Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities

Reference:
Zhang Helin, Bearup Daniel, Nijs Ivan, Wang Shaopeng, Barabas Gyorgy, Tao Yi, Liao Jinbao.- Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities
Ecology letters - ISSN 1461-023X - Hoboken, Wiley, 24:1(2021), p. 50-59
Full text (Publisher's DOI): https://doi.org/10.1111/ELE.13619
To cite this reference: https://hdl.handle.net/10067/1726690151162165141

Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities

Helin Zhang[1], Daniel Bearup[2], Ivan Nijs[3], Shaopeng Wang[4], György Barabás[5], Yi Tao[6,7], Jinbao Liao[1,*]

[1]*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*

[2]*University of Kent, School of Mathematics, Statistics and Actuarial Sciences, Parkwood Road, Canterbury, CT2 7FS, UK*

[3]*Research group Plants and Ecosystems, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium*

[4]*Key Laboratory for Earth Surface Processes of the Ministry of Education, Institute of Ecology, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China*

[5]*Division of Theoretical Biology, Department IFM, Linköping University, Linköping, Sweden*

[6]*Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing100101, China*

[7]*University of Chinese Academy of Sciences, Beijing 100049, China*

Emails: H.Z. (helinzh5@163.com) D.B. (d.bearup@kent.ac.uk),
I.N. (ivan.nijs@uantwerpen.be) S.W. (shaopeng.wang@pku.edu.cn)
G.B. (dysordys@gmail.com) Y.T. (yitao@ioz.ac.cn)

***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

Short running title: Dispersal heterogeneity promotes coexistence

Article type: Letters

Number of Abstract: 150 **Number of words in the main text: 4557**

Number of text box: 0 **Number of references: 77**

Number of tables: 0 **Number of figures: 5**

Keywords: dispersal heterogeneity, preemptive competition, competitive hierarchy, spatial coexistence, network theory, segregation-aggregation mechanism, landscape perception.

Statement of author contributions: J.L. designed this study, analyzed the results and wrote the manuscript; H.Z. wrote Matlab codes and performed simulations; all authors contributed substantially to revisions.

Data availability: This theoretical study has no data.

Abstract

Understanding the mechanisms of biodiversity maintenance is a fundamental issue in ecology. The possibility that species disperse within the landscape along differing paths presents a relatively unexplored mechanism by which diversity could emerge. By embedding a classical metapopulation model within a network framework, we explore how access to different dispersal networks can promote species coexistence. While it is clear that species with the same demography cannot coexist stably on shared dispersal networks, we find that coexistence is possible on unshared networks, as species can surprisingly form self-organized clusters of occupied patches with the most connected patches at the core. Furthermore, a unimodal biodiversity response to an increase of species colonization rates or average patch connectivity emerges in unshared networks. Increasing network size also increases species richness monotonically, producing characteristic species-area curves. This suggests that, in contrast to previous predictions, many more species can co-occur than the number of limiting resources.

Introduction

Global biodiversity is in ongoing decline due to anthropogenic pressures. Consequently, developing a better understanding of the mechanisms which create and maintain diversity in ecological communities is essential. Several mechanisms have been proposed (e.g. niche and neutral theories), and significant advances have been made in understanding species coexistence and consequently biodiversity maintenance (Chesson 2000; Hubbell 2001; Levine & HilleRisLambers 2009; Chu & Adler 2015). Among them, the competition-colonization trade-off has been a classic paradigm to explain biodiversity in natural ecosystems (Tilman 1994; Amarasekare 2000; Yu & Wilson 2001; Yu *et al*. 2004). However, in the absence of such a tradeoff between competitive ability and demographic traits, explaining stable coexistence in competitive communities remains a challenge for theoretical ecologists. Recently, non-hierarchical competition (i.e. competitive intransitivity) among species has been proposed as a potential endogenous mechanism for multispecies coexistence (Laird & Schamp 2006; Allesina & Levine 2011; Soliveres *et al*. 2015; Levine *et al*. 2017). However, a key question remains unsolved in hierarchical (transitive) competitive systems proposed by Tilman (1994): whether there exists any other factor fostering species coexistence in such system without involving the colonization-competition trade-off.

One such factor could be the effect of landscape heterogeneity on dispersal range (Hanski & Ovaskainen 2000). There is abundant evidence in nature that landscape structure, and other factors, can result in anisotropic (i.e. directionally biased) dispersal behavior (Urban & Keitt 2001; Fortuna *et al*. 2006; Grilli *et al*. 2015). For example, Montoya *et al*. (2008) observed that seed dispersal by birds, as opposed to by winds, is better described by an irregular network than a spatially uniform network. Fortuna *et al*. (2006) identified a large spatial network of temporary ponds, with a power-law degree distribution, which are used as breeding sites by amphibian species. Furthermore, species dispersal between sub-reefs within the Great Barrier Reef has been described with scale-free small-world networks (Kininmonth *et al*. 2010). However, with a few exceptions (e.g. Chesson 2000; Snyder & Chesson 2003), the majority of existing models assume that dispersal is isotropic within a two dimensional landscape.

As such, there has been an increasing interest in characterizing the effects of varying patch connectivities on the persistence and dynamics of species using network theory (Bode *et al*. 2008; Holland & Hastings 2008; Dale & Fortin 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 and links corresponding to habitat patches (or colony sites) and dispersal pathways respectively (Fortuna *et al*. 2006, 2009). These studies found that variation in the number of links between patches (i.e. network heterogeneity) greatly promotes species persistence by increasing local recolonization opportunities, demonstrating the importance of dispersal network structure for ecological dynamics (e.g. Holland & Hastings 2008; Gilarranz & Bascompte 2012).

Despite these advances, species-specific dispersal network connectivities have not been well integrated into our general understanding of how coexistence emerges among species. While a few models have considered the effect of variation in patch connectivities, they assumed that all species use the same dispersal pathways (i.e. shared networks; e.g. Holland & Hastings 2008). This assumption neglects the fact that different species may perceive the landscape differently (e.g. landscape perception; Hansbauer *et al.* 2010; Dondina *et al.* 2018) and therefore have distinct dispersal pathways, creating diverse patterns of patch connectivity (Yeaton & Bond 1991; Bunn *et al*. 2000; Nicholson & Possingham 2006; Fortuna *et al*. 2009; Bearup *et al*. 2013; Hirt *et al*. 2018; Germain *et al*. 2019). For example, plant species with wind-dispersed seeds could be described using a homogeneous dispersal network, while those with bird-dispersed seeds could be described with a heterogeneous one due to bird habitat preferences (Montoya *et al.* 2008). Furthermore, Fortuna *et al.* (2009) found that the importance of individual patches within a dispersal network can vary significantly between species. Thus, there is an urgent need for spatial coexistence theory to incorporate species-specific dispersal networks that are widespread in nature (Amarasekare 2008).

