disaggregated, due to habitat heterogeneity or habitat fragmentation, and thus consist of relatively isolated subcommunities linked by species dispersal (Poisot et al., 2014; Galiana et al., 2018; Guimarães, 2020). Thus, a model for the landscape scale must encompass both small-scale subcommunities, with individual interaction networks, and the overall metacommunity, which includes all possible interactions (illustrated in Fig. 1; Kissling and Schleuning, 2015; Tylianakis and Morris, 2017). Luckily, the patch-dynamic framework (Fortuna and Bascompte, 2006; Pillai et al., 2011; Jabot and Bascompte, 2012; Liao et al., 2020), which was conceived to model such spatially disaggregated communities, provides a straightforward approach to address these open questions.

In this study, we thus constructed patch-dynamic models for both mutualistic and antagonistic metacommunities and challenged them with a single invasive species (Fig. 1). Using these models, we performed a systematic comparative analysis of the effects of invader properties, community type, and interaction network structure on robustness of the resident metacommunity to invasion. Here, robustness refers to the number of native species expected to become extinct after invasion, with fewer species losses indicating higher robustness (Lonsdale, 1999; Hui et al., 2016; Liao et al., 2020).

2. Methods

2.1. Theoretical framework

At the landscape scale, populations are often monitored by recording the presence or absence of a species in habitat patches. The metapopulation framework, originally developed by Levins (1969),

$$\frac{dP}{dt} = \underbrace{cP(1-P)}_{Colonization}\underbrace{-eP}_{Extinction} \tag{1}$$

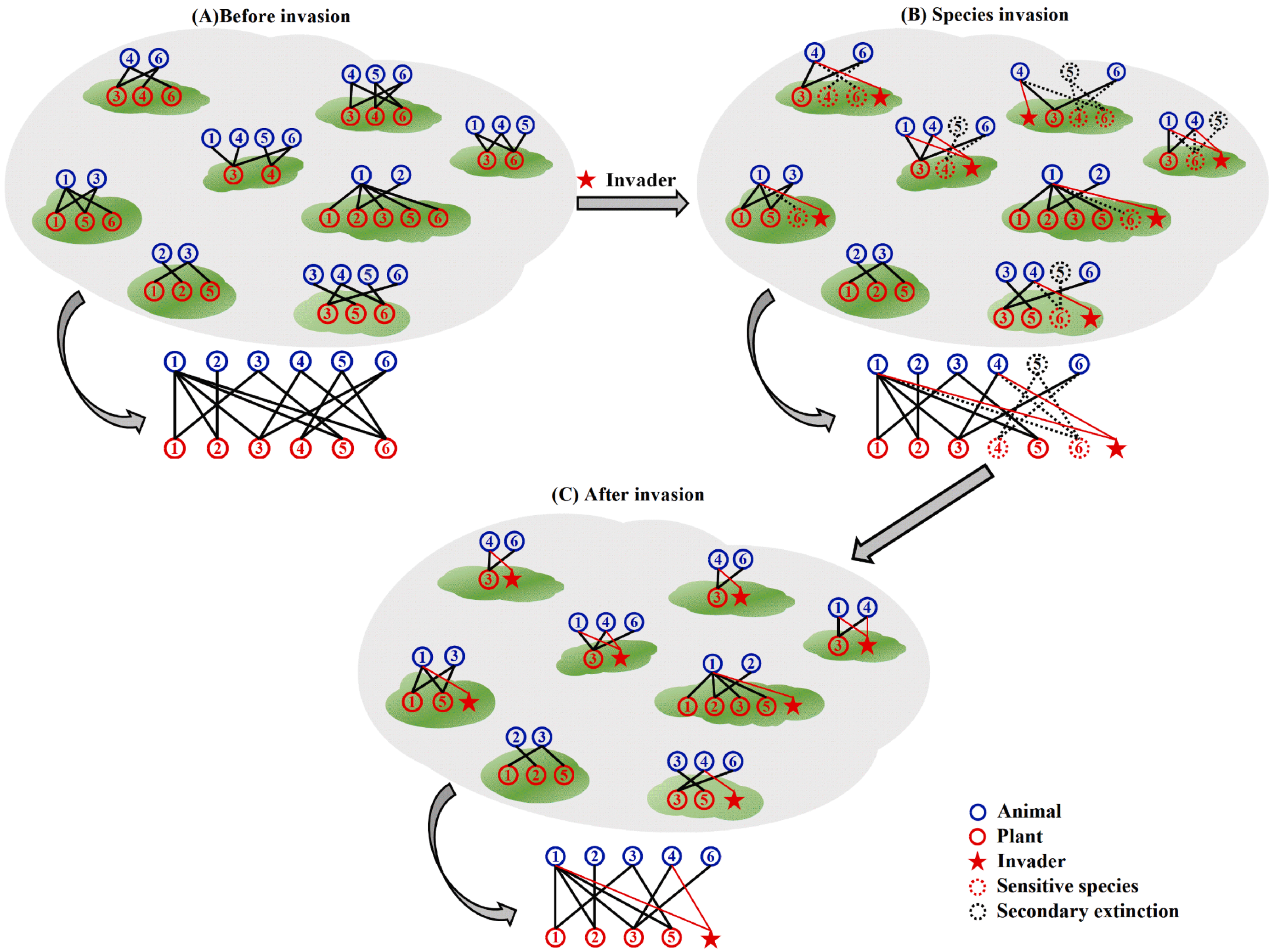

Fig. 1. Conceptual metacommunity framework of bipartite networks before and after species invasion. (A) Before invasion: a patch-dynamic framework allowing a metacommunity perspective on ecological networks by viewing networks as the regional assembly of simpler, spatially distributed subnetworks. Each patch is assumed to accommodate a local community (i.e. subnetwork) consisting of multiple interacting species, and the metacommunity is defined as a set of local communities linked by species dispersal; (B) Species invasion: the alien plant is introduced and invaded into local communities, with some native plants being sensitive to the invader and some native animals interacting with the invader; (C) After invasion: some sensitive plants would go extinct because of their all local patches being occupied by the invader, and some native animals would become extinct as their interacting plants are all extinct (i.e. secondary extinction).

is ideally suited to characterizing such dynamics (t is time) of patch occupancy (P) by a species (so-called patch-dynamic models; Hastings, 1980; Tilman, 1994). The parameters c and e describe the rates at which patches transition from unoccupied to occupied and vice versa. Colonization is restricted by the availability of unoccupied patches (i.e. $1 - P$). Such patch-dynamic models have been extended to describe the assembly of communities of species on patches of suitable habitat (i.e. metacommunities) based on colonization and extinction processes (Hanski and Ovaskainen, 2000; Melián and Bascompte, 2002; Pillai et al., 2011; Liao et al., 2020).

In this study, we consider metacommunities consisting of two classes of species, for example, plants and animals with a single common interaction type: mutualism or antagonism. These two classes are distinguished by their resource requirements; plants are able to colonize any patch, while animals are only able to colonize a patch already occupied by a suitable plant (Armstrong, 1987; Amarasekare, 2004). The interaction types are distinguished by the effect of animals on their interacting plants. In mutualistic communities, plants are only able to reproduce and colonize other patches if they co-occur with a suitable animal (e.g. representing pollination). In antagonistic communities, the extinction rate of plant species is increased when they co-occur with a suitable animal (e.g. representing top-down predator pressure). In order to focus on the effects of interactions between these classes, we assume that intra-guild competition is weak and thus that competitive exclusion does not occur within patches (e.g. Fortuna and Bascompte, 2006; Liao et al., 2020). Thus, each patch can accommodate a local community of interacting species.

In order to capture the differences between these two classes of species, and the possibility of multiple interacting species in each patch, we must modify the original patch dynamics in Eq. (1). For animals, we are able to use the same equation

$$\frac{dA_j}{dt} = c_j^A A_j\left[\Omega_j(t) - A_j\right] - e_j^A A_j, \tag{2}$$

regardless of whether interactions are mutualistic or antagonistic (Fortuna and Bascompte, 2006; Liao et al., 2020). Note that A_j, c_j^A, and e_j^A are the patch occupancy, colonization rate and extinction rate of animal j (in a metacommunity of n_P plants and n_A animals, i.e. total species richness $S = n_P + n_A$) as in Eq. (1). The key difference introduced is that the habitat available to the animal is not the entire landscape, but rather the patches already occupied by a suitable plant at a given time t, i.e. $\Omega_j(t)$. As an animal may interact with more than one plant species, $\Omega_j(t)$ is determined by the union of patches occupied by at least one suitable plant. Given that species are randomly distributed across the landscape, $\Omega_j(t)$ can be approximated from the patch occupancies of the plant species, i.e. the probability that a given patch is occupied by a given plant i (P_i). In particular, we estimate $\Omega_j(t)$ by calculating the probability that a patch is not occupied by any plant species that can interact with animal j

$$\Omega_j(t) = \left[1 - \prod\nolimits_{i=1}^{n_P}\left(1 - \theta_{ji}P_i\right)\right], \tag{3}$$

where $\theta_{ji} = 1$ if plant i interacts with animal j, and $\theta_{ji} = 0$ otherwise (Fortuna and Bascompte, 2006; Liao et al., 2020).

The two types of interaction differ in how the presence of an animal affects the plant. We describe the patch dynamics for plant i in mutualistic communities by

$$\frac{dP_i}{dt} = c_i^P\Phi_i(t)P_i(1 - P_i) - e_i^P P_i, \tag{4}$$

and in antagonistic communities by

$$\frac{dP_i}{dt} = c_i^P P_i(1 - P_i) - \left[e_i^P + \mu_i^P\Phi_i(t)\right]P_i. \tag{5}$$

Parameters c_i^P and e_i^P are the colonization and extinction rate of plant i respectively. The variable $\Phi_i(t)$ represents the fraction of patches occupied by plant i which are also occupied by at least one suitable animal (that can interact with plant i). In a mutualistic network, $\Phi_i(t)$ modifies the colonization rate in Eq. (4), while in an antagonistic network, it increases the extinction rate in Eq. (5) (with the top-down extinction rate μ_i^P). Like $\Omega_j(t)$, the value of $\Phi_i(t)$ can be estimated from the system state. Animals can only occur in patches where at least one suitable plant is present, i.e. in a sub-habitat of size $\Omega_j(t)$ for animal j. We can estimate $\Phi_i(t)$ by determining the probability that a given patch (occupied by plant i) is not occupied by any suitable animal that can interact with plant i

$$\Phi_i(t) = \left[1 - \prod_{j=1}^{n_A}\left(1 - \theta_{ij}A_j\frac{P_i}{\Omega_j(t)}\frac{1}{P_i}\right)\right], \tag{6}$$

in which $A_j\frac{P_i}{\Omega_j(t)}\frac{1}{P_i} = \frac{A_j}{\Omega_j(t)}$ represents the proportion of the i-patches (i.e. occupied by plant i) occupied by animal j when both of them can interact ($\theta_{ij} = 1$), with $\frac{P_i}{\Omega_j(t)}$ being the fraction of the i-patches accounting for all the potential patches that animal j can colonize.

The term $\Phi_i(t)P_i$ in Eqs (4 & 5) thus represents the probability that a given patch is both occupied by plant i and at least one animal with which it interacts across the landscape.

