Non-shared dispersal networks with heterogeneity promote species coexistence in hierarchical competitive metacommunities

Helin Zhang, Jinbao Liao*

Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed Research, School of Geography and Environment, Jiangxi Normal University, Ziyang Road 99, 330022 Nanchang, China

***Corresponding author:** Prof. Dr. Jinbao Liao (jinbaoliao@163.com)

Address: Ziyang Road 99, 330022 Nanchang, Jiangxi Province, China.

Tel.: +86-(0)791-88133622 Fax: +86-(0)791-88120538

Abstract

Exploring the mechanism of biodiversity maintenance has become a fundamental issue in ecology. To date, many mechanisms have been proposed subject to the niche and neutral theories or the colonization-competition tradeoff. Despite these advances, species-specific dispersal heterogeneities are not well integrated into our general understanding of how coexistence emerges between competitors. Combining both network and metapopulation approaches, we construct a discrete, spatially explicit patch-dynamic model for metacommunities with hierarchically preemptive competition, to explore species coexistence in the shared vs. non-shared dispersal networks with contrasting heterogeneities (including regular, random, exponential and scale-free networks). Our model shows that, in spite of dispersal heterogeneity, species with the same demography (i.e. identical colonization and extinction rates) cannot coexist stably in the shared networks (i.e. the same dispersal pathways). In contrast, increasing dispersal heterogeneity in the non-shared networks greatly promotes regional coexistence, due to the segregation-aggregation mechanism by which each species is restricted to the self-organized clusters with the core of the most connected patches. However, these competitive patterns are largely mediated by species life-history attributes, for example, a unimodal biodiversity response to an increase of species dispersal emerges in the non-shared heterogeneous networks, with species richness peaked at intermediate dispersal levels. Interestingly, increasing network size can foster more species coexistence, leading to a monotonic increase in species-area curves. This strongly suggests that unexpectedly, many more species can co-occur regionally than the number of limiting resources. Overall, this modelling study, filling the gap between network structure and spatial competition, provides new insights into the spatial mechanisms of multispecies coexistence, theoretically demonstrating the importance of species-specific dispersal heterogeneity for biodiversity maintenance.

Keywords: Dispersal heterogeneity, preemptive competition, competitive hierarchy, regional coexistence, network theory, segregation-aggregation mechanism.

Introduction

Understanding the mechanisms of how species can coexist in natural communities has already become a central issue in ecology (Tilman 1982; Chesson 2000; Amarasekare & Nisbet 2001; Kraft et al. 2015). To date, many mechanisms have been proposed subject to the niche and neutral theories or the colonization-competition tradeoff, and significant advances have been made in our understanding of species coexistence and consequently biodiversity maintenance (Tilman 1994; Hubbell 2001; Yu & Wilson 2001; Levine & HilleRisLambers 2009; Chu & Adler 2015). Yet, these theories suffer their own shortcomings. For instance, many field studies fail to detect the evidence for the classic resource-based niche differences or the colonization-competition tradeoff (Harrison et al. 1995; Amarasekare 2000; Levine & Rees 2002), while the species equivalence assumption of neutral theory is hard to reconcile with nature (Turnbull et al. 1999; Yu and Wilson 2001; Jakobsson and Eriksson 2003; Allesina & Levine 2011). This suggests that there should be a fundamental disconnect between empirical findings and modelling assumptions (Cadotte et al. 2006). To solve this mismatch between theory and experiment, non-hierarchical competition (e.g. intransitivity) among multiple species has been recently proposed to be a potential mechanism for biodiversity maintenance (Huisman & Weissing 1999; Kerr et al. 2002; Laird & Schamp 2006; Allesina & Levine 2011). However, there remains one unsolved question: whether and how species in nature can coexist stably in a spatial system with hierarchical competition even without involving the colonization-competition trade-off?

To probe the possible underlying mechanism above, we should switch our focus on species dispersal in spatial patchy environments. It is well known that most previous models of spatial coexistence often assumed species dispersal interactions in a regular or random landscape (i.e. dispersal networks are assumed to be lattice-structured or randomly-structured), ignoring the more realistic dispersal heterogeneity across the landscape. In nature, evidence of dispersal networks with heterogeneity abounds (Fortuna et al. 2006; Grilli et al. 2015). For example, Kininmonth et al. (2010) found that the GBR (Great Barrier Reef) including 321 reefs is a scale-free small-world dispersal network for the species, i.e. most of reefs have one or a few links, and a very small proportion of reefs are extremely well-connected, following a power-law degree distribution. Furthermore, while trees with wind-dispersed seeds perceive the landscape as a homogeneous network, trees with bird-dispersed seeds move through a heterogeneous network (Montoya et al. 2008). Recently, there has been an increasing interest in characterizing the persistence and dynamics of interacting species with dispersal heterogeneity using network theory (Urban & Keitt 2001; Bode et al. 2008; Holland & Hastings 2008; Dale & Fortin 2010; Kininmonth et al. 2010; Gilarranz & Bascompte 2012; Grilli et al. 2015; Gilarranz et al. 2017). In these representations, each network is described as a graph consisting of a set of nodes (i.e. patches), and links between these nodes indicate dispersal pathways of individuals or sub-populations (Fortuna et al. 2006, 2009). These studies found that the spatial heterogeneous networks greatly promote species persistence relative to the homogeneous networks, demonstrating the importance of dispersal network structure for ecological dynamics (e.g. Holland & Hastings 2008; Gilarranz & Bascompte 2012).