In this study, we embed a classical model for metapopulation dynamics (Levins 1969) in a spatially heterogeneous landscape represented by a dispersal network (*Appendix* Fig. S1). We then use this model to investigate how the coexistence of competing species is affected by shared *vs.* unshared networks of varying heterogeneity. In particular, we systematically explore: (i) whether and how competitors can co-occur in shared vs. unshared networks when they have the same demographic traits; and (ii) which properties of dispersal network structure can best maintain species diversity.

Methods

Dispersal networks with heterogeneity

In metapopulation models, the landscape is typically divided into patches (or colony sites) which can be inhabited by a sub-population of a species. In this model, we assume that individuals can move between patches only along a pre-defined set of dispersal pathways (*Appendix* Fig. S1). The result is a network model, with patches and dispersal pathways being represented by network nodes and links respectively.

The primary advantage of this approach is that it allows us to make use of the extensive literature that has been developed to describe network structure. In particular, a key feature of network structure is its *degree distribution*. The *degree* of a node is the number of other nodes to which it is connected directly. The degree distribution describes the frequency with which nodes have a particular degree. Dispersal is isotropic or directionally unbiased, relative to the landscape, if the dispersal network is *homogeneous*, i.e. all nodes have the same degree. Anisotropic, directionally biased, dispersal can be represented by a *heterogeneous* network in which the degree of nodes varies. Similar to Gilarranz & Bascompte (2012) and Liao *et al*. (2020), we consider four typical dispersal network structures (illustrated in Fig. 1a-d):

(i) A homogeneous (or regular) network where all patches have the same degree. For example, Figure 1e shows a completely regular network in which each patch has four links to other patches (k=4). This is equivalent to a lattice-structured model with nearest neighbour dispersal under periodic boundary conditions (Bascompte & Sole 1995; Hiebeler 2000).

(ii) A randomly structured network with randomly connected patches (Watts & Strogatz 1998). In particular, node degrees are drawn from a Poisson distribution with the variance equal to the mean degree within the network (e.g. $\sigma^2 \approx \bar{k}$=4 in Fig. 1f). Thus, all patches have a similar number of connections though there is some variation (heterogeneity) (Erdös & Rényi 1959).

(iii) An exponential network constructed based on the generic algorithm of random attachment (Barabási & Albert 1999), which produces an exponential degree distribution. Such networks have a higher variability in degree for a given mean degree than the random network (ii) (e.g. $\bar{k}$=4 and variance $\sigma^2 \approx 5.86$ in Fig. 1g) (Fortuna *et al*. 2006), producing a greater heterogeneity in patch connectivities.

(iv) A scale-free network constructed according to the algorithm of Barabási & Albert (1999) with preferential attachment (i.e. increasing the probability that new patches connect to already well-connected patches), which yields a power-law degree distribution. This type of network has a very high variability in degree for a given mean degree (e.g. $\bar{k}$=4 and $\sigma^2 \approx 27.4$ in Fig. 1h). Thus, a few patches are highly connected while most have only few connections.

In these networks, all patches are reachable by every species, that is, each patch has at least one link to another patch. Species are assumed to use dispersal links in either direction without preference, i.e. when patches i_1 and i_2 are linked, dispersal can occur from either i_1 to i_2 or vice versa.

Competitive dynamics

Metapopulation models are typically based on the concept of patch occupancy, i.e. whether a species is present or absent on a patch. Patches are assumed to be of the minimum size required to sustain a viable population of the species studied. In this model, we additionally assume that each patch (or colony site) can either be vacant or host a single species (cf. Tilman 1994), producing competition for available colony sites. Monoculture patches of this sort have been observed in garden plot ecosystems (Tilman & Wedin 1991; Wedin & Tilman 1993) and insect communities (Hanski 1990; Shorrocks 1991). Due to the priority effect, displacing an established population/adult is typically more difficult than colonizing an empty patch (Comins & Noble 1985; Calcagno *et al*. 2006; Fukami 2015). Additionally, ignoring this effect, by permitting a strong competitor to displace weaker species, always leads to monoculture (i.e. only the best competitor survives) when all species have the same demographic traits (*Appendix* Fig. S2). Consequently, we focus on preemptive competition, i.e. species compete only for empty patches, and assume that strong competitors have priority. Thus, a species can colonize an empty patch only if no superior competitor simultaneously colonizes that patch.

We consider a system of n species with a strict competitive hierarchy, i.e. species are ranked from the best competitor (species 1) to the poorest (species *n*). In order to focus on the effect of network structure, we assume that all species have the same demographic traits (colonization and extinction probabilities, *c* and *e* respectively). This explicitly precludes the existence of any colonization-competition tradeoff (Tilman 1994).

The result is a stochastic model in which the probability that a given empty patch *i* is colonized by the *S*-th competitor ($1 \leq S \leq n$) is

$$P_i(S) = (1-c)^{\sum_{j=1}^{S-1} x_j} \cdot [1-(1-c)^{x_S}]. \tag{1}$$

Here x_j (≥ 0) denotes the number of *j*-patches (occupied by species *j*) directly linked to the empty patch i, and $(1-c)^{\sum_{j=1}^{S-1} x_j}$ denotes the probability that the superior competitors (species 1, 2, 3…*S*-1) do not establish a population on this patch. Note that an empty patch can only be colonized from a patch that is directly connected to it.

Spatially explicit simulations

Initially each patch is occupied by a species randomly sampled from the species pool. When dispersal networks are not shared, we generate a dispersal network for each species with given network properties (e.g. variation in patch degrees). For each time step, we first check whether the population in each occupied patch becomes extinct (with probability *e*). We then determine whether any empty patches become occupied by the species directly connected to it (see Eq. 1). Finally, we record the patch occupancy for each species at each time step, calculated as its number of occupied patches divided by the network size (i.e. the total number of patches).

To reduce the effects of stochasticity (*Appendix* Figs S3-S4), we model patch occupancy dynamics (via Matlab R2018b) using large networks consisting of 1024 patches and 2048 undirected links (cf. Gilarranz & Bascompte 2012). As such, all types of network have the same number of patches and links with the same average degree $\bar{k}$=4, allowing us to compare species coexistence in dispersal networks with contrasting levels of heterogeneity. It was observed from simulations that these systems approached steady state after 5000 time steps. We estimated these steady states by simulating a system for 10,000 time steps and then averaging its occupancies over the last 1000 steps. To eliminate effects of specific dispersal network structures, 100 replicates were simulated for each case. Each replicate used different, randomly generated, dispersal networks but with the same properties (i.e. the same network size, total links, and degree distribution). The mean steady-state patch occupancy (mean ± standard deviation SD) was then calculated from these replicates. A broad range of biologically reasonable parameter combinations were explored and found to yield qualitatively similar outcomes (*Appendix* Figs S1-S27), thus allowing us to present our general results in Figs 1-5 by choosing one of those parameter combinations as a reference.

