Spatial network structure and metapopulation persistence

Luis J. Gilarranz*, Jordi Bascompte

Integrative Ecology Group, Estación Biológica de Doñana, CSIC, C/Américo Vespucio s/n, E-41092 Sevilla, Spain

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ABSTRACT

We explore the relationship between network structure and dynamics by relating the topology of spatial networks with its underlying metapopulation abundance. Metapopulation abundance is largely affected by the architecture of the spatial network, although this effect depends on demographic parameters here represented by the extinction-to-colonization ratio (e/c). Thus, for moderate to large e/c-values, regional abundance grows with the heterogeneity of the network, with uniform or random networks having the lowest regional abundances, and scale-free networks having the largest abundance. However, the ranking is reversed for low extinction probabilities, with heterogeneous networks showing the lowest relative abundance. We further explore the mechanisms underlying such results by relating a node's incidence (average number of time steps the node is occupied) with its degree, and with the average degree of the nodes it interacts with. These results demonstrate the importance of spatial network structure to understanding metapopulation abundance, and serve to determine under what circumstances information on network structure should be complemented with information on the species life-history traits to understand persistence in heterogeneous environments.

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1. Introduction

Recent papers have applied network theory to ecological problems. Spatial ecology, in particular, has used graph theory to describe persistence in fragmented habitats (Urban and Keitt, 2001; Dale and Fortin, 2010). In these representations, nodes indicate suitable habitat patches, and links between such nodes indicate dispersal pathways of individuals or gene flow (Fortuna et al., 2009). By treating space as a network, one emphasizes the relationship between habitat patches rather than their individual properties. Since many habitats are intrinsically patchy, while others are being fragmented at a high rate, it is important to predict under what circumstances a network of habitat patches will support a metapopulation. This understanding hinges on two aspects, namely, describing the architecture of realistic spatial networks, and modelling ecological dynamics on such networks.

Regarding spatial dynamics, intense research was performed in the 90s on spatially explicit models (Bascompte and Solé, 1995; Tilman and Kareiva, 1997; Hanski and Gilpin, 1997). Among others, we obtained important insight on the coexistence of competitors and natural enemies (Hassell et al., 1991), the formation of complex spatial patterns due to simple rules (Bascompte and Solé, 1995), or the rate and shape of metapopulation decline as habitat is progressively destroyed (Lande, 1987; Bascompte and Solé, 1996). Although

this research was important in exploring the population and community effects of short-range dispersal, it was mainly based on spatially homogeneous lattice models, where one patch is linked to its 4 or 8 nearest neighbours. An important exception are the spatially realistic metapopulation models, where the exact positions and areas of patches are explicitly modelled (Hanski, 1998).

Network structure, on the other hand, has been the hallmark of recent research on complex networks, including spatial networks (Fagan, 2002; Fortuna et al., 2006; Dale and Fortin, 2010). Originally, work on complex networks was mainly descriptive, focusing on relevant statistical patterns. One such a pattern is provided by the degree distribution, i.e., the probability of finding a patch with a certain number of links. The shape of this distribution is a first description of the heterogeneity of the network. Beyond this first descriptor, other topological characteristics may be relevant to describing complex networks. One such example is the connectivity correlation, measured as the correlation between a node's degree and the average degree of the nodes it interacts with (Maslov and Sneppen, 2002; Melián and Bascompte, 2002).

The ultimate rational for studying complex networks, however, has been the belief that network structure highly affects its dynamics, and more recent papers have explicitly explored the dynamical implications of network patterns (Bode et al., 2008; Holland and Hastings, 2008; Economo and Keitt, 2008; Muneepeerakul et al., 2008).

A network approach has the promise of providing an assessment of persistence merely from topological information. For example, to what degree the topology of the network by itself

* Corresponding author.
 E-mail address: lj.gilarranz@ebd.csic.es (L.J. Gilarranz).

provides information on metapopulation persistence even in the absence of demographic information? This is a relevant question since describing how the invisible road map of patches looks like is simpler than measuring demographic variables. Second, what specific property of network structure better predicts metapopulation abundance? Here we build on previous work relating network structure and spatial ecological dynamics (Bode et al., 2008; Holland and Hastings, 2008; Economo and Keitt, 2008; Muneepeerakul et al., 2008) by studying ecological dynamics on spatial networks with contrasting architectures, and exploring what properties of structure best explain the differences in their ability to support a metapopulation.