2.2. Introduction of an invasive species

As is typical in invasion studies, we investigate the effect of introducing a single alien species into an established metacommunity. To focus on the network structure as the main factor determining metacommunity robustness to invasion, we assume that: (i) there is no strong competition among resident species; and (ii) an invading species can displace those sensitive resident species (i.e. the resident species are sensitive to the invader) via competitive superiority. The first assumption can increase species coexistence both locally and globally without imposing any tradeoff (cf. Fortuna and Bascompte, 2006; Liao et al., 2020). The second assumption is represented by disallowing the sensitive resident species (i.e. the inferior competitor) to colonize the patches that the invader (i.e. the superior competitor) occupies, following previous patch-dynamic models (Hastings, 1980; May and Nowak, 1994; Tilman, 1994; Pillai et al., 2010, 2011).

If the invading species is an animal $j = n_A + 1$, we modify Eq. (2) to represent the effect of the invader on resident animals as follows.

$$\frac{dA_j}{dt} = c_j^A A_j\left[\Omega_j(t)\left(1 - \phi_j A_{n_A+1}\right) - A_j\right] - e_j^A A_j. \tag{7}$$

Similarly for mutualistic or antagonistic communities, we modify Eq. (4) or Eq. (5) respectively to represent the effect of an invading plant $i = n_P + 1$ on resident plants

$$\frac{dP_i}{dt} = c_i^P\Phi_i(t)P_i[(1 - \phi_i P_{n_P+1}) - P_i] - e_i^P P_i, \tag{8}$$

$$\frac{dP_i}{dt} = c_i^P P_i[(1 - \phi_i P_{n_P+1}) - P_i] - \left[e_i^P + \mu_i^P\Phi_i(t)\right]P_i. \tag{9}$$

In Eqs (7-9), the sensitivity coefficient ϕ_i (or ϕ_j) is either 1 or 0 depending on whether resident plant i (or animal j) is sensitive to the invader. For example, when $\phi_i = 1$ (i.e. the resident is sensitive), the fraction of the habitat available to the plant i is reduced to suitable patches which are not occupied by the invader, e.g. the term $(1 - \phi_i P_{n_P+1})$ in Eqs (8 & 9).

As, in general, an invading species must be able to integrate into the existing community Richardson et al., 2000; Memmott and Waser, 2002; Olesen et al., 2002; Morales and Aizen, 2006), we assume that it is able to interact with some of the resident species and vice versa. Thus, the variables $\Omega_j(t)$ and $\Phi_i(t)$ must be updated to include the invader Eqs (3 &

(6) become

$$\Omega_j(t) = \left[1 - \prod_{i=1}^{n_P+1} \left(1 - \theta_{ji} P_i\right)\right], \tag{10}$$

$$\Phi_i(t) = \left[1 - \prod_{j=1}^{n_A+1} \left(1 - \theta_{ij} \frac{A_j}{\Omega_j(t)}\right)\right], \tag{11}$$

where, as before, θ_{ij} indicates that plant i interacts with animal j.

2.3. Model setup and analysis

The structure of interactions within a metacommunity can be represented by a bipartite network of plants and animals (with links corresponding to interactions). We constructed a wider range of such community structures by varying the following four network structure metrics (Lau et al., 2017): network size (the number of species $S = n_P + n_A = 32, 64, 96$ with $n_P = n_A$), connectance (the relative number of interactions $C = 0.1{\sim}0.5$ with increasing intervals 0.05), nestedness (the level of sharing of interaction partners among species $N = \text{NODF}/100$; using the '*vegan*' R package to calculate NODF; Almeida-Neto et al., 2008; Oksanen et al., 2013) and modularity (the degree of compartmentalization Q; using the '*igraph*' R package; Newman and Girvan, 2004; Guimerà and Amaral, 2005). For each combination of network size and connectance, we built networks of varying levels of nestedness and modularity independently, following the algorithm of Thébault and Fontaine (2010 and more details therein). The resulting ensemble of community structures is represented graphically in Fig. S2 (see *Appendix B*).

The interactions between resident species and an invader were determined as follows. We set fractions $F_1 \in [0,\ 1]$ and $F_2 \in [0,\ 1]$ of resident species which would be sensitive to or able to interact with the invader. The appropriate number of species were then selected to be sensitive either randomly (Random) or systematically based on their number of connections within the native metacommunity. We considered two systematic cases: Most - sensitivity was assigned to resident species in order from most connected (i.e. resident generalists) to least connected ones (i.e. resident specialists); and Least - the reverse (from least connected to most connected species). Similarly, the appropriate number of species were assigned to interact with the invader either randomly or using a preferential attachment algorithm (Barabási and Albert, 1999), i.e. with highly connected species being more likely to interact with the invader. Note that there was little difference in results between random and preferential attachments (Figs S5-S7 in *Appendix B*), so results for random attachment are used throughout.

The resulting models increase in complexity with network size and, as such, are difficult to investigate analytically for ecologically relevant cases (but see *System analysis* for a simplified neutral model in *Appendix A*). Consequently, we primarily adopted numerical methods (via ODE45 in Matlab R2016a) to derive the non-trivial steady states of systems. The dynamics of the resident metacommunity were run until they reached a long-term steady state (either reaching a fixed point or a periodic cycle). We then introduced an invasive plant or animal and re-ran the dynamics until a new steady state was reached (see Fig. S1 in *Appendix B*). Species were deemed extinct if their patch occupancies fell below 10^{-6}, and the number of native species remaining before and after invasion was recorded for each simulation. The demographic traits of all native species, including species colonization rates (c_i^P& c_j^A), extinction rates (e_i^P & e_j^A) and top-down extinction rates (μ_i^P), were randomly drawn from appropriate uniform distributions $U[min,\ max]$. In each case, patch dynamics were simulated with 20 replicates for each network structure to reduce the effect of random assignment of sensitivity and attachment. In each replicate, we used different random seeds to avoid generating the same uniformly-distributed values for species demographic traits. From numerous preliminary simulations for a variety of parameter combinations, we found that changing initial species patch occupancies does not alter system steady states, thereby demonstrating the stability of these steady states. A broad range of parameter combinations were explored initially and found to yield qualitatively consistent metacommunity patterns. Thus, we chose a set of parameter values for all native species (see Fig. 2) as a representative case throughout, and interestingly, in most cases, no species loss occurs for either community type before invasion. With the model, we attempt to explore the relationship between network structures (i.e. linking patterns) and metacommunity robustness to invasion for antagonism and mutualism.

3. Results

The proportions of resident species being sensitive to (F_1) and able to interact with (F_2) the invader are key determinants of the effect of an invasion (Figs 2-3&Figs S3-S7 in *Appendix B*). Regardless of how they are selected, increasing the proportion of sensitive species reduces proportion of resident species which survive after invasion (Figs 2, 3A-B&E-F). This follows naturally from the assumption that the invader excludes sensitive species from patches that it occupies, which can significantly increase their extinction risk (see *System analysis* in *Appendix A*). This effect can be offset by the invader's suitability for connections with resident species (Fig. 3C-D, G-H). Resident losses are generally lowest when the invader disproportionately displaces resident specialists ("Least"; Figs 2&3), in contrast to the "Most" case (Figs 2&3) where the sensitivity of resident generalists to the invader leads to highest species losses. Additionally, invaders which require interactions with other species (mutualistic animals or any plants) must form sufficient connections with residents to invade successfully. If they do not reach this threshold, such invaders are unable to invade and thus cause few losses in the resident metacommunity (Figs 2D-L, 3D&G-H). Similarly, invading plants with more connections to animals (Figs 2B-C, 3C) suffer greater predation pressure and thus are less likely to successfully invade. Furthermore, we note that the impact of invaders of mutualistic metacommunities saturates as they form more connections with residents and thus cause fewer secondary extinctions (Figs 2E-F&K-L and 3D&H).

We observe some small deviations from these, relatively intuitive, trends. Firstly, in animal invasions of antagonistic metacommunities, resident losses are highest when the invader disproportionately displaces resident specialists (Fig. 3E&G). This can be explained by the fact that specialist animals are more vulnerable to extinction than generalist animals which are better able to tolerate direct competition from the invader. Additionally, there is an increase in resident survival at very high levels of resident sensitivity to the invader in antagonistic communities (Fig. 3A), due to the positive feedback loop, i.e. the release of top-down predation pressure from some resident animals can promote the abundances of associated resident plants, which in turn is just sufficient to support other associated resident animals that would otherwise go extinct. More specifically, this can be explained with reference to Fig. S12 (see *Appendix B*) for the case of an invading plant. When almost all resident plants are sensitive to the invader, the insensitive plants survive in sufficient abundance to support animals. These animals can impose predation pressure on sensitive plants which might otherwise survive, driving them to extinction. By contrast, when all plants are sensitive to the invader, only animals which directly feed on the invader can survive and any plants which do not interact with these animals are released from predation pressure, permitting them to survive at low abundance.

The finer details of interaction network structure (including network size, connectance, nestedness and modularity) also influence the robustness of a metacommunity to invasion (Figs 4&5 and Figs S8-S11 in *Appendix B*). Increasing network connectance preserves species richness post-invasion (Fig. 4 and Fig. S8 in *Appendix B*). This effect saturates quickly in larger networks, indicating that the effect is due to each resident attaining a particular threshold number of links within the community, i.e. sufficient to minimize the risk of secondary extinction.