Results

Two-species system

To get insight into the competitive dynamics, we first simply analyze two species (A – superior competitor and B – inferior competitor) competing for an empty patch i

locally. Thus the probability of the superior species *A* successfully colonizing the empty patch is

$$P_i(A) = 1 - (1 - c)^{x_A}, \tag{2}$$

with 0< *c* <1. The inferior species *B* can colonize the patch only if species *A* does not. Hence the probability of this event is

$$P_i(B) = (1 - c)^{x_A} \cdot \left[1 - (1 - c)^{x_B}\right]. \tag{3}$$

Note that x_A and x_B denote the number of species *A* and *B* directly linked to the patch *i*. We can now determine whether it is possible for the inferior species *B* to have a greater probability to occupy the focal empty patch *i* than the superior species *A*. By setting $P_i(B) > P_i(A)$, we have

$$(1 - c)^{x_A} \cdot \left[1 - (1 - c)^{x_B}\right] > 1 - (1 - c)^{x_A}. \tag{4}$$

As such, the conditions for $P_i(B) > P_i(A)$ can be derived as

$$\begin{cases} x_B > ln\left[2 - (1 - c)^{-x_A}\right]/\ln(1 - c) \\ x_A < -\ln 2/\ln(1 - c) \end{cases}, \tag{5}$$

otherwise $P_i(B) < P_i(A)$ (see phase diagram in *Appendix* Fig. S5). Thus, when the inferior species occupies more patches in a given area than the superior species, it is able to overcome its competitive inferiority locally. This indirectly demonstrates that species might coexist regionally if they do not share the same dispersal networks.

We then simulate the coexistence of two competitors with the same demography (i.e. identical colonization and extinction rate) on shared vs. unshared dispersal networks with contrasting heterogeneities, including (from most homogeneous to most heterogeneous) regular, random, exponential and scale-free networks (Fig. 1). For shared networks, we find that the two species cannot coexist regardless of the level of heterogeneity in the dispersal network, as the superior species eventually excludes the inferior species (Fig. 1I-IV). However, for unshared dispersal networks (with the same heterogeneity), stable coexistence becomes possible (Fig. 1VI-VIII; see coexistence pattern in *Appendix* Fig. S6), with the exception of regular networks (Fig. 1V). Interestingly, increasing the degree of dispersal network heterogeneity causes the long-term species occupancies to converge (Fig. 1VI-VIII), i.e. the competitive advantage of the superior species is reduced.

The coexistence patterns described above can, however, be altered by varying the species' relative extinction and colonization rates (Fig. 2; *Appendix* Figs S7-S15) or the average patch degree (*Appendix* Fig. S16). Again, no coexistence is possible when the species share the same dispersal network (*Appendix* Fig. S17I-IV), as the superior competitor excludes the inferior species. However, when dispersal networks are unshared, a coexistence (grey) region exists (Fig. 2II-IV & VI-VIII), except in regular networks (Fig. 2I & V). As expected, the global occupancy of both species declines as the relative extinction rate (e/c) increases (Fig. 2I-IV). This typically results in the weaker competitor becoming extinct first (Fig. 2I-IV; *Appendix* Fig. S17). However, species coexistence is maintained at much higher e/c-ratios if dispersal networks are unshared and the network heterogeneity is high.

By contrast, increasing the relative colonization rate (c/e) produces a quite different pattern (Fig. 2V-VIII). The abundance of the superior species increases monotonically with increasing relative colonization rate regardless of other factors, but tends to saturate at high *c/e*-ratios. On shared networks, the inferior species is simply excluded (*Appendix* Fig. S17V-VIII). However, on unshared heterogeneous networks, there is an intermediate range (grey) in which the species coexist, which expands as the networks become more heterogeneous (Fig. 2V-VIII). In particular, the patch occupancy of the inferior species initially increases with the relative colonization rate before declining to extinction at high *c/e*-ratios. Intermediate levels of *c/e* thus maximize the inferior species' occupancy and consequently promote species coexistence, as opposed to lower or higher colonization rate which would speed up species exclusion (a unimodal response). This outcome is similar to the case where the average patch degree is increased (*Appendix* Fig. S16) and follows directly from the observation that increasing *c* reduces the area of parameter space in which the inferior species can locally outcompete the superior species (*Appendix* Fig. S5).

Finally, for this two-species system, we explore how coexistence is affected when the species utilize differing dispersal modes, corresponding to the dispersal networks with different heterogeneities (Fig. 3). When the inferior species has a longer dispersal range (i.e. it disperses on a non-local network, including random, exponential and scale-free networks), it can exclude a locally dispersing superior species (Fig. 3I-III). By contrast, when the inferior competitor uses local dispersal (i.e. a regular dispersal network), it is always outcompeted by the superior competitor (Fig. 3IV-VI). Thus, non-local dispersal modes can compensate for competitive disadvantage and overturn the competitive outcome. In other cases, where both competitors use non-local dispersal modes, we observe that the species can coexist stably (Fig. 3VII-XII) and that species abundances are very similar when the inferior competitor disperses on the network with highest heterogeneity (Fig. 3X & XI).

Multispecies system

We now extend this investigation to a multi-species system (Fig. 4; *Appendix* Figs S18-S20) showing that the behaviours described above transfer well to this more complex case. Again, increasing the relative extinction rate (*e/c*) reduces species richness on both shared and unshared dispersal networks. Furthermore, on shared networks, only the best competitor survives (*Appendix* Fig. S18a), while on unshared networks, coexisting sub-communities are possible (Fig. 4a). Greater degrees of dispersal network heterogeneity promote species diversity. Similarly when the relative colonization rate (*c*/*e*) is varied, we find that, only the best competitor can survive on shared networks (*Appendix* Fig. S18b). Moreover, on unshared networks, the greatest community diversity is attained at intermediate levels of *c*/*e* (a unimodal response, similar to the effect on patch degree; see *Appendix* Fig. S21). Again, increasing dispersal network heterogeneity increases community diversity.

Finally, we examine the effect of network size on biodiversity (i.e. the species-area curve) in shared (*Appendix* Fig. S22) and unshared dispersal networks (Fig. 5). In shared networks, only the best competitor survives regardless of network size and heterogeneity (*Appendix* Fig. S22). By contrast, increasing the network size in unshared networks leads to a monotonic increase in species richness, with greater species richness on more heterogeneous dispersal networks (Fig. 5a). Additionally, we observe that patches which are highly connected within the dispersal network of a particular species are normally occupied by that species (Fig. 5b-d; *Appendix* Fig. S23).