Despite these advances, species-specific dispersal heterogeneities are not well integrated into our general understanding of how coexistence emerges between species. Even though a few models considered spatial dispersal with different heterogeneities, they still assumed that all species share the same dispersal networks (i.e. with the same dispersal pathways; e.g. Holland & Hastings 2008). This assumption greatly neglects the fact that different species may perceive the landscape differently and therefore display distinct dispersal pathways (i.e. non-shared dispersal networks due to difference in habitat preference or dispersal traits), shaping different patterns of patch connectivity (Bunn et al. 2000; Nicholson & Possingham 2006; Fortuna et al. 2009). For instance, Codeco & Grover (2001) have empirically shown that spatial variation in the supply ratio of Carbon and Phosphorous can favor different algal or bacterial species at different spatial locations, therefore avoiding competitive exclusion via dispersal. In addition, some species often exhibit markedly different dispersal patterns, even though they disperse at similar times through similar mechanisms (Nathan & Muller-Landau 2000; Kinlan & Gaines 2003; Becker et al. 2007; Clobert et al. 2009). Thus, there is an urgent need for spatial coexistence theory to incorporate the non-shared dispersal networks with heterogeneity that is widespread in nature (Amarasekare 2008).

In this study, we construct a discrete, spatially explicit patch-dynamic model for multiple species with hierarchically preemptive competition, in order to make a systematic comparative analysis of species coexistence in shared *vs.* non-shared dispersal networks with contrasting heterogeneities. Four typical types of spatial dispersal networks are considered (illustrated in Fig. 1): regular (Bascompte & Solé 1995), random (Erdös & Rényi 1959; Watts & Strogatz 1998), exponential and scale-free networks (Barabasi & Albert 1999). Using this model, we attempt to explore: (i) whether and how competitors with dispersal heterogeneity can co-occur in shared vs. non-shared networks without involving the colonization-competition tradeoff; and (ii) under what properties of dispersal network structure can best maintain species diversity.

Methods

Model description

We model a competition system structured in a large number of discrete habitat patches connected by species dispersal. Each patch can be vacant or host a single species. The system consists of n species with competitive hierarchy (i.e. ranking species according to their competitive abilities), in which the first species is the best competitor while the n-th species being the worst competitor ($1>2>3>\cdots>n$). According to the more realistic situation that colonizing a patch already occupied by another species may be intrinsically more difficult than colonizing an empty patch (e.g. plant propagule) because of preemptive effect (Comins & Noble 1985; Calcagno et al. 2006), we only consider the preemptive competition (no replacement among species), i.e. species only compete for empty patches, with strong competitors having priority to colonize empty patches. Thus, the inferior species can colonize the empty patch only if those superior species fail to establish there. All species in the landscape are assumed to have the same colonization (with rate *c*) and extinction rates (*e*), in order to exclude the colonization-competition tradeoff. As such, we can unambiguously attribute any species coexistence to our explicit structural properties of dispersal networks. In each time step, each occupied patch becomes extinct with a probability *e* regardless of species identity. At the same time, whether the empty patch is colonized by its directly connected occupied patches depends on species competitive hierarchy as well as species abundances (i.e. patch occupancy). Therefore, the probability that a given empty patch *i* is colonized by the *S*-th competitor ($1 \leq S \leq n$) should be

$$P_i(S) = 1 - (1 - c)^{\sum_{j=1}^{S} x_j}, \qquad (1)$$

where x_j (≥0) is the number of *j*-patches (occupied by species *j*) directly linked to the empty patch *i*, and $(1 - c)^{\sum_{j=1}^{S} x_j}$ is the probability of the patch *i* being unoccupied by those superior competitors (including species 1,2,3…*S*). Note that each empty patch is colonized by one of its directly connected occupied patches with an independent probability (*c*) regardless of species identity.

Dispersal networks with heterogeneity

We represent the landscape as a graph (spatial network) consisting of a set of nodes (patches) connected by links. The link between two nodes indicates the dispersal potential or frequency between patches. Each node denotes a suitable patch linked with a number of other patches (i.e. linking degree *k*), and links between patches represent species dispersal pathways (i.e. functional connectivity among populations). As such, each type of dispersal network can be characterized by its linking degree distribution. Similar to Gilarranz & Bascompte (2012), four structures of dispersal networks are considered (illustrated in Fig. 1a-d):

(i) A regular network with all patches having the same linking degree. For example, Fig. 1a shows a completely homogeneous network where each patch owns four links to other patches (k=4), equal to the lattice-structured model with nearest neighbour dispersal (Bascompte & Sole 1995; Hiebeler 2000; Liao et al. 2013a,b).