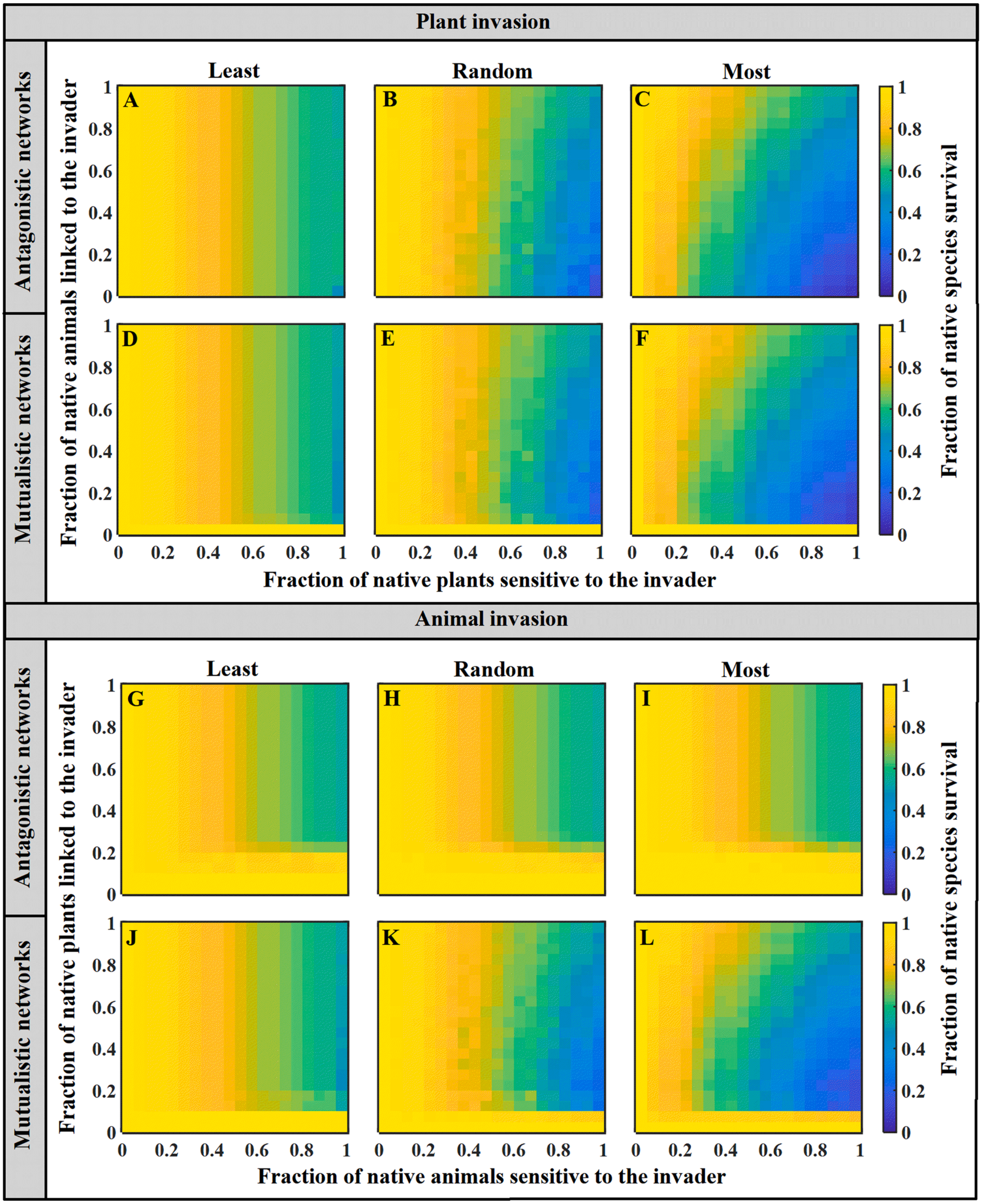

Fig. 2. Metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both antagonistic and mutualistic networks (network size $S = 32$, connectance $C = 0.25$ and nestedness $N = NODF/100 = 0.65$), simultaneously varying both the fraction of native (plant or animal) species sensitive to the invader ($0 \leq F_1 \leq 1$) and the fraction of native (plant or animal) species linked to the invader ($0 \leq F_2 \leq 1$) via random attachment. Three selective modes for species sensitivity to the invader are considered: randomly selecting species irrespective of their linking degree (Random), species selection in decreasing order of their linking degree, i.e. starting from most connected species (Most), and species selection in increasing order of their linking degree, i.e. starting from least connected ones (Least). The colonization rates of all native plant (c_i^P) and animal (c_j^A) species are randomly drawn from a uniform distribution $U[0.4,\ 0.6]$, their extinction rates (e_i^P & e_j^A) are sampled from $U[0.08,\ 0.12]$, and the top-down extinction rates $\mu_i^P \in U[0.08,\ 0.12]$, while the demographic traits of the invader are set as $c_{n_P+1}^P = c_{n_A+1}^A = 0.8$, $e_{n_P+1}^P = e_{n_A+1}^A = 0.1$ and $\mu_{n_P+1}^P = 0.1$.

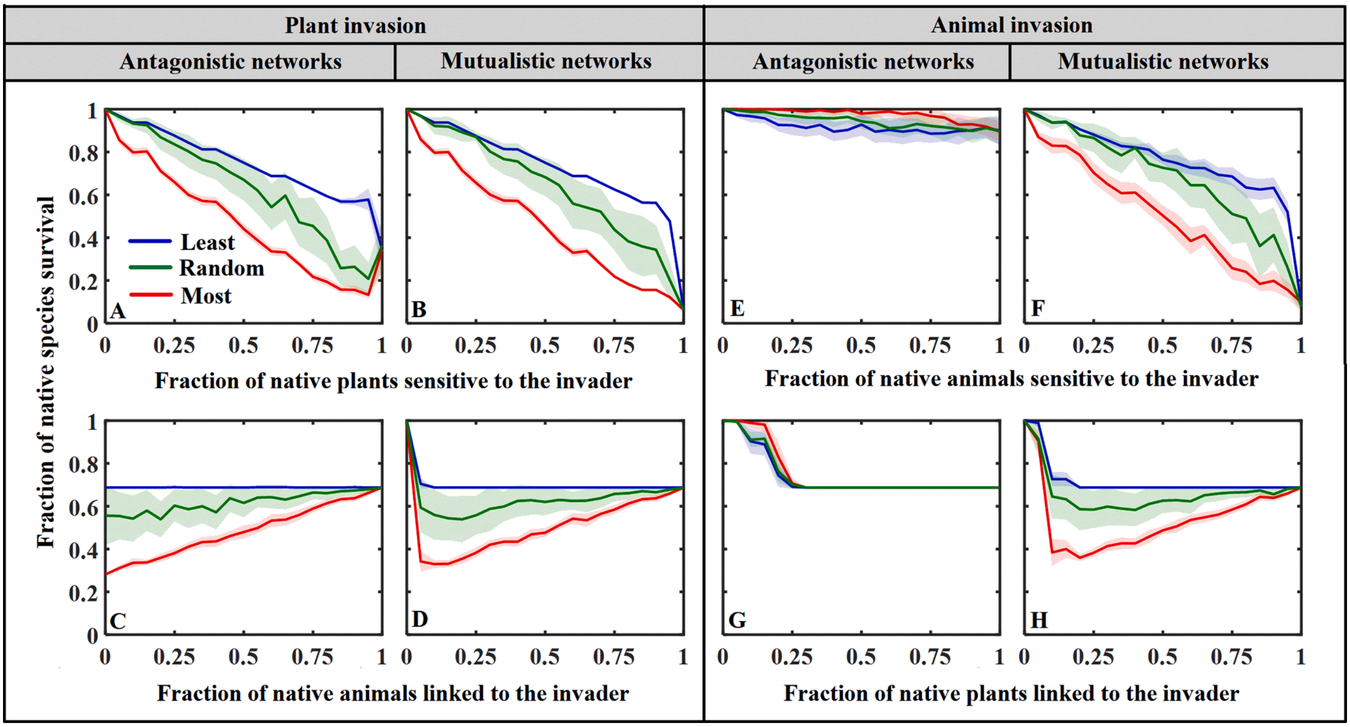

Fig. 3. Individual effects of species sensitivity to the invader and species interaction with the invader (via random attachment) on metacommunity persistence at steady state (mean ± standard deviation SD of 20 replicates) for both antagonism and mutualism, separately by fixing the fraction of native (plant or animal) species linked to the invader (F_2=0.1) and the fixing the fraction of native (plant or animal) species sensitivity to the invader (F_1=0.6). Again three selective modes for species sensitivity to the invader are included: Random, Most and Least (see *SubSection 2.3*). Other parameters are the same as in Fig. 2.

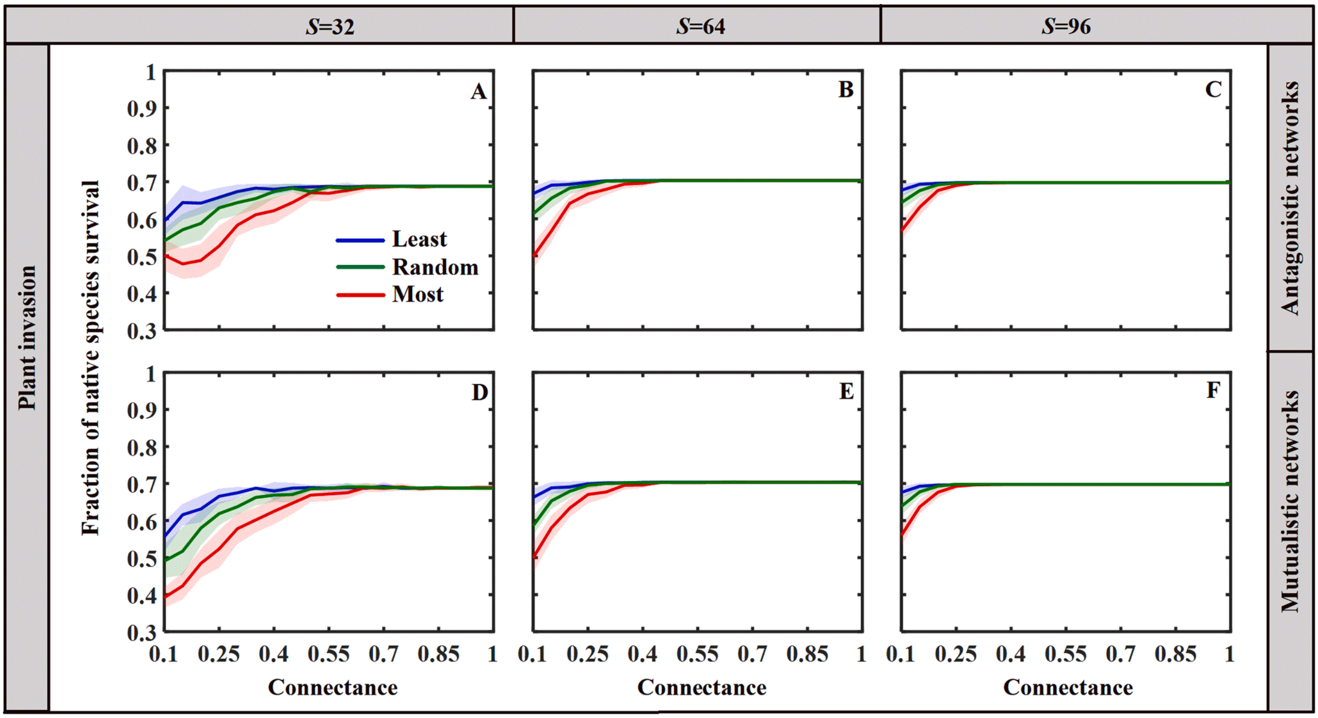

Fig. 4. Effect of initial network connectance on metacommunity persistence (mean ± SD of 20 replicates) facing plant invasion at steady state, by varying network size (S = 32, 64 and 96). Note that all bipartite networks used here are randomly structured (i.e. each plant–animal pair has the same probability to interact). Others are the same as in Fig. 3.