Discussion

The key innovation of our model is to place metapopulation dynamics on an irregular dispersal network. Existing theoretical studies of the mechanisms controlling community diversity are based on models which assume regular connections between landscape patches. However, in natural systems such connections can be far from regular (Hanski & Ovaskainen 2000; Fortuna *et al*. 2006; McIntire *et al*. 2007). Our study demonstrates that such heterogeneity can allow species with differing dispersal connections (i.e. species-specific dispersal networks) to coexist, thereby promoting community diversity. Thus, previous patch-dynamic models focusing only on shared regular networks, might have largely underestimated species diversity, as species in natural communities often exhibit diverse dispersal patterns with more or less heterogeneity.

When dispersal networks are shared, all species have the same ability to access any given colony site. Consequently, the outcome of competition events is not influenced by this spatial structure. By contrast, when each species disperses differently (i.e. on a different dispersal network), any given species will have greater access to some areas of the landscape than others. This creates refuges for inferior competitors within the landscape, i.e. areas which the superior competitors have limited access to, allowing the inferior competitor to outcompete them locally.

This explanation is confirmed by comparing the spatial distribution of each species to its dispersal network (*Appendix* Figs S6 & S23), where we observe that species form self-organized clusters of occupied patches with the most connected patches at the core. This mechanism can be explored further by relating the incidence of a species upon a patch (i.e. the proportion of time steps that a patch is occupied by that species) to the degree of that patch and the mean degree of patches it is connected to (*Appendix* Figs S24-S27). Species incidence on a patch increases with the patch degree (*Appendix* Figs S24-S25) and with the mean degree of the connected patches (*Appendix* Figs S26-S27). This can be explained by the observation that a patch is more likely to be recolonized by a species, if it is adjacent to a large number of sites occupied by that species (Eq. 1). In turn, if a patch is likely to be occupied by a specific species, it is more likely that the patches connected to it will be colonized by that species. This creates a positive feedback between highly connected patches and those that connect to them. The result is a segregation-aggregation process (*sensu* Pacala 1997; Murrell *et al*. 2001; Holyoak & Loreau 2006), which permits species to coexist on the landscape scale; although single species dominate in any given region. Thus, our study shows that unshared dispersal networks offer a mechanism for the emergence of landscape scale community diversity (γ-diversity).

It is well known that a dispersal range advantage can compensate for a disadvantage in direct competition or permit coexistence of competitors (e.g. Liao *et* *al*. 2013a). We observe exactly the same trends when competing species disperse on networks with differing levels of heterogeneity (Fig. 3). This can be explained by the observation that a higher level of heterogeneity within a dispersal network permits longer-range dispersal. In particular, if we regard the regular network as representing the physical arrangement of the habitat (i.e. a regular lattice), it describes short range dispersal (dispersal only between "nearest neighbours"). However, when the degree distribution is heterogeneous, some patches have more connections than the mean. In the context of the physical arrangement described above, this means they must connect to more than only their "nearest neighbours" (in that lattice), allowing longer range dispersal. As the level of heterogeneity increases, the number of connections possessed by highly connected patches increases, allowing a species occupying such a site to access a greater proportion of the total sites. This corresponds to increasing dispersal range. Interestingly, these patterns have been observed empirically by Yeaton & Bond (1991), where two competing shrub species with dispersal differences (one with ant-dispersed seeds and another with wind-dispersed seeds) can co-occur stably.

In order for these mechanisms to operate, colonization success rates cannot be too high. In particular, we find a unimodal biodiversity response to colonization success rate (Figs 2 & 4). This follows from the observation that, if the colonization success rate is high, the best competitors will almost always successfully colonize any unoccupied patch which they can access. Consequently, even large aggregations of an inferior competitor are not able to resist invasion. For similar reasons, we also find a unimodal biodiversity response to average patch degree (*Appendix* Figs S16 & S21). The aggregation-segregation mechanism relies on inferior competitors forming relatively isolated clusters (*Appendix* Figs S6 & S23). As landscape connectivity increases, all patches become more accessible and such isolated clusters become harder to form.

A final observation is that increasing network size monotonically increases species richness in unshared networks and that the strength of this response increases with dispersal network heterogeneity (Fig. 5). Essentially, as network (or landscape) size increases, the chance that each species can achieve local competitive dominance within a specific region of the landscape increases. The resulting monotonically increasing species-area curves refute the previous view that the number of species coexisting cannot exceed the number of limiting resources (Levin 1970; Tilman 1982). Instead, we theoretically demonstrate that, when there are species-specific differences in dispersal networks, many more species than the number of limiting resources should be able to coexist, as empirically observed in several natural systems (Tilman 1982; Kotler & Brown 1988; Wellborn *et al.* 1996). Previously, coexistence of an unlimited number of species in a spatial context was ascribed to the colonization-competition tradeoff (Tilman 1994) rather than to differences in the dispersal opportunities available to individual species (Adler & Mosquera 2000). Our model provides an alternative explanation; i.e. if the landscape is large enough, unshared heterogeneous dispersal networks can support the coexistence of many more species than expected, due to a segregation-aggregation mechanism.

By demonstrating that the structure of dispersal networks strongly governs species coexistence, mediated by species life-history attributes, our work helps fill the gap between landscape structure and spatial competition. We find that incorporating species-specific dispersal networks into the traditional hierarchical competitive systems can greatly promote regional coexistence owing to the formation of self-organized clusters. This implies that traditional shared lattice- or randomly-structured models might have severely underestimated biodiversity maintenance. More importantly, the model suggests significant implications for biodiversity conservation and management. For instance, as different species often display diverse patterns of patch connectivity based on their dispersal traits (e.g. wind-dispersed *vs.* bird-dispersed seeds; walking *vs.* flying species), it is essential to characterize the dispersal networks of species of interest. We could then overlay or intersect these networks to find hub locations, so as to design multispecies conservation plans (e.g. Bunn *et al*. 2000; Urban & Keitt 2001; Nicholson & Possingham 2006; Bearup *et al*. 2013).

Furthermore, the unimodal diversity response to an increase of species colonization rate or average patch degree observed in our model (Figs 2 & 4; *Appendix* Figs S16 & S21), indirectly supports the intermediate heterogeneity hypothesis (cf. Duelli 1997; Tscharntke *et al.* 2005; Sirami *et al.* 2019). In particular, we find that intermediate levels of patch connectivity (inversely related to habitat fragmentation) maximize species coexistence as predicted. This contradicts existing strategy for biodiversity conservation, which calls for increasing habitat connectivity (e.g. constructing ecological corridors) as much as possible (reviews in Fahrig 2002, 2003; Ewers & Didham 2006; Fischer & Lindenmayer 2007). Such interventions might lead to more species losses because of increasing competitive exclusion. Thus, we suggest that several small reserves would conserve more species than a single large reserve (see SLOSS debate in Ovaskainen 2002), if the patch size meets the minimum area required for a viable population. This conclusion has been supported by empirical studies (Fahrig 2003, 2017), which found that habitat fragmentation generally enhanced species diversity though the effects were small. However, we make the additional point that local aggregation of weaker competitors can prevent invasions. This suggests a complementary strategy for species conservation, i.e. establishing enclaves of species endangered by non-native invaders and limiting access to them. Similar concepts have, in fact, been applied to the problem of red squirrel conservation in the UK (Parrott *et al.* 2009).