2. Methods

2.1. Spatial structure

Here we consider four network architectures as represented in Fig. 1. Each node or habitat patch will be described by its degree k, defined as its number of links to other nodes. Similarly, each network can be defined by its degree distribution.

In regular networks (Fig. 1a), every patch has four links to nearby patches, as traditionally modelled by spatially explicit models such as cellular automata and coupled map lattices (Bascompte and Solé, 1995). This network describes a totally homogeneous habitat with short-range dispersal.

In a landscape where patches are connected randomly (Fig. 1b), long-distance interactions are allowed (Watts and Strogatz, 1998). Even when the average degree per node is the same than before, there is some variability. This variability in degree across nodes can be seen in Fig. 1, where the size of a node is proportional to its number of links. In this case, the probability of finding a patch with a certain number of links follows a Poisson distribution (Erdös and Rényi, 1959).

Exponential networks such as the one displayed in Fig. 1c also allow long-distance interactions, but as can be seen by the variability in node sizes, they show a more heterogeneous range of node's degree (Fortuna et al., 2006). These networks were constructed following the algorithm by Barabasi and Albert (1999) with random attachment.

Finally, scale-free networks (Fig. 1d) are extremely heterogeneous (Kininmonth et al., 2010). The majority of nodes have one or a few links, but a few nodes are extremely well-connected. The degree distribution follows a power law (Barabasi and Albert, 1999).

To make results comparable, all networks must have the same number of nodes and the same number of links. Here we used networks with a large enough number of nodes to reduce the role of stochastic effects. Specifically, the network here analyzed contains 1024 nodes and 2048 undirected links. By an undirected link we refer that if nodes i and j are connected, dispersal can occur from either i to j or vice-versa.

2.2. From structure to dynamics

The previous spatial networks are the physical template over which the dynamics of a metapopulation is simulated. We use a discrete, spatially explicit version of Levins', 1969 model, where a patch is either occupied or empty. Each time step has two phases: an extinction phase, when occupied nodes become extinct with a certain probability e, and a colonization phase, when an unoccupied node i is colonized from one of the occupied nodes it interacts with an independent colonization probability per node c. The overall, node-specific effective colonization probability $C(i)$ is then given by

$$C(i) = 1-(1-c)^x, \tag{1}$$

where x is the number of occupied nodes linked to node i.

We estimate the metapopulation regional abundance at each time step along the dynamics as the number of occupied patches divided by the total number of patches. To avoid transient dynamics we discard the first 1000 time steps, and then average the proportion of occupied patches of the next 9000 time steps (Fig. 2).

Since the metapopulation regional abundance depends on the extinction-to-colonization ratio, we calculate this amount for every e/c ratio on every network type.
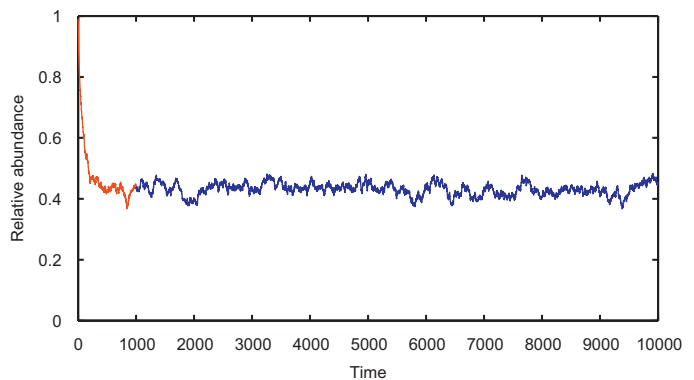
Fig. 2. Example of model dynamics. The figure depicts the simulated relative abundance of a metapopulation on an exponential spatial network. The first 1000 time steps, which are removed from the estimation of the average relative abundance, are highlighted in red. $e/c=2$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
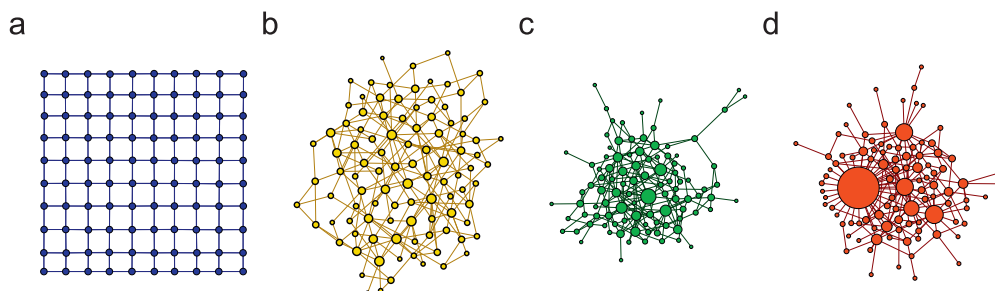
Fig. 1. The four different spatial networks used in this study, from the most homogeneous to the most heterogeneous. Node size is proportional to its degree. Networks represented in this figure have 100 nodes and are drawn for representation purposes, while the networks used in the simulations have 1024 nodes. (a) Regular network, (b) random network, (c) exponential network, (d) scale-free network.