We note that, following from the trends noted above, this effect is generally strongest when the invader has the largest impact on the resident community, i.e. when the invader disproportionately affects generalists in all but the case of an animal invasion of an antagonistic community (see Fig. S8A-C in *Appendix B*). In this exception, increasing network size initially does not affect resident species richness, but then

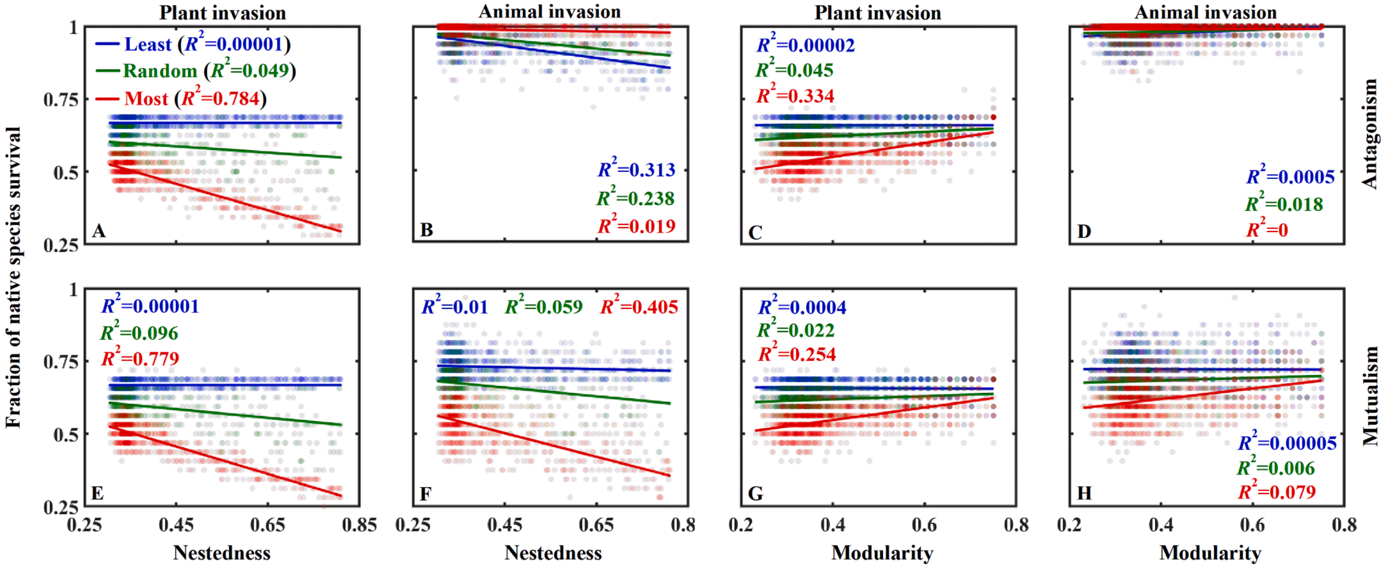

Fig. 5. Individual effects of initial nestedness (N=$NODF$/100; 620 networks) and modularity (Q; 1010 networks) on metacommunity persistence at steady state (linear fitting with R^2) under plant or animal invasion in both mutualistic and antagonistic networks (fixed $S = 32$ and $C = 0.25$). Parameters: fraction of (plant or animal) species sensitivity to the invader F_1=0.6 (containing three selective ways: Random, Most and Least), and fraction of native (plant or animal) species linked to the invader (F_2=0.1) via random attachment. Other parameter values are the same as in Fig. 2.

results in a sudden decline to a constant fraction of the initial community size (see Fig. S9I-L in *Appendix B*), indicating a critical threshold below and above which a further increase in network size does not affect species survival. This also suggests that the invader can only exclude resident sensitive animals when it preys on a sufficient number of resident plants. The nestedness and modularity of the interaction network structure have opposite effects on the impact of invasion (Fig. 5 and Figs S10-S11 in *Appendix B*). Specifically, increasing nestedness or modularity, decreases or increases respectively metacommunity robustness to invasion. In line with our previous observation, these effects are strongest when resident generalists are sensitive to the invader, again except for animal invasion in antagonistic communities (Fig. 5B&D).

4. Discussion

Successful invasive species are typically able to integrate themselves into the network of interactions present in the resident community (Memmott and Waser, 2002; Lopezaraiza-Mikel et al., 2007; Aizen et al., 2008; Bartomeus et al., 2008; Vilà et al., 2009; Albrecht et al., 2014). As such, it is natural to suppose that the structure of this network plays an important role in invasion success or failure. Our results refine this hypothesis, setting out the key structural features which determine how robust a community is to invasion.

The effects of invasion by a plant are qualitatively similar regardless of whether the invaded community is mutualistic or antagonistic (Figs 2&3). By contrast, invasion by an animal has greater impact in mutualistic communities than in antagonistic ones. From a metacommunity perspective, animals are always more vulnerable than plants; as they can colonize only patches where a suitable plant is already present. Consequently, the displacement of resident plants by an invader will always induce secondary extinctions among animals. Only in mutualistic communities are plants similarly reliant on animals and, as such, animal invasion of antagonistic communities does not produce the same extinction cascade. The impact of an invading species on the resident metacommunity is, naturally, dependent on whether the invading species is able to establish itself. For animals and mutualistic plants, invasion success is, thus, dependent on the number of residents with which the invader is able to interact. Consequently, such invaders have negligible impact on the metacommunity if they do not interact with more resident species than some, system dependent, critical threshold (Figs 2&3). Only plants invading antagonistic communities avoid this limitation as their invasion success is not dependent on other species. Interestingly, above this threshold, the impact of an invader tends to decline as the number of interactions it has with resident species increases, i.e. the invader is most detrimental to the metacommunity when it has only sufficient links to resident species to successfully invade. This trend arises because generalist invaders cause fewer secondary extinctions most likely through providing the same interactions as the species they displace. Animals invading antagonistic communities are the only exception. By displacing resident animals, they reduce predation pressure on plants, but as the number of plants they prey on increases, they replace that predation pressure themselves (Fig. 3G).

Similarly, it is natural that increasing the proportion of species that are vulnerable to displacement by the invader results in more vulnerable metacommunities. It is, however, noteworthy that the selection of these sensitive species also has an important effect (Figs 2-3). In most cases, it is the generalists (i.e. highly connected species; Fig. 2) which are most important in determining the impact of invasion. Since these species are highly connected, their losses are more likely to induce secondary extinctions. Yet, we have tended to find animals in antagonistic communities deviate from this trend, as other species do not rely on them for survival (i.e. without secondary extinctions). Consequently, animal invasions of antagonistic communities have most impact when the invader displaces specialists (Fig. 3E&G), which are naturally more vulnerable to extinction than generalists due to their more limited colonization options.

In addition to these direct interactions between an invader's attributes and the resident metacommunity, the underlying structure of interactions within the metacommunity also plays an important role in determining a community's robustness to invasion. Increasing resident community diversity and the proportion of resident species which interact (connectance) increases system robustness to invasion. This results from the fact that in larger, more connected, metacommunities, the displacement of species by an invader is less likely to cause secondary extinctions, and the remaining species are more likely to retain essential interactions (Wardle, 2001; Baiser et al., 2010; Smith-Ramesh et al., 2017). This effect saturates as community size and connectance increase, because any individual species only needs to retain a critical number of interactions to remain viable. Smith-Ramesh et al. (2017) 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, indirectly supporting this modeling outcome. Thus, our results suggest that more diverse metacommunities should have a greater tolerance of invaders, showing more robust to invasion.

The effects of nestedness and modularity of the interaction network depend on whether the invader disproportionately displaces resident specialists or generalists (Fig. 5). Nestedness describes the degree to which the metacommunity generalists form a single dense core interacting with all other species (Fortuna and Bascompte, 2006; Strona et al., 2013; Strona and Lafferty; 2016). Consequently, if an invader displaces these core generalists in a nested structure of beneficial interactions, it has the potential to significantly disrupt the metacommunity through secondary extinctions. On the other hand, if it displaces specialists, it will induce few secondary extinctions, and may, in fact, provide greater interaction redundancy increasing community robustness to disturbances. Thus, increasing nestedness increases the impact of an invader in the former case while having little effect in the latter. Naturally, if the interactions are detrimental, as in the case of antagonistic animals, these effects are reversed (Fig. 5B and Fig. S10 in *Appendix B*). In Fig. 5C-D&G-H, we show that the effect of increasing modularity is the reverse of that obtained when increasing nestedness (see Fig. S11 in *Appendix B*). Modularity measures the degree to which a community is compartmentalized into independent, disconnected, subcommunities. Thus, increasing network modularity is more likely to limit the impact of an invader to a subcommunity and thus buffer the propagation of secondary extinctions throughout the whole metacommunity (cf. Stouffer and Bascompte, 2011), explaining the reversed effect. The opposite effects of nestedness and modularity on metacommunity robustness to invasion suggest a negative correlation between nestedness and modularity, consistent with the statistical analysis for those empirical networks at high connectivities (see Fortuna et al., 2010).

Our model demonstrates that, on the landscape scale, metacommunity robustness to invasion is a complex function of native species sensitivity to the invader, alien species integration, network structural properties and the type of interaction. Generally, both mutualistic and antagonistic metacommunities display similar responses to species invasion, except for animal invasion in antagonistic networks where plants are not dependent on animals. Regardless of the type of interaction, increasing network size and connectance promotes metacommunity robustness to invasion, while both nestedness (negative) and modularity (positive) show the opposite effects. 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 (Wei et al., 2015), in line with our theoretical predictions. However, these structural effects can be significantly affected by whether the invader disproportionately displaces generalist or specialist species and whether it is a generalist or specialist itself. To simplify the modeling framework, we only focus on antagonistic and mutualistic interactions between plants and animals, while ignoring other potential interactions (e.g. intraguild predation among animals, interference competition among plants or animals, etc.). One can anticipate that considering these potential interactions might have a substantial effect on metacommunity robustness to invasion, thus future study can conceptualize these different interactions into models for comparison. Overall, the patch-dynamic framework provides new and more general insights into how alien species are well integrated into native networks and how they affect metacommunity persistence.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that cdocould have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.109949.

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Supplementary Material

Appendix A - *System analysis*

Under the neutral assumption that all native species, including plants and animals, have the same demographic traits (i.e. $c_i^P = c_j^A = c,\ e_i^P = e_j^A = e$), and that top-down extinction rates are equivalent ($\mu_i^P = \mu$), some analytic, general, results can be obtained from Eqs (2, 4 & 5) (see Section 2: *Methods*). Specifically, the following non-trivial coexistence steady states

$$P_i^*(mut) = 1 - \frac{e}{c\Phi_i^*} \text{ or } P_i^*(ant) = 1 - \frac{e+\mu\Phi_i^*}{c} \qquad (0 \le \Phi_i^* < 1) \tag{A.1}$$

and

$$A_j^* = \Omega_j^* - e/c \tag{A.2}$$

exist for mutualistic or antagonistic communities respectively. These steady states are ecologically reasonable, i.e. all species have positive occupancy, when $\Phi_i^* > e/c$ & $\Omega_j^* > e/c$ or $\Phi_i^* < (c-e)/\mu$ & $\Omega_j^* > e/c$ for each species in mutualistic or antagonistic communities respectively.

After plant invasion, we obtained the patch occupancy for native plants at steady state

$$P_i^*(mut) = 1 - \varphi_i P_{n_P+1}^* - \frac{e}{c\Phi_i^*} \ \&\ P_i^*(ant) = 1 - \varphi_i P_{n_P+1}^* - \frac{e+\mu\Phi_i^*}{c}, \tag{A.3}$$

where $0 \le \Phi_i^* < 1$ and φ_i =0 or 1. Similarly for the plant invader, $P_{n_P+1}^*(mut) = 1 - \frac{e}{c\Phi_{n_P+1}^*}$ and $P_{n_P+1}^*(ant) = 1 - \frac{e+\mu\Phi_{n_P+1}^*}{c}$ if it has the same demographic traits as the natives. This suggests that the invader is required to interact with a sufficient number of resident animals for survival in mutualistic metacommunities ($\Phi^*_{n_P+1} > e/c$), while this would reduce the survival of the invader in antagonistic metacommunities ($\Phi^*_{n_P+1} < \frac{c-e}{\mu}$). When the plant invader is well integrated into the resident metacommunity, the sensitive native plants ($\varphi_i = 1$) face a greater extinction risk than those which are insensitive ($\varphi_i = 0$) due to lower patch availability. The decline in abundances of these sensitive plants would also affect the abundance of linked native animals (see Eqs A.2 & A.3), which do not interact with the invader, by reducing their potential patch availability (Ω^*_j). In turn, this could lead to secondary extinctions. Interestingly, if both the invader and the sensitive plant share highly similar characteristics of interactions with resident animals (i.e. similar niche; $\Phi^*_i = \Phi^*_{n_P+1}$), then the sensitive plant would become extinct much easily.