Two caveats should be addressed when applying our model to terrestrial ecosystems. Firstly, although there have been a large number of studies on scale-free graphs (Barabási & Albert 1999), actual patch mosaics seem to not quite fit the definitions of such well-studied networks so that they tend to not include the extremely connected patches that characterize scale-free networks (Urban *et al*. 2009). Secondly, it may be inappropriate to apply a graph representation for some landscapes if habitat patches are poorly resolved spatially (Urban & Keitt 2001). For example, habitat quality varies continuously and subtly over the landscape, thus aggregating this variability into discrete patches may be inappropriate (e.g. Liao *et al*. 2013b).

However, our modelling predictions could be further validated by both controlled micro- or mesocosms and field observations. For example, by manipulating habitat connectivity in protist/microarthropod experiments (e.g. Violle *et al.* 2010; Staddon *et al.* 2010; Chischolm *et al.* 2011; Carrara *et al.* 2012, 2014), it would be possible to test spatial coexistence of hierarchical competitors with different dispersal patterns. For mesocosms, it would be possible to perform long-term competition experiments for glass plants in gardens by controlling species dispersal between plots, e.g. via addition of propagules of plant species (Tilman & Wedin 1991; Wedin & Tilman 1993). Furthermore, open field experiments, such as those performed by Ding *et al.* (2013) and Wang *et al.* (2015) on dispersal of forest birds in Thousand Island Lake, China, could be extended to explore the effect of variation in dispersal pathways on their coexistence. Overall, by integrating both network and metapopulation approaches, our modelling study provides a new way to understand the coexistence mechanism of spatial dispersal heterogeneity, thereby strengthening our comprehension of biodiversity maintenance in hierarchical competitive communities.

Acknowledgements

This study was supported by the National Science Foundation of China (No. 31760172 & 31901175) and the Key Joint Youth Project of Jiangxi Province (No. 20192ACBL21029). Comments from two reviewers greatly improved this manuscript.

Competing interests: The author declares no competing interests.

Supplementary Information is available for this paper.

References

Adler, F.R. & Mosquera, J. (2000). Is space necessary? Interference competition and limits to biodiversity. *Ecology*, 81, 3226-3232.

Allesina, S. & Levine, J.M. (2011). A competitive network theory of species diversity. *PNAS*, 108, 5638-5642.

Amarasekare, P. (2000). Coexistence of competing parasitoids on a patchily distributed host: local vs. spatial mechanisms. *Ecology*, 81, 1286-1296.

Amarasekare, P. (2008). Spatial dynamics of food webs. *Annu. Rev. Ecol. Evol. Syst.*, 39, 479-500.

Barabási, A.L. & Albert, R. (1999). Emergence of scaling in random networks. *Science*, 286, 509-512.

Bascompte, J. & Solé, R.V. (1995). Rethinking complexity: modelling spatio-temporal dynamics in ecology. *Trends Ecol. Evol.*, 10, 361-366.

Bearup, D., Petrovskii, S., Blackshaw, R.P. & Hastings, A. (2013). Synchronized Dynamics of *Tipula paludosa* Metapopulation in a Southwestern Scotland Agroecosystem: Linking Pattern to Process. *Am. Nat.*, 182, 393-409.

Bode, M., Burrage, K. & Possingham, H.P. (2008). Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. *Ecol. Model.*, 214, 201-209.

Bunn, A.G., Urban, D.L. & Keitt, T.H. (2000). Landscape connectivity: a conservation application of graph theory. *J. Environ. Manage.*, 59, 265-278.

Calcagno, V., Mouquet, N., Jarne, P. & David, P. (2006). Coexistence in a metacommunity: the competition-colonization trade-off is not dead. *Ecol. Lett.*, 9, 897-907.

Carrara, F., Altermatt, F., Rodriguez-Iturbe, I. & Rinaldo, A. (2012). Dendritic connectivity controls biodiversity patterns in experimental metacommunities. *PNAS*, 109, 5761-5766.

Carrara, F., Rinaldo, A., Giometto, A. & Altermatt, F. (2014). Complex interaction of dendritic connectivity and hierarchical patch size on biodiversity in river-like landscapes. *Am. Nat.*, 183, 13-25.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343-366.

Chisholm, C., Lindo, Z. & Gonzalez, A. (2011). Metacommunity diversity depends on connectivity and patch arrangement in heterogeneous habitat networks. *Ecography*, 34, 415-424.

Chu, C. & Adler, P.B. (2015). Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. *Ecol. Monogr.*, 85, 373-392.

Comins, H.N. & Noble, I.R. (1985). Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *Am. Nat.*, 126, 706-723.

Dale, M. & Fortin, M.J. (2010). From graphs to spatial graphs. *Annu. Rev. Ecol. Evol. Syst.*, 41, 21-38.

Ding, Z., Feeley, K.J. Wang, Y., Pakeman, R. & Ding, P. (2013). Patterns of bird functional diversity on land-bridge island fragments. *J. Anim. Ecol.*, 82, 781-790.

Dondina, O., Orioli, V., Colli, L., Luppi, M. & Bani, L. (2018). Ecological network design from occurrence data by simulating species perception of the landscape. *Landscape Ecol.*, 33, 275-287.

Duelli, P. (1997). Biodiversity evaluation in agricultural landscapes: An approach at two different scales. *Agr. Ecosyst. Environ.*, 62, 81-91.

Erdös, P. & Rényi, A. (1959). On random graphs I. *Publ. Math.*, 6, 290-297.

Ewers, R.M. & Didham, R.K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.*, 81, 117–142

Fahrig, L. (2002). Effect of habitat fragmentation on the extinction threshold: a synthesis. *Ecol. Appl.*, 12, 346-353.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.*, 34, 487-515.

Fahrig, L. (2017). Ecological responses to habitat fragmentation *per se*. *Ann. Rev. Ecol. Evol. Syst.*, 48, 1-23.

Fischer, J. & Lindenmayer, D.B. (2007). Landscape modification and habitat fragmentation: A synthesis. *Glob. Ecol. Biogeogr.,* 16, 265-280.

Fortuna, M., Gómez-Rodríguez, C. & Bascompte, J. (2006). Spatial network structure and amphibian persistence in stochastic environments. *Proc. R. Soc. B*, 273, 1429-1434.