(ii) A randomly structured network with randomly connected patches (Watts & Strogatz 1998). In particular, patch linking degrees follow a Poisson distribution with the variance equal to the average degree per patch (e.g. $\bar{k}$=4 in Fig. 1b), thus there exists a small variation in patch linking degrees (Erdős & Rényi 1959).

(iii) An exponential network constructed based on the algorithm of Barabasi & Albert (1999) with random attachment. For instance, Fig. 1c displays an exponential network with the same average linking degree $\bar{k}$=4 but more variability in linking degrees than the random network (i.e. higher heterogeneity; Fortuna et al. 2006).

(iv) A scale-free network constructed according to the algorithm by Barabasi & Albert (1999) with preferential attachment. For example, Fig. 1d exhibits a scale-free network (keeping average patch linking degree at $\bar{k}$=4) with extremely high heterogeneity, i.e. most patches have a few links, while a few patches are extremely well-connected, following a power-law degree distribution (Kininmonth et al. 2010).

In these networks, species are assumed to disperse equally in all directions with no preference, i.e. when both patches i_1 and i_2 are linked, dispersal can occur from either i_1 to i_2 or vice versa.

Spatially explicit simulations

Initially all patches are assumed to be fully occupied by randomly assigning one of competitors to each patch. Within each time step, we determine local population extinction for each occupied patch with a given probability (e). Then we calculate the probability that each empty patch becomes occupied by its directly connected species according to their competitive hierarchy as well as population abundances (see Eq. 1). Finally we record patch occupancy for each species at each time step using their number of occupied patches divided by the network size (i.e. the total number of patches).

To find the steady state, we preliminarily run the system for a long time, and find that 5000 time steps are sufficient to achieve system stability. Thus we run each case until 10,000 time steps, and estimate patch occupancy for each species at steady state by averaging their patch occupancies between t=9000~10,000 time steps to avoid transient dynamics. Each case is explored with 100 replicates, starting from different dispersal architectures in each replicate but with identical network properties (e.g. the same network size, total links and their degree distribution). Ultimately, the mean of these 100 replicates (mean ± standard deviation SD) yields species abundance at steady state. A broad range of biologically reasonable parameter combinations are explored and found to yield qualitatively similar outcomes (Figs S1-S21 in *Appendix*), thus allowing us to present our general results in Figs 1-5 by choosing one of parameter combinations as a reference case.

Results

Two-species system

We first explore the coexistence of two competitors with the same demography (i.e. identical colonization and extinction rates) in shared vs. non-shared dispersal networks with contrasting heterogeneities, including (from most homogeneous to most heterogeneous) regular, random, exponential and scale-free networks (Fig. 1). All types of network have the same number of 1024 patches and 2048 links with the same average linking degree $\bar{k}$=4, which is large enough to reduce the role of stochastic effects (see Figs S1-S2 in *Appendix*), thereby allowing us to compare species coexistence in different heterogeneous networks. In general, both species cannot coexist regionally in the shared networks in spite of dispersal heterogeneity, eventually with the superior species excluding the inferior species (Fig. 1I-IV). In contrast, when their dispersal networks are non-shared, i.e. both competitors have species-specific dispersal pathways but with the same heterogeneity (e.g. scale-free networks in Fig. S3), they can co-occur stably (Fig. 1VI-VIII), except in the regular networks where the poor competitor is competitively excluded (Fig. 1V; see coexistence pattern in Fig. S4 in *Appendix*). Meanwhile, increasing dispersal heterogeneity in the non-shared networks interestingly decreases the amplitude of stochastic fluctuations on patch dynamics and increases the inferior species abundance.

The coexistence patterns described above, however, can be altered by varying species relative extinction or/and colonization rates (Fig. 2; Figs S5-S13 in *Appendix*) as well as average patch linking degree (Fig. S14 in *Appendix*). On the one hand, both species intuitively display a monotonic decline in global patch occupancy (mean ± SD of 100 replicates) as relative extinction rate (*e*/*c*) increases irrespective of whether the heterogeneous networks are shared or not, therefore speeding up species exclusion. Yet, species coexistence in the non-shared networks with higher heterogeneity can tolerate much higher ratios of *e*/*c*. On the other hand, in the shared networks even with high heterogeneity, increasing relative colonization rate (*c/e*; i.e. dispersal rate) expectedly leads to an increase in the superior species abundance, while the inferior species is always outcompeted. In the non-shared networks, increasing values of *c/e* promotes the superior species occupancy, but the patch occupancy of the inferior species initially increases but latter declines to extinction, except in the regular networks where the inferior species always goes extinct. Interestingly, we find that intermediate levels of *c/e* can maximize the inferior species abundance and therefore promote species coexistence, while further decreasing or increasing species dispersal would speed up species exclusion. This outcome is similar to the case of increasing average linking degree (Fig. S14 in *Appendix*). Furthermore, we find that increasing network heterogeneity increases the parameter space (*c/e*) for regional coexistence.