The steady state for native animals, after animal invasion

$$A^*_j = \Omega^*_j\left(1 - \varphi_j \cdot A^*_{n_A+1}\right) - e/c, \qquad \text{(A.4)}$$

suggests the same trend, with sensitive animals ($\Omega^*_j > \frac{e}{c(1-A^*_{n_A+1})}$) more susceptible to extinction than insensitive animals ($\Omega^*_j > e/c$). In mutualistic communities, this could result in secondary extinctions among plants which interact with these species, while in antagonistic communities, prey plants would increase in abundance, due to release from top-down predation pressure (see Eq. A.1), unless the invader consumes the same species. Likewise, the steady state for the animal invader in both types of interaction $A^*_{n_A+1} = \Omega^*_{n_A+1} - e/c$ indicates that the invader must interact with a sufficient number of resident plants for survival ($\Omega^*_{n_A+1} > e/c$), otherwise the invasion fails. If the invader is well integrated into the resident community, the sensitive animals should meet $\Omega_j^* > \frac{e}{c - c\Omega_{n_A+1}^* + e}$ for survival, suggesting that they are more vulnerable to extinction when the invader interacts with more resident plants.

Appendix B – *Figures S1-S12*

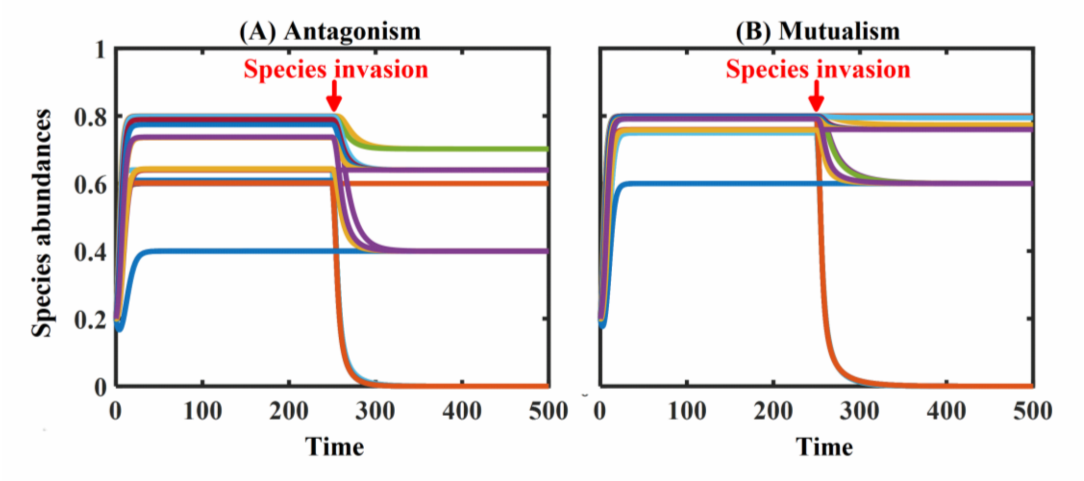

Figure S1. Metacommunity dynamics for both antagonistic (A) and mutualistic (B) bipartite networks before and after a plant species invasion (different colors – different species). Parameter values: fraction of native plants sensitive to the invader F_1=0.9, selected in increasing order of their linking degree (i.e. starting from least connected to most connected species), fraction of native animals linked to the invader F_2=0.1 with random attachment, all native species with the same demographic traits: $c_i^P = c_j^A = 0.5$, $e_i^P = e_j^A = 0.1$ and $\mu_i^P = 0.1$, while the invader: $c_{n_P+1}^P$=0.8, $e_{n_P+1}^P = 0.1$ and $\mu_{n_P+1}^P = 0.1$.

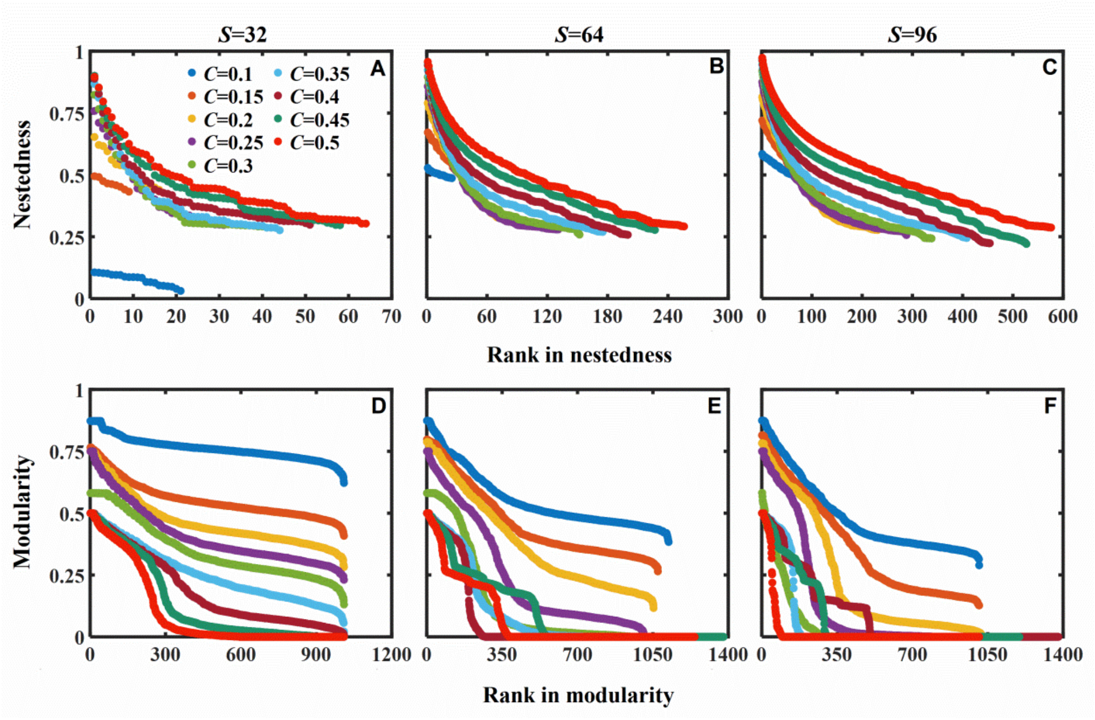

Figure S2. The generated bipartite networks of varying levels of nestedness and modularity independently at each combination of network size (*S*) and connectance (*C*). These networks are used as initial metacommunity structures for both mutualism and antagonism in our study.

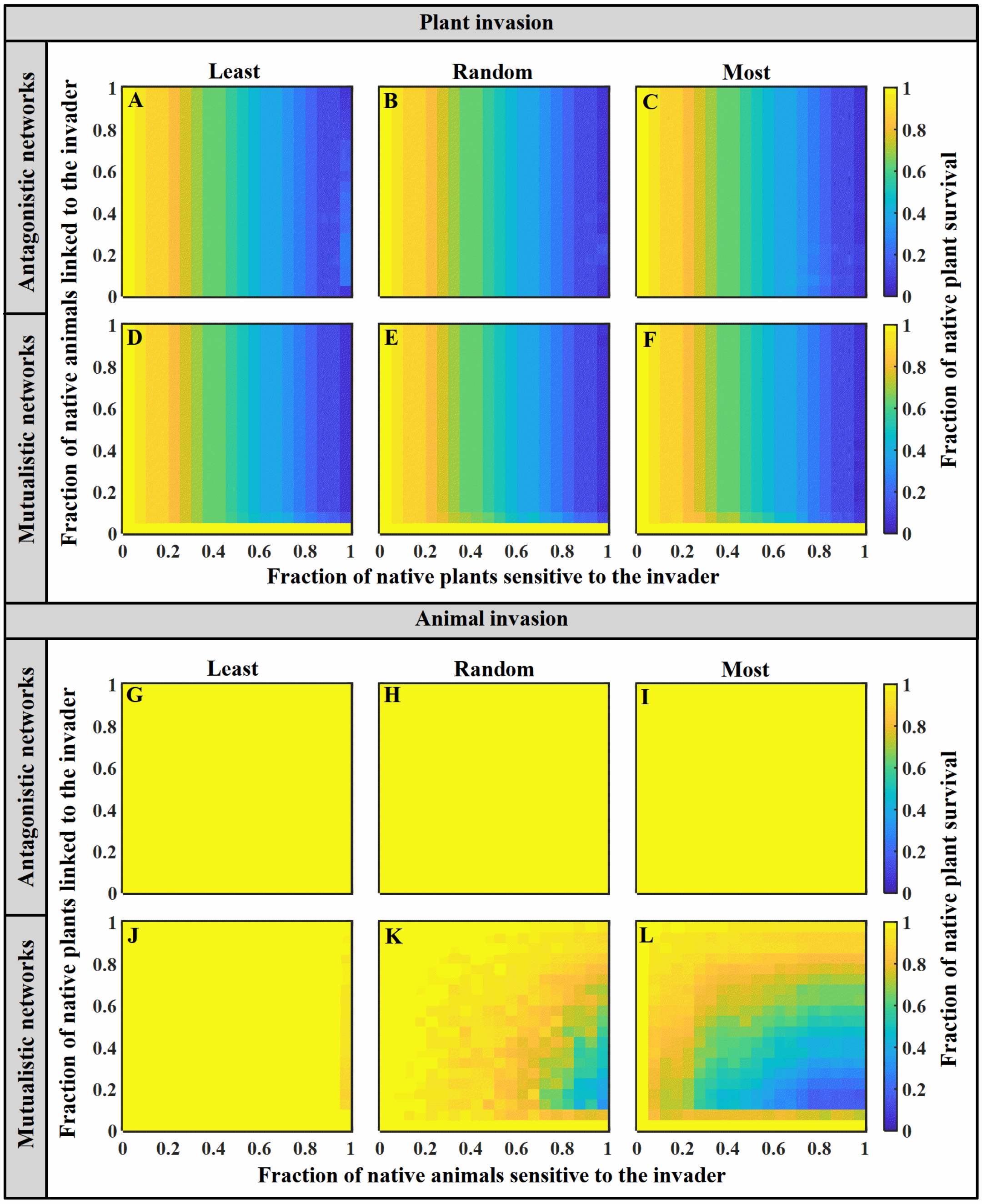

Figure S3. Plant metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both mutualistic and antagonistic networks (S=32, C=0.25 and N=0.65). Others are seen in Fig. 2.