Fortuna, M., Albaladejo, R., Fernández, L., Aparicio, A. & Bascompte, J. (2009). Networks of spatial genetic variation across species. *PNAS*, 106, 19044-19049.

Fukami, T. (2015). Historical Contingency in Community Assembly: Integrating Niches, Species Pools, and Priority Effects. *Ann. Rev. Ecol. Evol. S.*, 46, 1, 1-23.

Germain, R.M., Jones, N.T. & Grainger, T.N. (2019). Cryptic dispersal networks shape biodiversity in an invaded landscape. *Ecology*, 100, e02738.

Gilarranz, L.J. & Bascompte, J. (2012). Spatial network structure and metapopulation persistence. *J. Theor. Biol.*, 297, 11-16.

Gilarranz, L.J., Rayfield, B., Liñán-Cembrano, G., Bascompte, J. & Gonzalez, A. (2017). Effects of network modularity on the spread of perturbation impact in experimental metapopulations. *Science*, 357, 199-201.

Grilli, J., Barabás, G. & Allesina, S. (2015). Metapopulation Persistence in Random Fragmented Landscapes. *PLoS Comput. Biol.*, 11, e1004251.

Hansbauer, M.M. *et al.* (2010). Landscape perception by forest understory birds in the Atlantic Rainforest: black-and-white versus shades of grey. *Landscape Ecol.*, 25, 407-417.

Hanski, I. (1990). Dung and carrion insects. In: (Eds. Shorrocks, B.& Swingland, I.R.) *Living in a patchy environment*. Oxford University Press, Oxford, England, pp. 127-145

Hanski, I. & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, 404, 755-758.

Hiebeler, D. (2000). Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. *Ecology*, 81, 1629-1641.

Hirt, M.R., Grimm, V., Li, Y., Rall, B.C., Rosenbaum, B. & Brose, U. (2018). Bridging scales: allometric random walks link movement and biodiversity research. *Trends Ecol. Evol.*, 33, 701-712.

Holland, M.D. & Hastings, A. (2008). Strong effect of dispersal network structure on ecological dynamics. *Nature*, 456,792-794.

Holyoak, M. & Loreau, M. (2006). Reconciling empirical ecology with neutral community models. *Ecology*, 87, 1370-1377.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Kininmonth, S.J., De'ath, G. & Possingham, H.P. (2010). Graph theoretic topology of the great but small barrier reef world. *Theor. Ecol.*, 3, 75-88.

Kotler, B.P. & Brown, J.S. (1988). Environmental heterogeneity and the coexistence of desert rodents. *Ann. Rev. Ecol. Syst.*, 19, 281-307.

Laird, R.A. & Schamp, B.S. (2006). Competitive intransitivity promotes species coexistence. *Am. Nat.*, 168, 182-193.

Levin, S.A. (1970). Community equilibria and stability, and an extension of the competitive exclusion principle. *Am. Nat.*, 104, 413-423.

Levine, J.M. & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254-257.

Levine, J. M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56-64.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, 15, 237-240.

Liao, J.B., Li, Z., Quets, J.J. & Nijs, I. (2013a). Effects of space partitioning in a plant species diversity model. *Ecol. Model.*, 251, 271-278.

Liao, J.B., Li, Z., Hiebeler, D.E., Iwasa, Y., Bogaert, J. & Nijs, I. (2013b). Species persistence in landscapes with spatial variation in habitat quality: A pair approximation model. *J. Theor. Biol.*, 335, 22-30.

Liao, L.M., Shen, Y. & Liao, J. (2020). Robustness of dispersal network structure to patch loss. *Ecol. Model.*, 424, e109036.

McIntire, E.J.B., Schultz, C.B. & Crone, E.E. (2007). Designing a network for butterfly habitat restoration: where individuals, populations and landscapes interact. *J. Appl. Ecol.*, 44, 725-736.

Montoya, D., Zavala, M.A., Rodríguez, M.A. & Purves, D.W. (2008). Animal versus wind dispersal and the robustness of tree species to deforestation. *Science*, 320, 1502-1504.

Murrell, D.J., Purves, D.W. & Law, R. (2001). Uniting pattern and process in plant ecology. *Trends Ecol. Evol.*, 16, 529-530.

Nicholson, E. & Possingham, H.P. (2006). Objectives for multiple-species conservation planning. *Conserv. Biol.*, 20, 871-881.

Ovaskainen, O. (2002). Long-term persistence of species and the SLOSS problem. *J. Theor. Biol.*, 218, 419-433.

Pacala, W. (1997). Dynamics of plant communities. In: (Ed. Crawley, M.) *Plant Ecology*. Blackwell Science Ltd., Oxford, pp. 532-555.

Parrott, D., Quy, R., Van, D., Lurz, P., Rushton, S., Gurnell, J. *et al.* (2009). Review of red squirrel conservation activity in northern England. *Natural England Commissioned Report*.

Shorrocks, B. (1991). Competition on a divided and ephemeral resource: a cage experiment. *Biol. J. Linnean Soc.*, 43, 211-220.

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A. *et al.* (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *PNAS*, 116, 16442-16447.

Snyder, R.E. & Chesson, P. (2003). Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecol. Lett.*, 6, 301-309.

Soliveres, S., Maestre, F.T., Ulrich, W., Manning, P., Boch, S., Bowker, M.A. *et al.* (2015). Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol. Lett.*, 18, 790-798.

Staddon, P., Lindo, Z., Crittenden, P. D., Gilbert, F. & Gonzalez. A. (2010). Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecol. Lett.*, 13, 543-552.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2-16.

Tilman, D. & Wedin, D. (1991). Dynamics of nitrogen competition between successional grasses. *Ecology*, 72, 1038-1049.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2010). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecol. Lett.*, 8, 857-874.

Urban, D. & Keitt, T. (2001). Landscape connectivity: a graph-theoretic perspective. *Ecology*, 85, 1205-1218.

Urban, D.L., Minor, E.S., Treml, E.A. & Schick, R.S. (2009). Graph models of habitat mosaics. *Ecol. Lett.*, 12, 260-273.

Violle, C., Pu, Z. & Jiang, L. (2010). Experimental demonstration of the importance of competition under disturbance. *PNAS*, 107, 12925-12929.

Wang, Y., Thornton, D.H., Ge, D., Wang, S. & Ding, P. (2015). Ecological correlates of vulnerability to fragmentation in forest birds on inundated subtropical land-bridge island. *Biol. Conserv.*, 191, 251-257.

Watts, D.J. & Strogatz, S.H. (1998). Collective dynamics of ‘small-world’ networks. *Nature*, 393, 440-442.

Wellborn, G.A., Skelly, D.K. & Werner, E.E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Ann. Rev. Ecol. Syst.*, 27, 337-363.