We further explore species coexistence when both competitors (again with the same demography) display different heterogeneous networks (Fig. 3). If the poor competitor shows the regular dispersal network, the strong competitor with higher dispersal heterogeneity (including random, exponential and scale-free) can outcompete the poor competitor (Fig. 3II-IV). In contrast, the inferior species with higher heterogeneity surprisingly can exclude the superior species with the regular dispersal network. This strongly indicates that dispersal heterogeneity can compensate the competitive disadvantage, thereby overturning the competitive outcome (Fig. 3I, V & IX). In other cases where both competitors choose different dispersal networks with more or less heterogeneity (excluding regular networks), we observe that both species can co-occur regionally, and higher dispersal heterogeneity decreases the fluctuation amplitude of patch occupancy dynamics (Fig. 3VI-VIII vs. X-XII).

Multispecies system

Then we investigate how many competitors (with the same demography) can coexist stably in multispecies metacommunities, again considering shared vs. non-shared dispersal networks by varying relative extinction or/and colonization rates (Fig. 4; Figs S19-S20 in *Appendix*). Generally, increasing relative extinction rate (e/c) reduces species richness in both shared and non-shared dispersal networks, but there exist differences in biodiversity maintenance among networks with different dispersal heterogeneities (Fig. 4a & c). For example, if all species have the same dispersal pathways, we surprisingly observe that more species can co-occur regionally in the regular networks than in other heterogeneous networks but only at relatively low values of *e/c*. In contrast, in the non-shared networks, higher dispersal heterogeneity can result in more species persistence (i.e. scale-free > exponential > random > regular). When varying relative colonization rate (*c*/*e*), we find that, in most cases, only the best competitor can survive in the shared networks regardless of dispersal heterogeneity, whereas more species can coexist with increasing dispersal heterogeneity in the non-shared networks. Similar to the case of increasing average linking degree (Fig. S21 in *Appendix*), an increase of *c*/*e* interestingly leads to a unimodal biodiversity response: moderate levels of *c/e* can maximize species diversity, while further increasing or decreasing ratios of *c/e* (i.e. dispersal rate) would result in more species extinctions.

Finally we examine the effect of network size on biodiversity maintenance (i.e. species-area curve) again in both shared and non-shared dispersal networks with contrasting heterogeneities (Fig. 5). In the shared networks, only the best competitor survives regardless of network size and dispersal heterogeneity. In contrast, increasing network size in the non-shared heterogeneous networks (except in the regular network where only the best competitor stays alive) can surprisingly lead to a monotonic increase in species richness, with more heterogeneity resulting in higher species diversity.

Discussion

Our spatially explicit model focuses on how species-specific dispersal networks and hierarchically preemptive competition interact to affect species coexistence, by assuming that all species have the same demographic traits to exclude the colonization-competition tradeoff. Yet, most current theoretical understanding comes from models with very regular connections among patches, by contrast with the heterogeneity in natural systems that are far from regular (Hanski & Ovaskainen 2000; Fortuna et al. 2006; McIntire et al. 2007). In our study, we thus concentrate on dispersal heterogeneity, specifically in network structure (including regular, random, exponential and scale-free), demonstrating the importance of spatial dispersal heterogeneity for species coexistence in the non-shared networks. Since we observe that in spite of dispersal heterogeneity, species cannot coexist stably in the shared networks if there is no colonization-competition tradeoff (Figs 1, 2 & 4). Intuitively, sharing the same dispersal pathways indicates that competitors encounter each other very frequently, and the best competitor would eventually drive all other inferior species to extinction by quickly seizing the empty patches. Thus, previous patch-dynamic models only focusing on the shared regular networks, might have largely underestimated species diversity, as species in natural communities always exhibit diverse dispersal patterns with more or less heterogeneity.