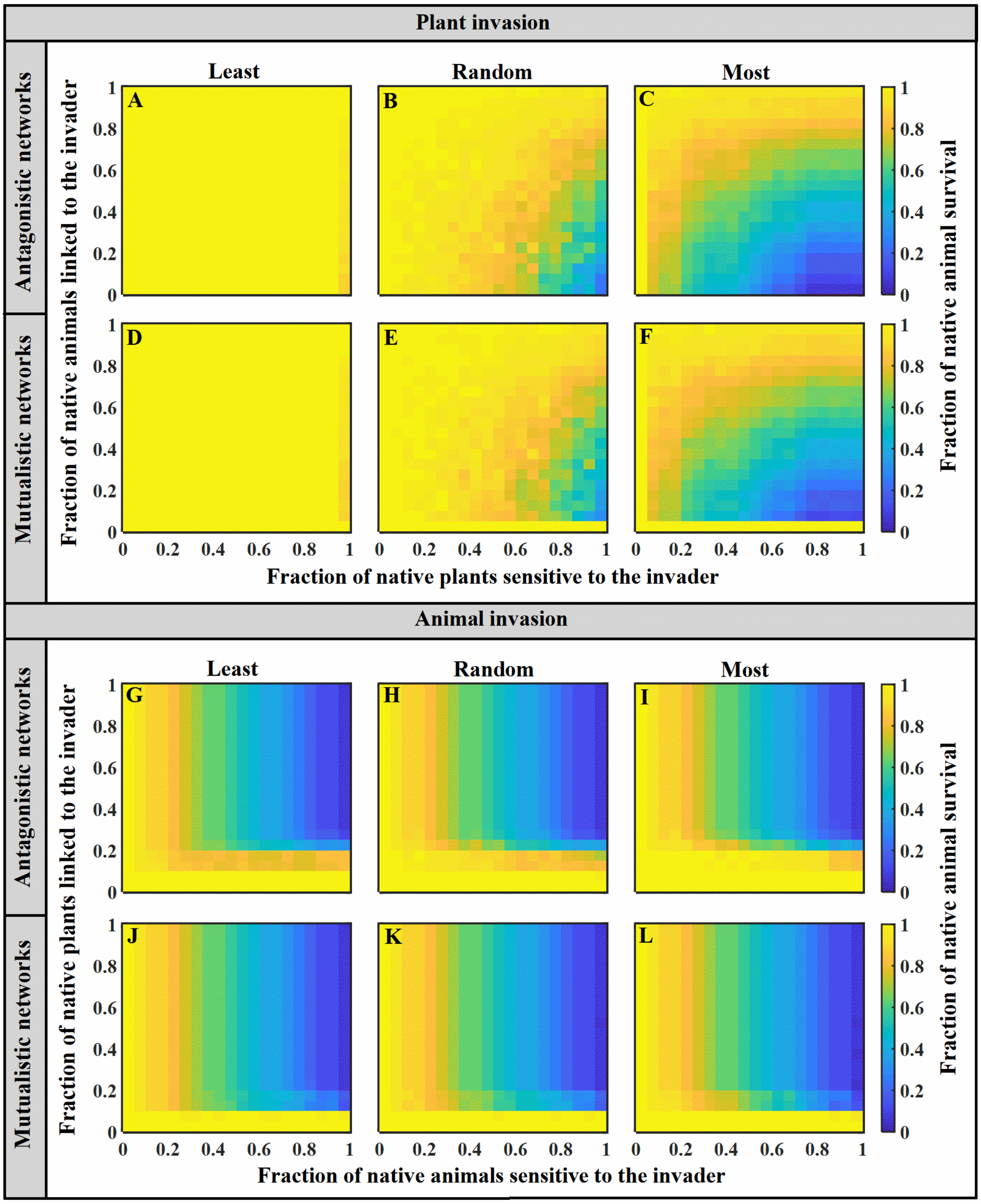

Figure S4. Animal metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both mutualistic and antagonistic networks (S=32, C=0.25 and N=0.65). Others are seen in Fig. 2.

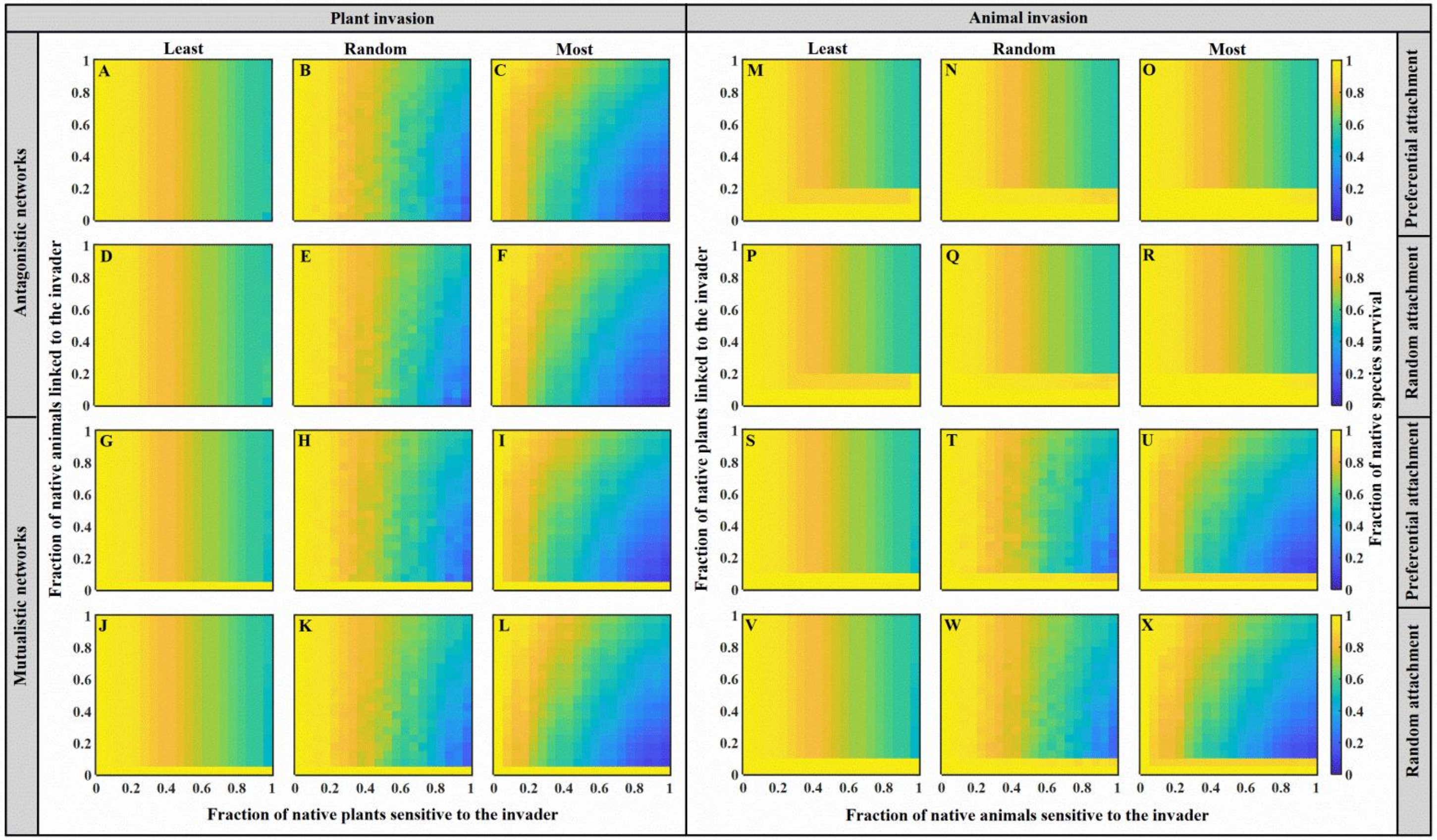

Figure S5. Metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both mutualistic and antagonistic networks (network size *S*=32, connectance *C*=0.25 and nestedness *N*=*NODF*/100=0.65), simultaneously varying both the fraction of native (plant or animal) species sensitive to the invader (F_1; three selective ways: Random, Most and Least; see *Methods*) and the fraction of native (plant or animal) species linked to the invader (F_2) via both random and preferential attachment. For simplicity, all native species with the same demographic traits: $c_i^P = c_j^A = 0.5$, $e_i^P = e_j^A = 0.1$ and $\mu_i^P = 0.1$, while the invader $c_{n_P+1}^P$=0.8, $e_{n_P+1}^P = 0.1$ and $\mu_{n_P+1}^P = 0.1$.

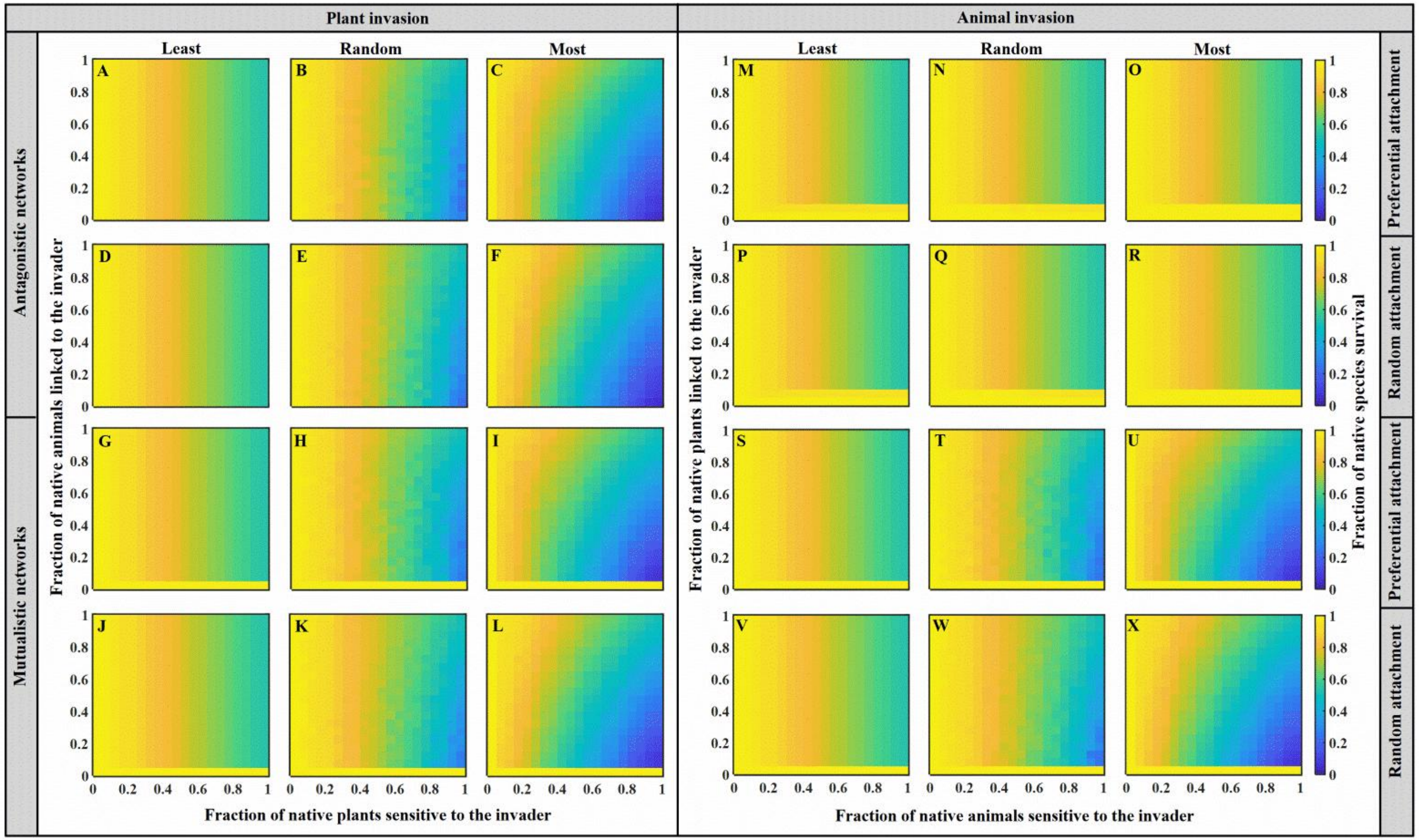

Figure S6. Metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both mutualistic and antagonistic networks (S=64, C=0.25 and N=0.65). Others are the same as in Fig. S5.