Wedin, D. & Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol. Monogr.*, 63, 199-229.

Yeaton, R.I. & Bond, W.J. (1991). Competition between Two Shrub Species: Dispersal Differences and Fire Promote Coexistence. *Am. Nat.*, 138, 328-341.

Yu, D.W. & Wilson, H.B. (2001). The competition–colonization trade-off is dead; long live the competition–colonization tradeoff. *Am. Nat.*, 158, 49-63.

Yu, D.W., Wilson, H.B., Frederickson, M.E., Palomino, W., De La Colina, R., Edwards, D.P. *et al*. (2004). Experimental demonstration of species coexistence enabled by dispersal limitation. *J. Anim. Ecol.*, 73, 1102-1114.

Figure legends

Figure 1. Patch dynamics of two competing species in shared (I-IV) vs. unshared (V-VIII) dispersal networks. Panels (a-d): Examples of networks for each level of heterogeneity with 256 patches (red nodes) with 512 links (green lines). Variation in patch degree (proportional to node size) increases from left to right. Panels (c-h): Degree distributions for networks of each type with 1024 patches and 2048 links, again with variation in degree increasing from left to right. Panels (I-IV): The species share the same dispersal network. The superior competitor always excludes the inferior competitor regardless of network heterogeneity. Panels (V-VIII): The species disperse on separate dispersal networks with the same level of heterogeneity. They are able to coexist except on regular networks. 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 (I-IV: e/c at fixed c=0.05) and colonization rate (V-VIII: c/e at fixed e=0.05) on patch occupancy of both inferior and superior competitors at steady state (mean ± SD of 100 replicates) in unshared networks but with the same levels of heterogeneity. The coexistence region (grey) expands as the level of heterogeneity increases in the dispersal networks. Panels (I-IV): Both species show a monotonic decline in patch occupancy as e/c increases, but with the inferior species becoming extinct first. Panels (V-VIII): Increasing c/e leads to a monotonic increase in patch occupancy of the superior competitor, while the occupancy of the inferior species initially increases but later declines to zero.

Figure 3. Patch dynamics of both inferior and superior competitors with different heterogeneous networks. Panels (I-III): The inferior competitor, which disperses on a network with higher heterogeneity, excludes the superior competitor which only has access to a regular dispersal network (i.e. local dispersal), in contrast to panels (IV-VI). Panels (VII-XII): both competitors can coexist when their dispersal networks have different levels of heterogeneity. Parameter values for both species are the same: c=e=0.05.

Figure 4. Effects of relative extinction (a: e/c at fixed c=0.05) and colonization rate (b: c/e at fixed e=0.05) on the number of coexisting species at steady state (mean ± SD of 100 replicates) on unshared networks with the same levels of heterogeneity. As shown in graphs (a & b), species diversity decreases monotonically with increasing e/c, while intermediate levels of c/e maximize species richness except in regular networks.

Figure 5. Panel (a): Species-area relationship between network size (i.e. total number of patches) and the number of coexisting species at steady state (mean ± SD of 100 replicates) on unshared networks with the same levels of heterogeneity, by fixing average patch degree at $\bar{k}$=4. As shown, increasing network size leads to a monotonic increase in species richness except in regular networks. Panels (b-d): Examples of species coexistence patterns at steady state on small heterogeneous networks with 256 patches (black nodes – empty patches, and nodes in other colors – patches occupied by other species). Node size is proportional to its degree. Parameter values for all species are the same: c=e=0.05.

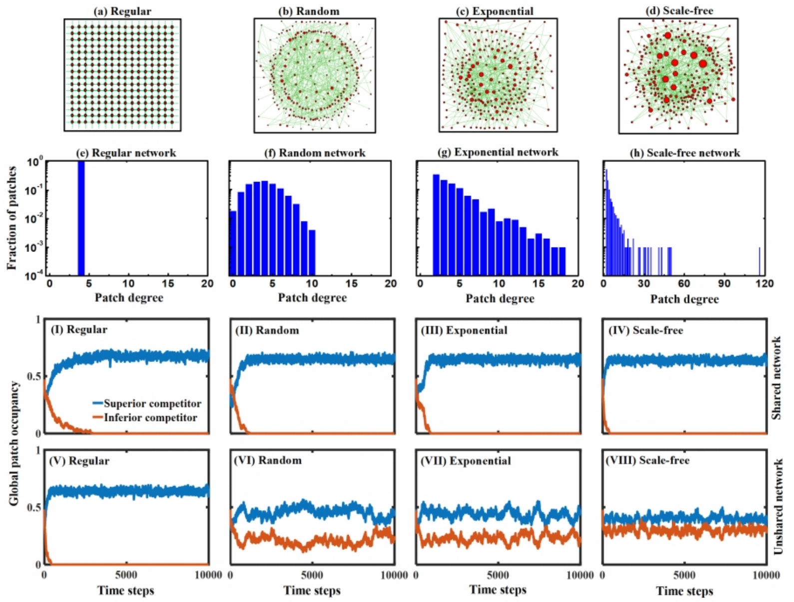

Figure 1. Patch dynamics of two competing species in shared (I-IV) vs. unshared (V-VIII) dispersal networks. Panels (a-d): Examples of networks for each level of heterogeneity with 256 patches (red nodes) with 512 links (green lines). Variation in patch degree (proportional to node size) increases from left to right. Panels (c-h): Degree distributions for networks of each type with 1024 patches and 2048 links, again with variation in degree increasing from left to right. Panels (I-IV): The species share the same dispersal network. The superior competitor always excludes the inferior competitor regardless of network heterogeneity. Panels (V-VIII): The species disperse on separate dispersal networks with the same level of heterogeneity. They are able to coexist except on regular networks. Parameter values are the same for both species: colonization rate c=0.05 and extinction rate e=0.05.

289x203mm (300 x 300 DPI)

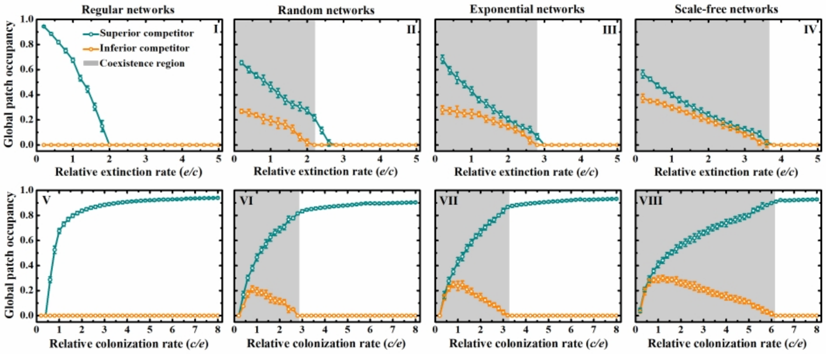

Figure 2. Effects of relative extinction (I-IV: e/c at fixed c=0.05) and colonization rate (V-VIII: c/e at fixed e=0.05) on patch occupancy of both inferior and superior competitors at steady state (mean ± SD of 100 replicates) in unshared networks but with the same levels of heterogeneity. The coexistence region (grey) expands as the level of heterogeneity increases in the dispersal networks. Panels (I-IV): Both species show a monotonic decline in patch occupancy as e/c increases, but with the inferior species becoming extinct first. Panels (V-VIII): Increasing c/e leads to a monotonic increase in patch occupancy of the superior competitor, while the occupancy of the inferior species initially increases but later declines to zero.