In contrast to the shared dispersal networks, the non-shared heterogeneous networks greatly promote species coexistence and therefore biodiversity maintenance, more obviously at higher dispersal heterogeneity (Figs 1, 2 & 4). We further explore the mechanism underlying the competitive outcome by analyzing spatial distribution for each species subject to their specific dispersal networks (Fig. S4 in *Appendix*), and relating a patch's incidence (i.e. the proportion of time steps that the node is occupied along the dynamics) with its linking degree as well as with the average degree of the patches it interacts with (Figs S15-S18 in *Appendix*). As observed in Fig. S4, species-specific dispersal networks with heterogeneity allow species to shape many clusters of occupied patches with the core of the most connected patches, locally forming many self-organized small worlds. This should be ascribed to variability in linking degree across patches, which results in variability across patches' incidence (Figs S15-S16 in *Appendix*). Obviously, patch incidence grows non-linearly with linking degree (Eq. 1), that is, patches require a minimum degree to stay occupied in the majority of time steps, but patch incidence would saturate after a threshold in degree. In turn, the highly connected patches for the focal species can provide benefit for their directly linked patches in terms of incidence (Figs S17 & S18 in *Appendix*). For example, when comparing patches with the same degree, those attached to the more well-connected patches have a larger incidence (positive feedback). Essentially, conspecifics tend to develop into clusters segregated from other species in space because of dispersal heterogeneity, which increases the frequency of neighbourhood dispersal within conspecifics but decreases competition among heterospecifics, thereby allowing demography-equivalent species to co-occur regionally in spite of preemptive competition (so-called the segregation-aggregation mechanism; Pacala 1997; Murrell et al. 2001; Holyoak & Loreau 2006). This mechanism can also be thought of as generating a type of spatial refugia for the poor competitors, i.e. locations within the clusters favoring persistence of the focal species after the extinction in surrounding areas.

When both competitors exhibit different dispersal heterogeneities, they are able to coexist stably, even though the poor competitor displays lower dispersal heterogeneity than the strong competitor (Fig. 3), again demonstrating that dispersal heterogeneity can weaken interspecific competition and therefore promote species coexistence. Furthermore, the poor competitor with higher dispersal heterogeneity can exclude the strong competitor of having the regular (homogeneous) dispersal, therefore altering the species' competitive rankings. Logically, even very low dispersal heterogeneity (e.g. random dispersal) can greatly promote population abundance for the poor competitor relative to the homogeneous dispersal, and such a large numerical advantage can overwhelm the competitive superiority, thereby excluding the strong competitor. This indicates that effects of spatial dispersal heterogeneity far outweigh the effect of preemptive competition, further confirming its important role in maintaining species diversity. However, these patterns of regional coexistence are greatly mediated by species life-history traits. Interestingly, a unimodal biodiversity response to an increase of dispersal rate emerges in the non-shared heterogeneous networks, showing diverse (positive as well as negative) effects of species dispersal on multispecies coexistence (Figs 2 & 4). More specifically, intermediate dispersal levels can maximize species richness, while further increasing or decreasing species dispersal results in more species exclusion. Intuitively, species is unable to persist locally at very low levels of dispersal rate. Yet, too much dispersal promotes patch colonization opportunities for the superior competitors, and consequently leads to the region-wide exclusion of the poor competitors under surplus dispersal, similar to the situation of increasing average patch linking degree (Figs S14 & S21 in *Appendix*).

A final observation is that increasing network size leads to a monotonic increase in species richness in the non-shared heterogeneous networks, with higher dispersal heterogeneity promoting more species persistence (Fig. 5). The resulting monotonically increased species-area curves refute the previous view that the number of species coexisting cannot exceed the number of limited factors (Levin 1970; Tilman 1982). Instead, we theoretically demonstrate that, when there is species-specific dispersal heterogeneity, there should be many more species coexisting regionally than the number of limiting resources, as empirically observed in several natural systems (Tilman 1982; Kotler & Brown 1988; Wellborn et al. 1996). Previously, coexistence of an unlimited number of species because of the colonization-competition tradeoff (Tilman 1994) was ascribed to a stepwise asymmetric model of competition rather than spatial heterogeneity (Adler & Mosquera 2000). However, our model provides another potential explanation that if the landscape is large enough, non-shared dispersal heterogeneities allow many more species to co-occur regionally than expected due to the segregation-aggregation mechanism.

Our work helps fill the gap between network structure and spatial competition, demonstrating that the architecture of dispersal networks largely affects species coexistence, greatly mediated by species life-history attributes. We find that incorporating species-specific dispersal heterogeneities into the traditional hierarchical competitive systems can greatly promote regional coexistence due to the formation of self-organized clusters. This strongly implies that traditional shared lattice- or randomly-structured models might have severely underestimated biodiversity maintenance. More importantly, this model suggests important implications for biodiversity conservation and management. For instance, as different species often display diverse patterns of patch connectivity based on their dispersal traits, we should first construct and analyze dispersal networks independently for multiple target species, and then overlay or intersect the multiple networks to find locations that are important for these species, so as to design multispecies conservation planning (e.g. Bunn et al. 2000; Urban & Keitt 2001; Nicholson & Possingham 2006). Overall, this modelling study, integrating both network and metapopulation approaches, takes an important step toward understanding the coexistence mechanism of multiple species with spatial dispersal heterogeneity, thereby strengthening our comprehension of biodiversity maintenance in hierarchical competitive metacommunities.

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Author contributions

J.L. conceived and wrote this manuscript, and H.Z. conducted simulations and analyzed results.

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Supplementary Material

Appendix accompanies this manuscript is also supplied.

Data accessibility

This is a theoretical modelling study and does not use data.