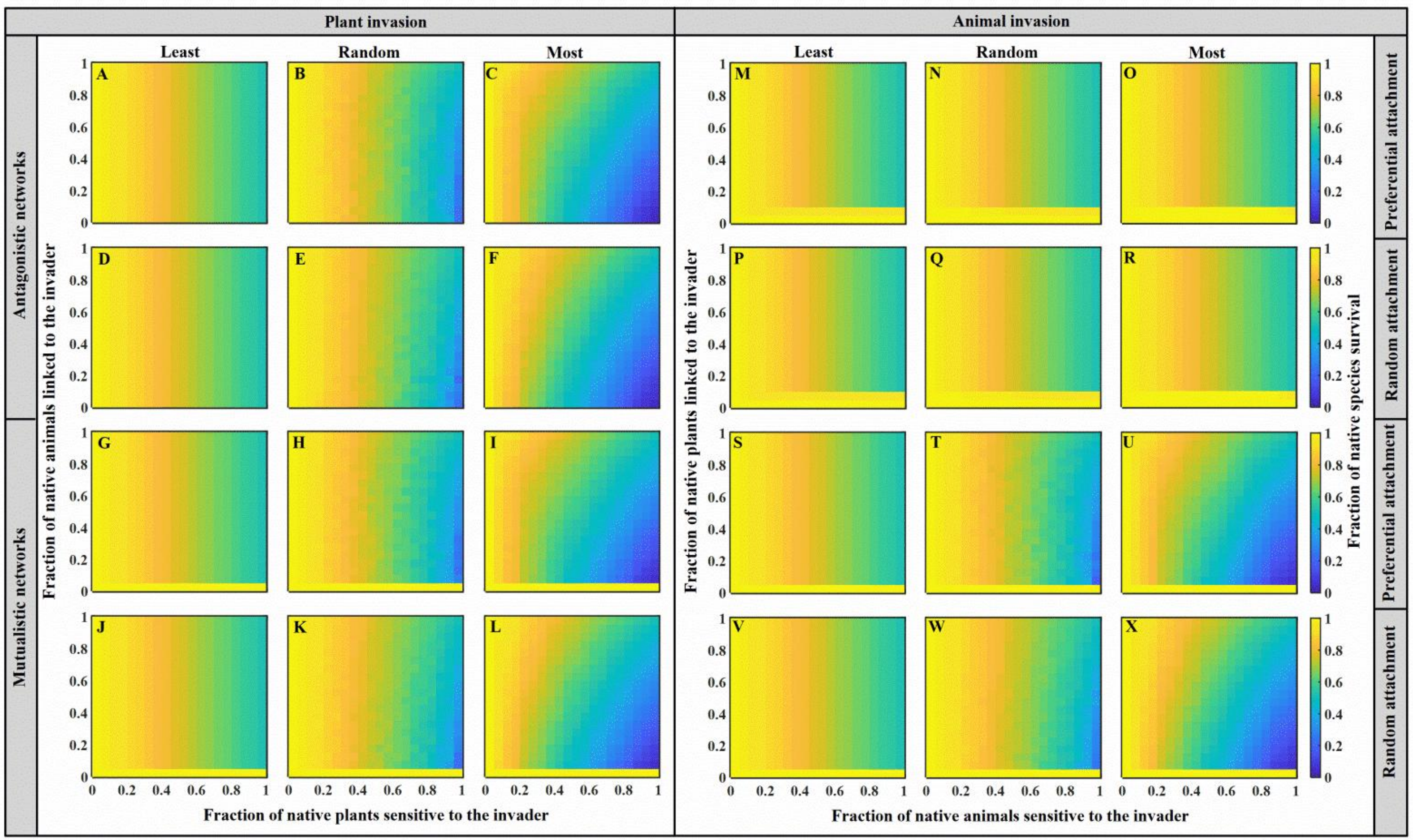

Figure S7. Metacommunity persistence at steady state (averaging on 20 replicates) after invasion in both mutualistic and antagonistic networks (***S*=96**, *C*=0.25 and *N*=0.65). Others are the same as in Fig. S5.

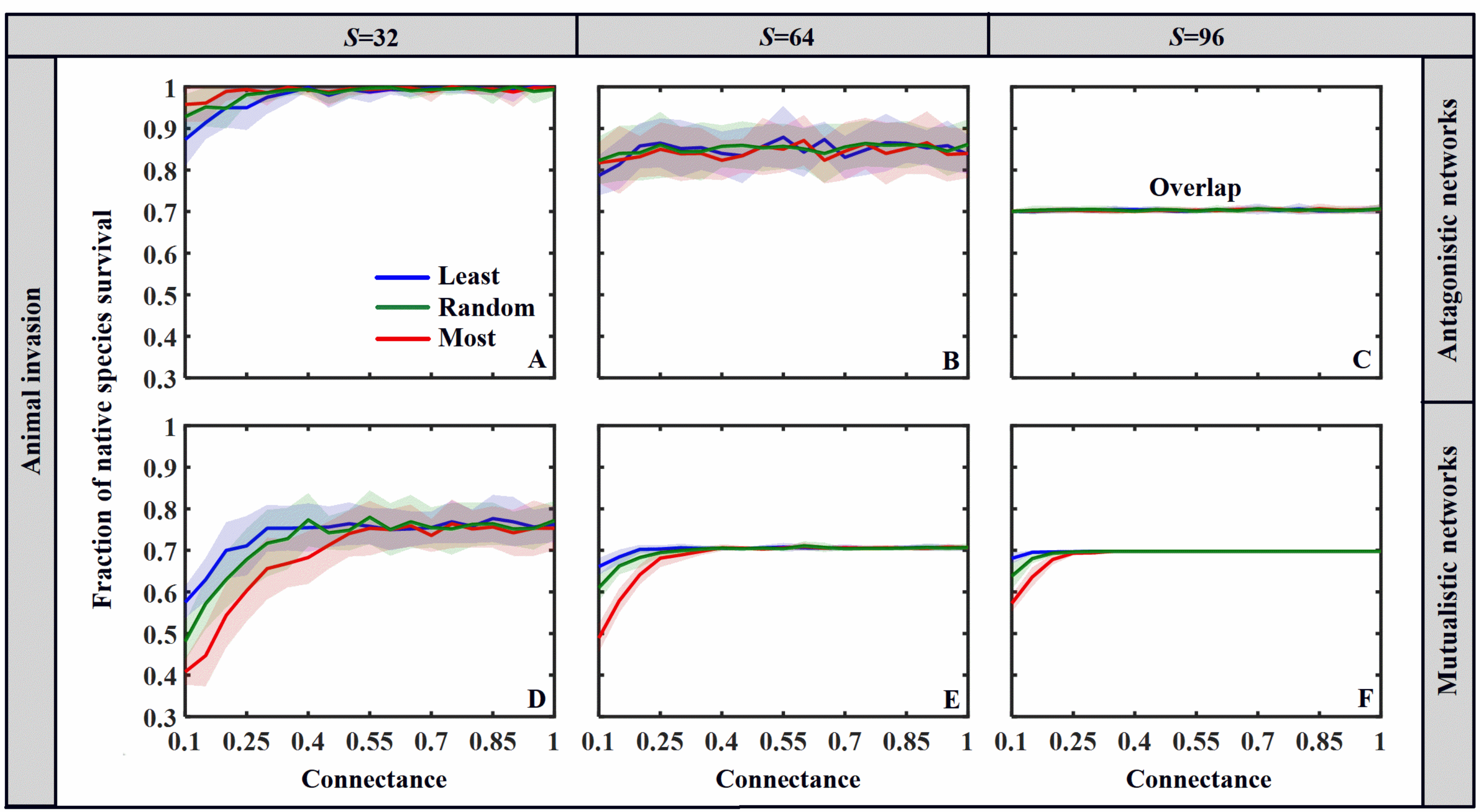

Figure S8. Effect of initial network connectance on metacommunity persistence (mean ± SD of 20 replicates) facing animal invasion at steady state, by varying network size (*S*=32, 64 and 96). Note that all bipartite networks used here are randomly structured (i.e. each plant–animal pair has the same probability to interact). Others are the same as in Fig. 4.

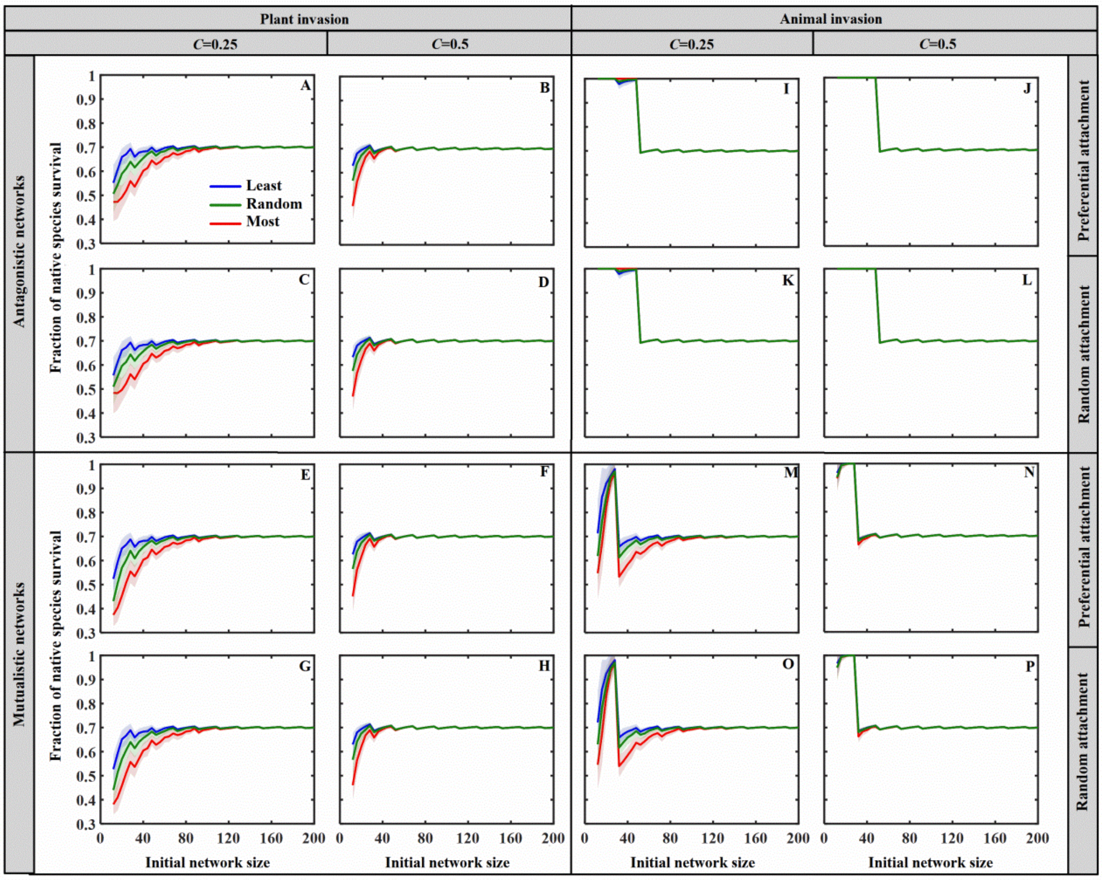

Figure S9. Effect of initial network size on metacommunity persistence at steady state (mean ± SD of 20 replicates) after invasion in mutualistic and antagonistic networks, by varying network connectance (C=0.25 and 0.5). Note that all bipartite networks used here are randomly structured (i.e. each plant–animal pair has the same probability to interact). The links between the invader and native species are shaped via random or preferential attachment. Other parameters: F_1=0.6, F_2=0.1, $c_i^P = c_j^A = 0.5$, $e_i^P = e_j^A = 0.1$ and $\mu_i^P = 0.1$, $c_{n_P+1}^P$=0.8, $e_{n_P+1}^P = 0.1$ and $\mu_{n_P+1}^P = 0.1$.