3. Results

Fig. 3 plots the metapopulation regional abundance of each network type, and the interception with the *x*-axis depicts the threshold in metapopulation persistence. Several results are worth noting. Overall, the more heterogeneous networks allow a metapopulation persistence for higher extinction-to-colonization (*e*/*c*) ratios. Interestingly enough, however, there are two broad areas of the parameter space where the ranking of each network type in terms of its ability to sustain a metapopulation shifts. Thus, for an extinction-to-colonization ratio below approximately 1.5, homogeneous networks described by a regular network display the highest regional abundance, albeit this is a small difference. However, as the extinction-to-colonization ratio becomes higher than 1.5, the order is reversed. Now, heterogeneous networks—and especially scale-free ones—show the highest regional abundance, and the difference across network types keeps growing with the relative extinction rate. Thus, the effect of network structure on metapopulation regional abundance depends on one property of the life history of the species, extinction-to-colonization ratio, not encapsulated in the topology of the network. In the appendices we compare these results with those obtained with the analytical approach by Hanski and Ovaskainen (2000). Next, we will explore the mechanism behind the pattern in Fig. 3 and what property of network architecture is best related to the shift in the ranking of network types in terms of their metapopulation abundance.

For low *e*/*c* ratios, each node in a regular network has a high effective colonization probability according to Eq. (1). All regions of the lattice have the same number of links, hence the same probability to maintain a population. In heterogeneous networks, however, isolated patches have a lower probability to be occupied than the patches of the lattice. This explains the topology ranking for low *e*/*c* ratios. But as the extinction probability increases, only highly connected clusters of patches can be frequently occupied. To have four links is not enough to be colonized. It is in this context of relatively high extinction probabilities when heterogeneous networks increase persistence. To further understand these differences, we will move from the scale of the entire network to the scale of a constituent node.