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Figures & Captions

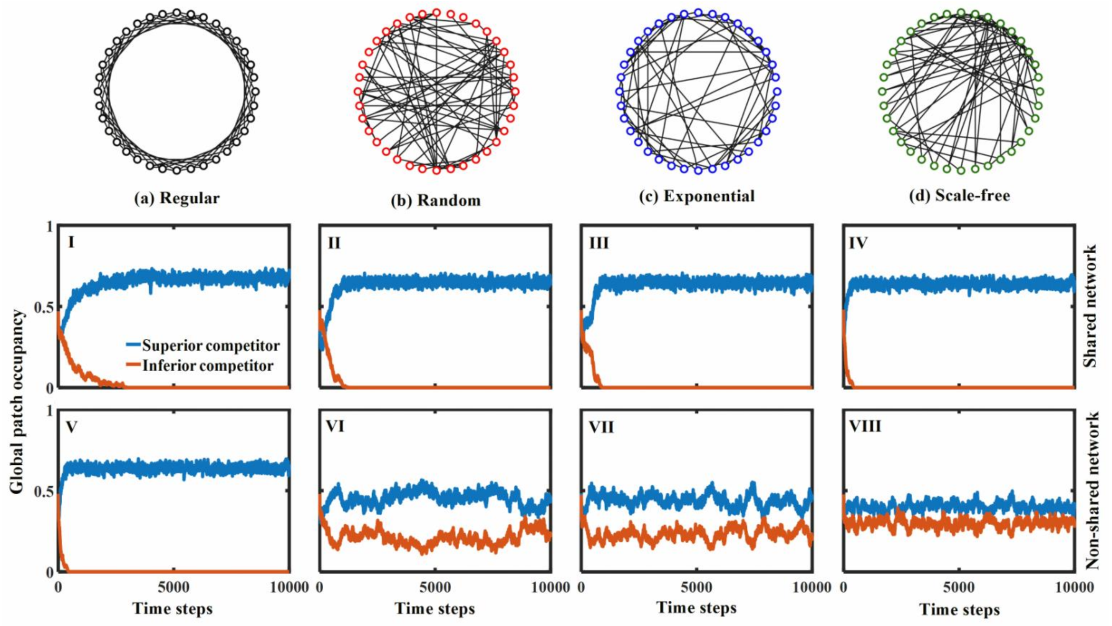

Figure 1. Patch dynamics of two competing species in shared (I-IV) vs. non-shared (V-VIII) dispersal networks (containing 1024 patches and 2048 links with average linking degree $\bar{k}$=4). Four typical networks from the most homogeneous to the most heterogeneous are included: (a) regular, (b) random, (c) exponential and (d) scale-free networks. For display purposes, these networks only consist of 36 patches (nodes) with 72 links. Here the shared networks indicate the same dispersal pathways for both competing species; while the non-shared networks mean that both competitors show different dispersal pathways but with the same heterogeneity. Parameter values are the same for both species: colonization rate *c*=0.05 and extinction rate *e*=0.05.