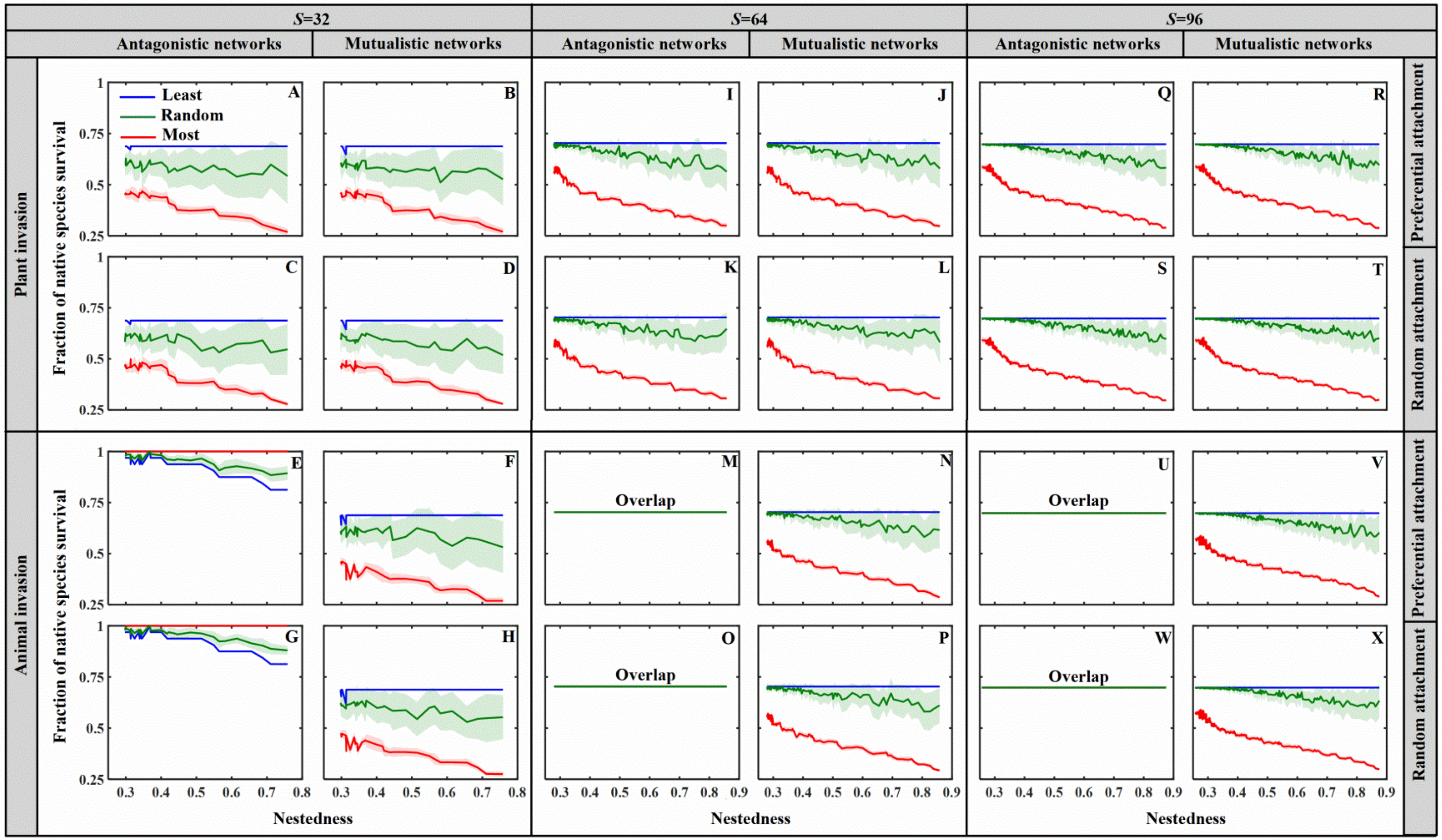

Figure S10. Effect of initial nestedness (*N*=NODF/100) on metacommunity persistence at steady state (mean ± SD of 20 replicates) under invasion for both antagonism and mutualism (*S*=32, 64, 96; *C*=0.25). Parameters: see Fig. S9.

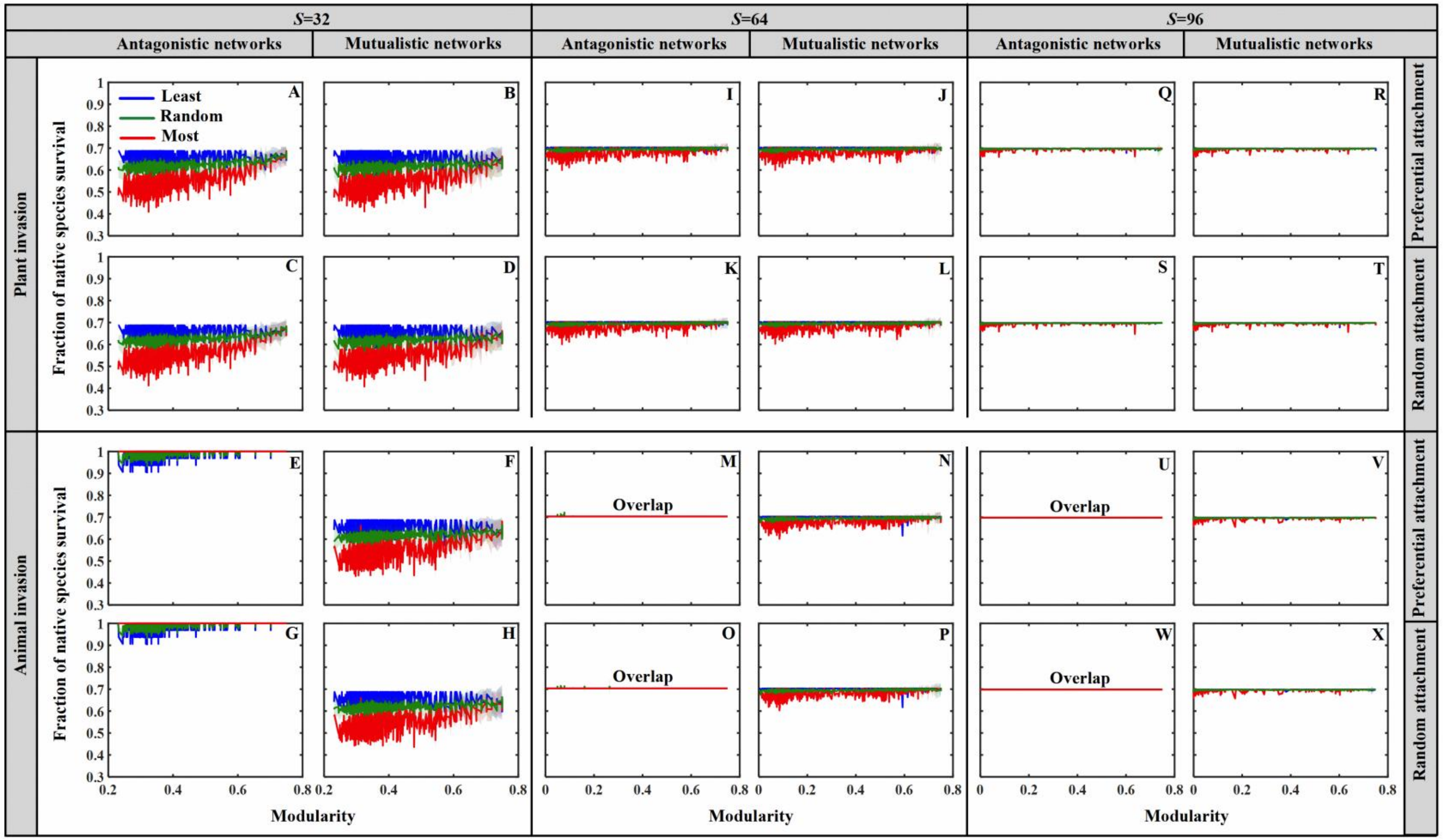

Figure S11. Effect of initial modularity (*Q*) on metacommunity persistence at steady state (mean ± SD of 20 replicates) under invasion for both mutualism and antagonism (*S*=32, 64, 96; *C*=0.25). Other parameters are the same as in Fig. S9.

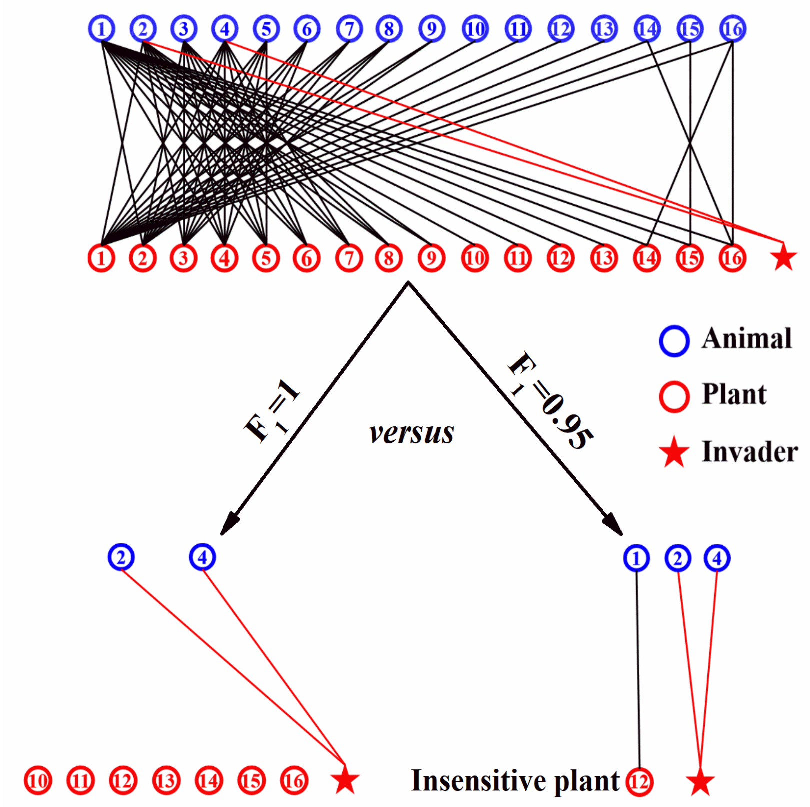

Figure S12. Illustration of increasing the fraction of native plants sensitive to the invader (F_1=0.95 *vs.* 1) increases metacommunity persistence at very high levels of F_1 when selecting sensitive plants from most connected to least connected ones (Most) in antagonsitic networks, as shown in Fig. 3A. At F_1=0.95, the insensitive plant survives in sufficient abundance to support the animal, which can impose predation pressure on sensitive plants which might otherwise survive, driving them to extinction. By contrast, when all plants are sensitive to the invader (F_1=1), only those animals that directly feed on the invader can survive, and any plant which do not interact with these animals are released from predation pressure, permitting them to survive at low abundance. Other parameters: see Fig. 3.