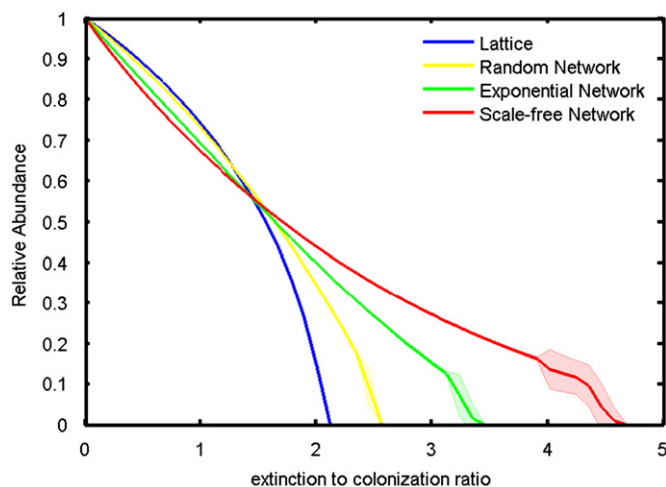Fig. 4 illustrates the variability across nodes in terms of their incidence, that is, the proportion of time steps that a certain patch is occupied (colour-coded). As can be observed, variability across nodes is higher in the more heterogeneous networks, although this is only observed for high extinction-to-colonization ratios. That is, the differential importance of each node depends on both the topology of the network and the demographic properties of the species inhabiting such a network. Only for highly heterogeneous networks and metapopulations with a high extinction-to-colonization ratios, the variability across nodes' incidence is really high. What property of the network does best explain whether a node's incidence will be higher or lower in the above scheme? A first candidate would be the degree of the node.
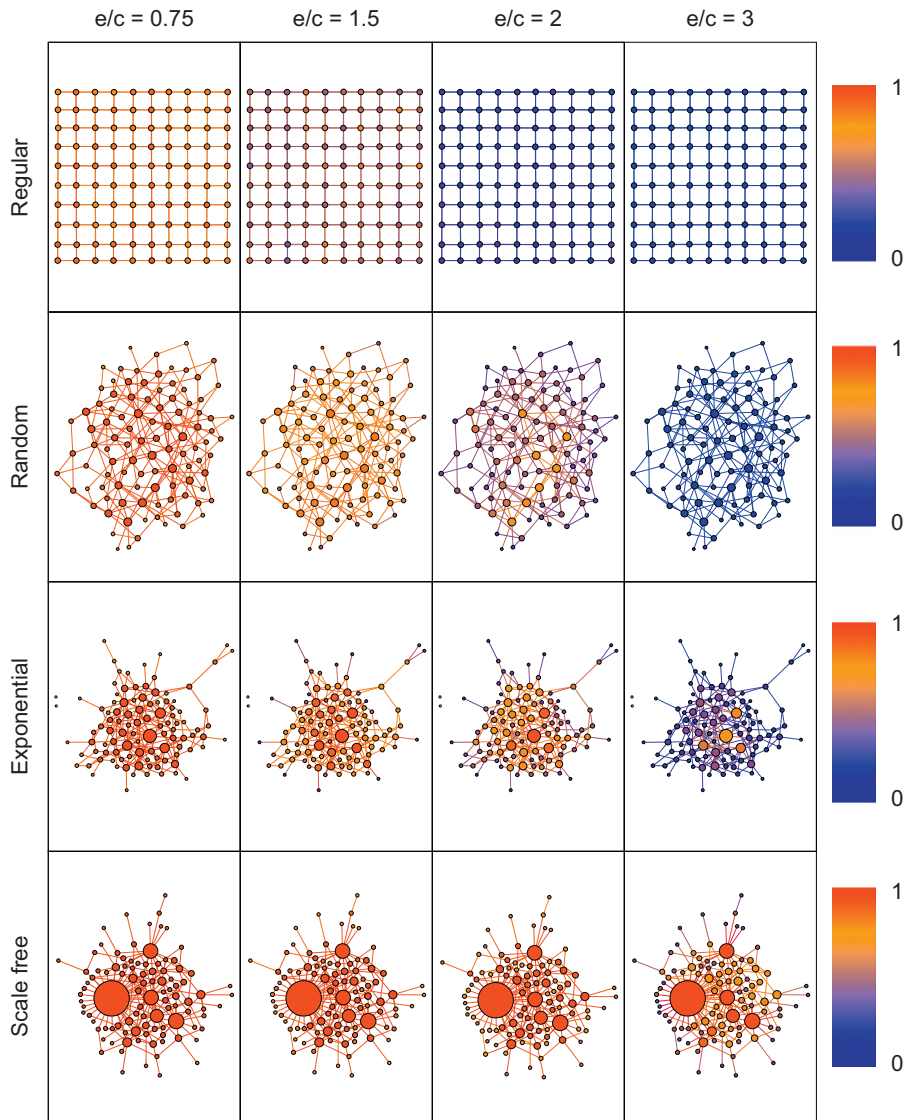
Fig. 5 plots the relationship between the incidence of a node and its degree in a scale-free network with high extinction-to-colonization rates (lower right-hand panel in Fig. 4). Not surprisingly, incidence grows with degree, but this is a highly non-linear relationship. Thus, nodes need a minimum degree to be able to stay occupied the majority of the time, but after a threshold in degree, there is no direct correspondence between degree and incidence. Since variability in degree is only one first description of network structure, and previous work has detected important variability in the connectivity correlation, we next explore to what extent being connected to a highly connected patch provides any benefit in terms of incidence.