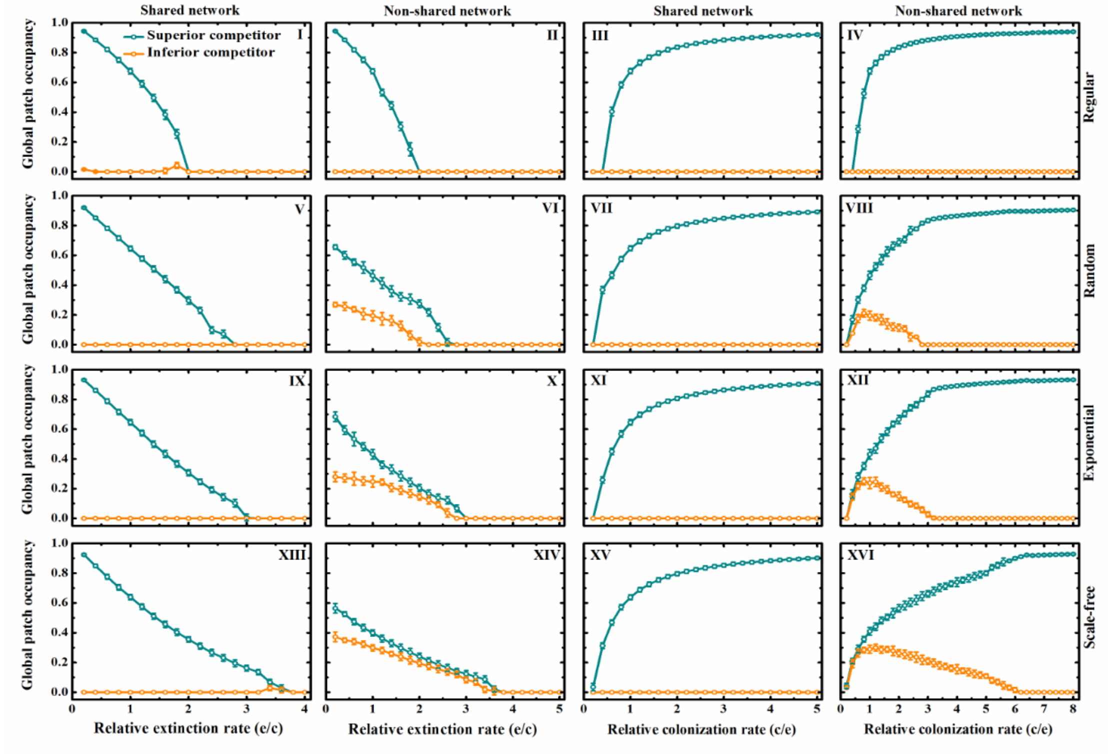

Figure 2. Effects of relative extinction (*e*/*c* at fixed *c*=0.05) and colonization (*c*/*e* at fixed *e*=0.05) rates on patch occupancy (mean ± standard deviation SD of 100 replicates) of both inferior and superior competitors at steady state in shared vs. non-shared networks with different heterogeneities, including regular, random, exponential and scale-free networks. These networks consist of 1024 patches and 2048 links, and non-shared networks indicate species-specific dispersal pathways for both competitors but with the same network property.

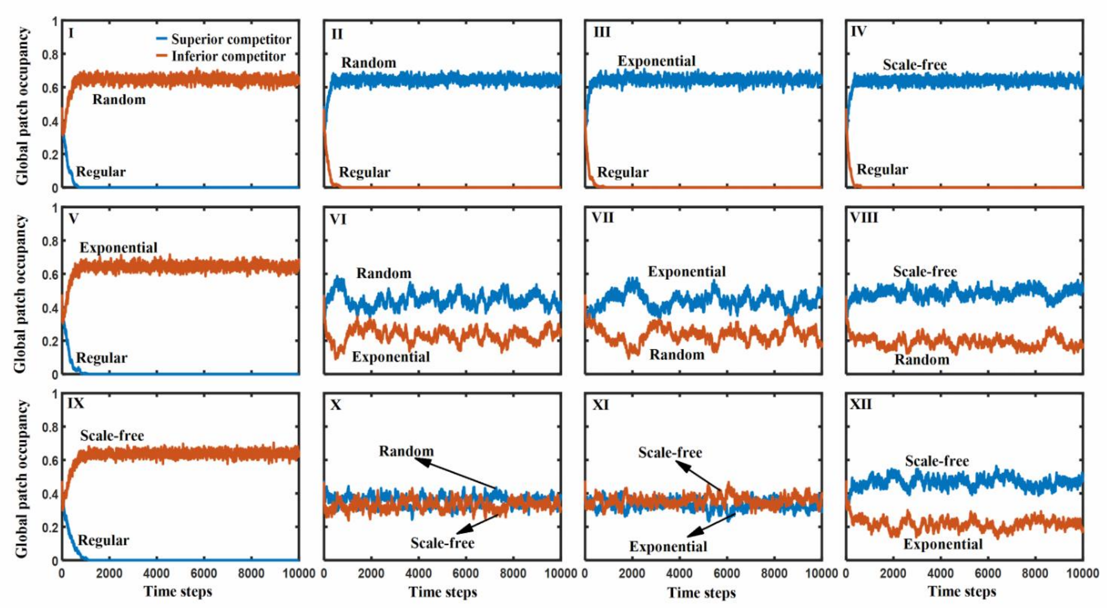

Figure 3. Patch dynamics of both inferior and superior competitors with different heterogeneous networks, consisting of 1024 patches and 2048 links. Four types of dispersal networks are considered: regular, random, exponential and scale-free networks. Parameter values for both species are the same: c=e=0.05.