289x203mm (300 x 300 DPI)

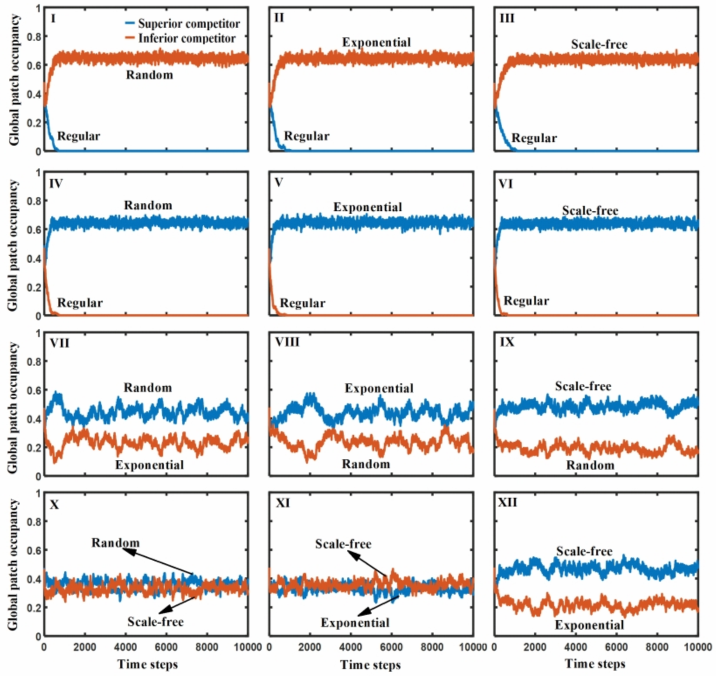

Figure 3. Patch dynamics of both inferior and superior competitors with different heterogeneous networks. Panels (I-III): The inferior competitor, which disperses on a network with higher heterogeneity, excludes the superior competitor which only has access to a regular dispersal network (i.e. local dispersal), in contrast to panels (IV-VI). Panels (VII-XII): both competitors can coexist when their dispersal networks have different levels of heterogeneity. Parameter values for both species are the same: c=e=0.05.

289x203mm (300 x 300 DPI)

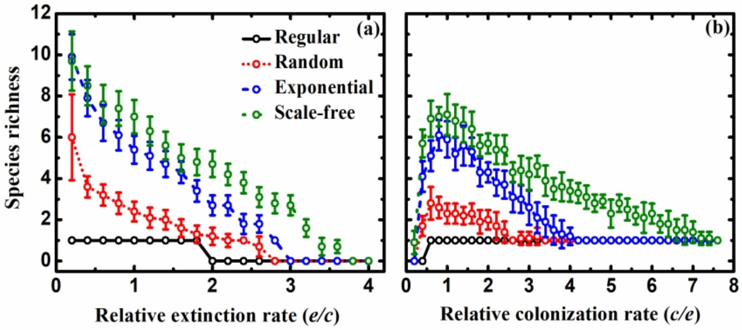

Figure 4. Effects of relative extinction (a: e/c at fixed c=0.05) and colonization rate (b: c/e at fixed e=0.05) on the number of coexisting species at steady state (mean ± SD of 100 replicates) on unshared networks with the same levels of heterogeneity. As shown in graphs (a & b), species diversity decreases monotonically with increasing e/c, while intermediate levels of c/e maximize species richness except in regular networks.

203x289mm (300 x 300 DPI)

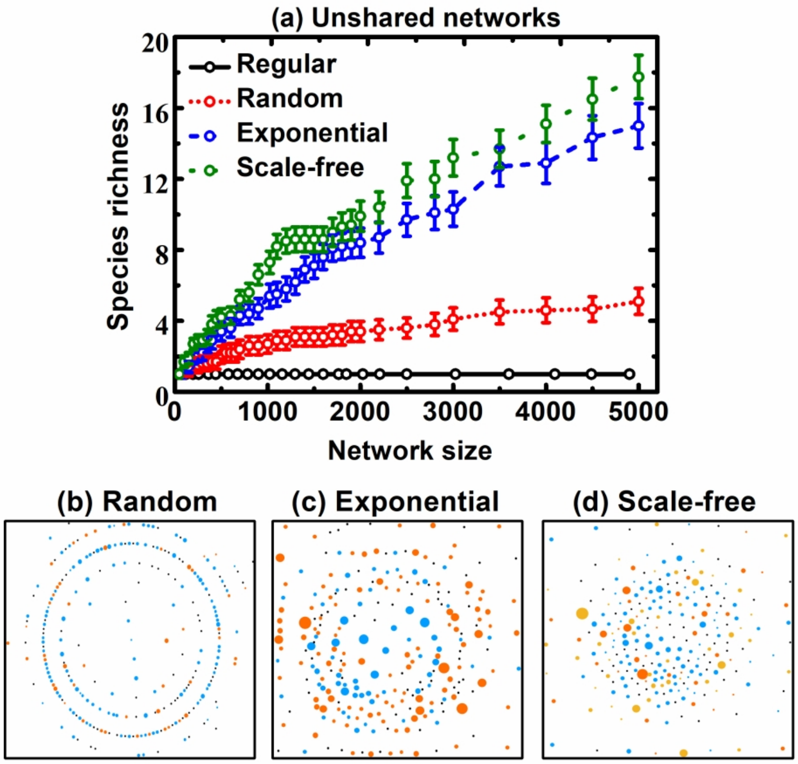

Figure 5. Panel (a): Species-area relationship between network size (i.e. total number of patches) and the number of coexisting species at steady state (mean ± SD of 100 replicates) on unshared networks with the same levels of heterogeneity, by fixing average patch degree at k =4. As shown, increasing network size leads to a monotonic increase in species richness except in regular networks. Panels (b-d): Examples of species coexistence patterns at steady state on small heterogeneous networks with 256 patches (black nodes – empty patches, and nodes in other colors – patches occupied by other species). Node size is proportional to its degree. Parameter values for all species are the same: c=e=0.05.

201x288mm (300 x 300 DPI)