We found that when comparing nodes with the same degree, those attached to well-connected patches have a larger incidence than those attached to patches with a low degree (Fig. 6). The benefit that a patch obtains from its nearest neighbours' degree is larger the larger is the patch's degree. Thus, the overall description of the network in terms of its degree distribution is not enough to estimate a node's incidence, which depends not only on its characteristics, but also on its position within the network. However, as happens for a node's degree, the relationship between incidence and average nearest neighbour's degree is highly non-linear. After a minimum nearest neighbour's degree, there is no increase in incidence for further increases of the degree of the nodes this node interacts with. Our results show that the relevance of the recolonization from highly connected patches is both induced by the topology of the network and the extinction-to-colonization ratio of the metapopulation (these examples are for high *e*/*c* displaying a higher heterogeneity in incidence as seen in Fig. 4).

4. Discussion

Let us emphasize our conclusions by the following remarks: (1) Network structure highly affects metapopulation persistence and abundance, with heterogeneous networks persisting for a wider range of parameter values. (2) Below an extinction-to-colonization ratio, homogeneous networks show the largest metapopulation abundance, while heterogeneous networks are the most abundant for higher relative extinction rates.

Persistence comes at a price. Poorly connected nodes become more easily unoccupied, and heterogeneous networks have many of these nodes. This explains our finding that for low *e*/*c* ratios, the more heterogeneous the network is, the lower its regional abundance. Thus, the network type maximizing relative abundance depends on the extinction-to-colonization ratio. If we were asked to engineer a landscape to improve a species relative abundance, the better habitat structure would depend on the species' life history. We have shown two domains in the extinction-to-colonization ratio where the ranking of network types is just reversed. Species with a relatively low extinction probability would do better in homogeneous spatial networks, while species with relatively high extinction probabilities would do better in highly heterogeneous networks.

Fig. 3. Long-term metapopulation abundance as a function of the relative extinction-to-colonization ratio for each network type illustrated in Fig. 1. We are plotting the average proportion of occupied nodes in the metapopulation, after ten thousand time steps. The average is calculated across 10 replicates, each with a different realization of the network with the same number of nodes, links, and degree distribution. Solid line represents the average of replicates, and shaded area replicates standard-deviation.

Fig. 4. Patch incidence for each network type and four values of the extinction-to-colonization ratio. Incidence is calculated as the proportion of time steps that a node is occupied along the dynamics. Node size is proportional to its degree, and colour represents patch incidence. As noted, heterogeneous networks show the largest differences on incidence across patches.
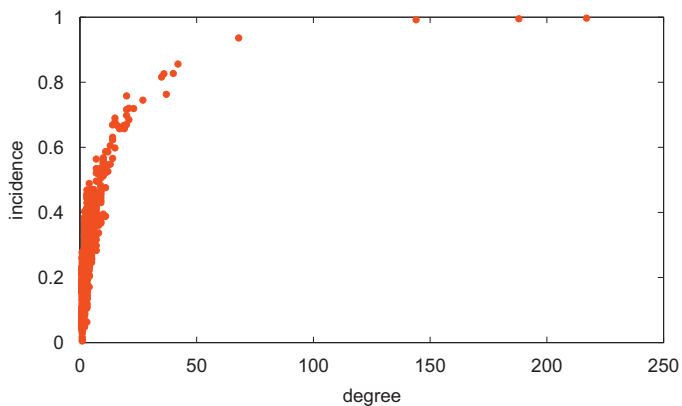
Fig. 5. Relationship between patch incidence and its degree for the scale-free network of Fig. 4. Every red dot in this figure indicates a patch of that network with a certain degree and a certain incidence. As noted, this is a highly non-linear relationship. $e/c = 3$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
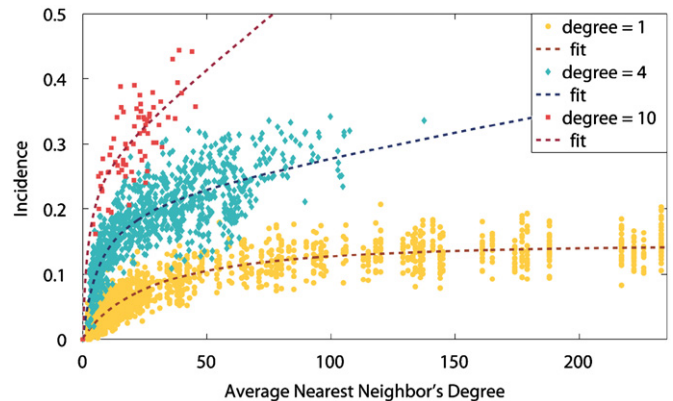
Fig. 6. A node's incidence is plotted as a function of its average nearest neighbour's degree, for nodes with three different number of links. Topologically, the nearest neighbours of a focal node are those nodes directly linked to the latter. Lines represent the local regression to improve graphic readability. Displayed results are obtained from the average dynamics of 10 different scale-free networks with an $e/c = 4$.