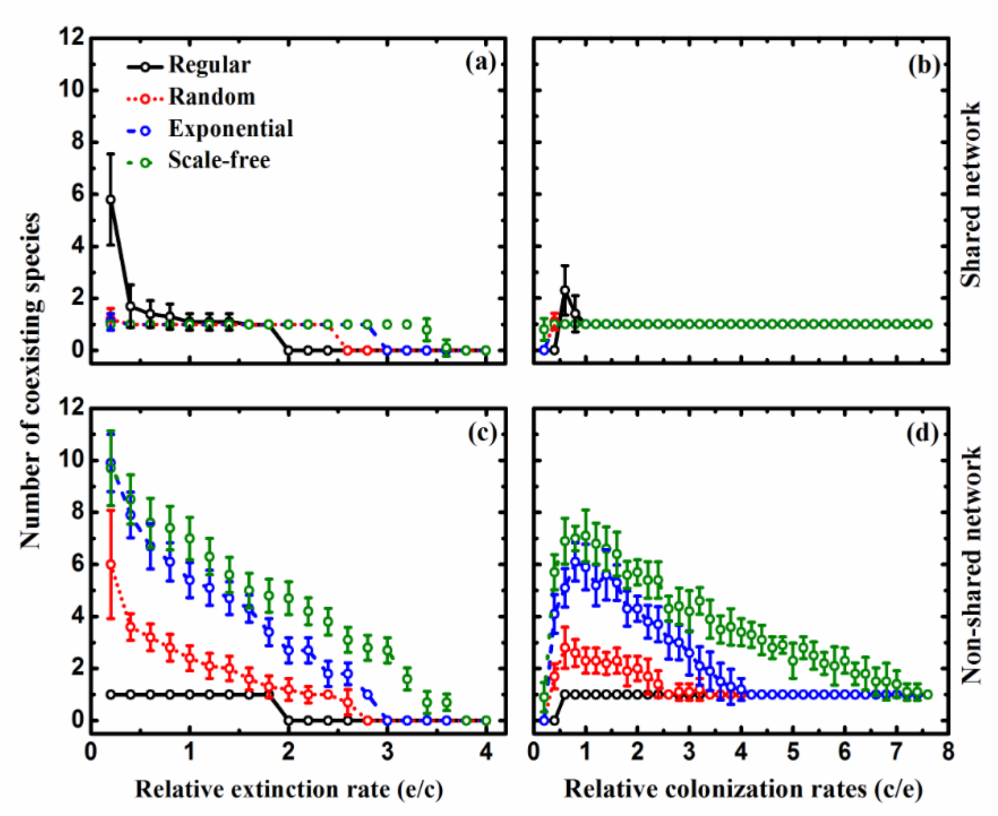

Figure 4. Effects of relative extinction (*e*/*c* at fixed *c*=0.05) and colonization rates (*c*/*e* at fixed *e*=0.05) on the number of coexisting species at steady state (mean ± SD of 100 replicates) in hierarchical competitive metacommunities, with preemptive competition that species only compete for empty patches. Initially the competitive system contain a sufficient number of species, and all species are assumed to have the same colonization and extinction rates in shared (graphs a & b) vs. non-shared (graphs c & d) networks, including regular, random, exponential and scale-free networks (again with 1024 patches and 2048 links). Here non-shared networks mean that all species have different dispersal pathways while keeping the same network property, which is realized by regenerating the dispersal network with the same heterogeneity and assigning them to each species.

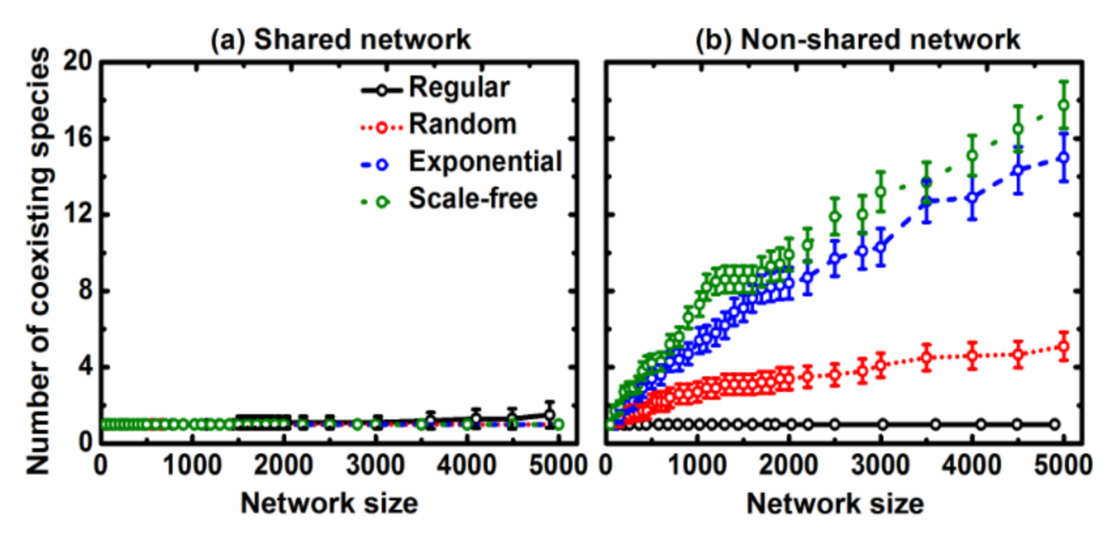

Figure 5. Relationship between network size (i.e. total number of patches) and the number of coexisting species at steady state (i.e. species-area curves) in hierarchical competitive metacommunities with preemptive competition (mean ± SD of 100 replicates). To exclude the colonization-competition tradeoff, all species are assumed to have the same colonization and extinction rates (c=e=0.05) in (a) shared vs. (b) non-shared networks (i.e. species-specific dispersal but with the same network property), by fixing the average patch linking degree ($\bar{k}$=4). Again four types of dispersal networks with contrasting heterogeneities are included: regular, random, exponential and scale-free networks.