Through this paper, we have treated spatial structure and demographic properties as independent from each other. In real scenarios, however, they may be interrelated. For example, a wind-pollinated plant may perceive its landscape in quite a different way than an animal-pollinated plant. Actually, it has been shown that animal-dispersed trees are less vulnerable to habitat fragmentation than wind-dispersed species (Montoya et al., 2008). One potential explanation is that while wind disperses seeds homogeneously or randomly trough the landscape, birds exert a strong habitat selection. As a consequence, trees with wind-dispersed seeds perceive the landscape as a homogeneous network, whereas trees with bird-dispersed seeds move through a heterogeneous network.

To advance further in our understanding of metapopulation persistence from a spatial network perspective, future studies should disentangle the effects of the species life-history traits and those of network structure. This will allow us to better quantify to what degree topological information by itself is enough to predict the fate of metapopulations in real landscapes. This will benefit not only from simulations, but also from mesocosm experiments.

Our work helps filling the gap between network structure and spatial ecological dynamics. The architecture of spatial networks largely affects its dynamics through recolonization processes, although this dependence is modulated by life-history attributes of the species. Specifically, homogeneous landscapes should maximize metapopulation abundance for species with small extinction-to-colonization ratios, while metapopulation abundance should be largest for highly heterogeneous landscapes when extinction-to-colonization ratios are higher.

Acknowledgements

Appendix A

Hanski and Ovaskainen (2000) derived an analytical approximation for the expected fraction of patches P occupied at equilibrium

$$P = 1 - e/(c\lambda_A). \tag{2}$$

In this equation, λ_A is the leading eigenvalue of the spatial network adjacency matrix.

When applied to the spatial networks used in this manuscript, Hanski and Ovaskainen's (2000) equation produces the results displayed in Fig. A1.

Comparing this result with those displayed in Fig. 3 of the main text clearly shows a similar overall result: higher metapopulation persistences are obtained for heterogeneous networks (extinction threshold takes place at higher extinction-to-colonization ratios). At a smaller scale, however, the analytical approach by Hanski and Ovaskainen (2000) does not show the shift in the ranking in metapopulation abundances at a given extinction-to-colonization ratio. A possible explanation for such a difference is that the above analytical approach was thought for a landscape where individuals can move from every patch to every other patch with a probability that inversely depends on distance. That landscape produces an adjacency matrix with no zeros and the
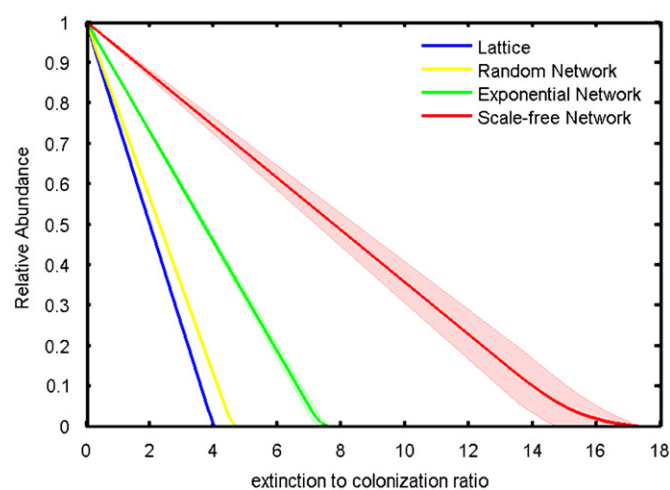

Fig. A1. Metapopulation relative abundance as a function of the extinction-to-colonization ratio using Hanski and Ovaskainen (2000) methodology. Shaded area represents the standard deviation of the replicates.

elements of the matrix are values between 0 and 1. The approach introduced in this paper, on the other hand, treats space as a binary network, and the adjacency matrix is a binary spare matrix. The leading eigenvalues of both approaches are therefore, very different.

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