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Zhang, Helin and Bearup, Daniel and Nijs, Ivan and Wang, Shaopeng and Barabás, György and Tao, Yi and Liao, Jinbao (2020) Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities. *Ecology Letters*. ISSN 1461-023X. (In press)

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ECOLOGY LETTERS

Dispersal network heterogeneity promotes species coexistence in hierarchical competitive communities

Journal:	<i>Ecology Letters</i>
Manuscript ID	ELE-00831-2020.R1
Manuscript Type:	Letters
Date Submitted by the Author:	11-Sep-2020
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4 **1 Dispersal network heterogeneity promotes species coexistence in**
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6 **2 hierarchical competitive communities**
7
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9
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26 **Short running title:** Dispersal heterogeneity promotes coexistence

27 **Article type:** Letters

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

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

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

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

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

37 **Data availability:** This theoretical study has no data.

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4 **38 Abstract**
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7 39 Understanding the mechanisms of biodiversity maintenance is a fundamental issue in
8
9
10 40 ecology. The possibility that species disperse within the landscape along differing
11
12 41 paths presents a relatively unexplored mechanism by which diversity could emerge.
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14
15 42 By embedding a classical metapopulation model within a network framework, we
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17
18 43 explore how access to different dispersal networks can promote species coexistence.
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20 44 While it is clear that species with the same demography cannot coexist stably on
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22 45 shared dispersal networks, we find that coexistence is possible on unshared networks,
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24 46 as species can surprisingly form self-organized clusters of occupied patches with the
25
26 47 most connected patches at the core. Furthermore, a unimodal biodiversity response to
27
28 48 an increase of species colonization rates or average patch connectivity emerges in
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30 49 unshared networks. Increasing network size also increases species richness
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32 50 monotonically, producing characteristic species-area curves. This suggests that, in
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34 51 contrast to previous predictions, many more species can co-occur than the number of
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36 52 limiting resources.
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53 **Introduction**

54 Global biodiversity is in ongoing decline due to anthropogenic pressures.
55 Consequently, developing a better understanding of the mechanisms which create and
56 maintain diversity in ecological communities is essential. Several mechanisms have
57 been proposed (e.g. niche and neutral theories), and significant advances have been
58 made in understanding species coexistence and consequently biodiversity
59 maintenance (Chesson 2000; Hubbell 2001; Levine & HilleRisLambers 2009; Chu &
60 Adler 2015). Among them, the competition-colonization trade-off has been a classic
61 paradigm to explain biodiversity in natural ecosystems (Tilman 1994; Amarasekare
62 2000; Yu & Wilson 2001; Yu *et al.* 2004). However, in the absence of such a tradeoff
63 between competitive ability and demographic traits, explaining stable coexistence in
64 competitive communities remains a challenge for theoretical ecologists. Recently,
65 non-hierarchical competition (i.e. competitive intransitivity) among species has been
66 proposed as a potential endogenous mechanism for multispecies coexistence (Laird &
67 Schamp 2006; Allesina & Levine 2011; Soliveres *et al.* 2015; Levine *et al.* 2017).
68 However, a key question remains unsolved in hierarchical (transitive) competitive
69 systems proposed by Tilman (1994): whether there exists any other factor fostering
70 species coexistence in such system without involving the colonization-competition
71 trade-off.

72 One such factor could be the effect of landscape heterogeneity on dispersal range
73 (Hanski & Ovaskainen 2000). There is abundant evidence in nature that landscape
74 structure, and other factors, can result in anisotropic (i.e. directionally biased)

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4 75 dispersal behavior (Urban & Keitt 2001; Fortuna *et al.* 2006; Grilli *et al.* 2015). For
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6 76 example, Montoya *et al.* (2008) observed that seed dispersal by birds, as opposed to
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8
9 77 by winds, is better described by an irregular network than a spatially uniform network.
10
11 78 Fortuna *et al.* (2006) identified a large spatial network of temporary ponds, with a
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14 79 power-law degree distribution, which are used as breeding sites by amphibian species.
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17 80 Furthermore, species dispersal between sub-reefs within the Great Barrier Reef has
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19 81 been described with scale-free small-world networks (Kininmonth *et al.* 2010).
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22 82 However, with a few exceptions (e.g. Chesson 2000; Snyder & Chesson 2003), the
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25 83 majority of existing models assume that dispersal is isotropic within a two
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28 84 dimensional landscape.

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30 85 As such, there has been an increasing interest in characterizing the effects of
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33 86 varying patch connectivities on the persistence and dynamics of species using
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36 87 network theory (Bode *et al.* 2008; Holland & Hastings 2008; Dale & Fortin 2010;
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39 88 Gilarranz & Bascompte 2012; Grilli *et al.* 2015; Gilarranz *et al.* 2017). In these
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41
42 89 representations, each network is described as a graph consisting of a set of nodes and
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44
45 90 links corresponding to habitat patches (or colony sites) and dispersal pathways
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47
48 91 respectively (Fortuna *et al.* 2006, 2009). These studies found that variation in the
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51 92 number of links between patches (i.e. network heterogeneity) greatly promotes
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54 93 species persistence by increasing local recolonization opportunities, demonstrating the
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57 94 importance of dispersal network structure for ecological dynamics (e.g. Holland &
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60 95 Hastings 2008; Gilarranz & Bascompte 2012).

60 96 Despite these advances, species-specific dispersal network connectivities have

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4 97 not been well integrated into our general understanding of how coexistence emerges
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6 98 among species. While a few models have considered the effect of variation in patch
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9 99 connectivities, they assumed that all species use the same dispersal pathways (i.e.
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12 100 shared networks; e.g. Holland & Hastings 2008). This assumption neglects the fact
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14 101 that different species may perceive the landscape differently (e.g. landscape
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17 102 perception; Hansbauer *et al.* 2010; Dondina *et al.* 2018) and therefore have distinct
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19
20 103 dispersal pathways, creating diverse patterns of patch connectivity (Yeaton & Bond
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22 104 1991; Bunn *et al.* 2000; Nicholson & Possingham 2006; Fortuna *et al.* 2009; Bearup
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25 105 *et al.* 2013; Hirt *et al.* 2018; Germain *et al.* 2019). For example, plant species with
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27 106 wind-dispersed seeds could be described using a homogeneous dispersal network,
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30 107 while those with bird-dispersed seeds could be described with a heterogeneous one
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33 108 due to bird habitat preferences (Montoya *et al.* 2008). Furthermore, Fortuna *et al.*
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35 109 (2009) found that the importance of individual patches within a dispersal network can
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38 110 vary significantly between species. Thus, there is an urgent need for spatial
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41 111 coexistence theory to incorporate species-specific dispersal networks that are
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43 112 widespread in nature (Amarasekare 2008).

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46 113 In this study, we embed a classical model for metapopulation dynamics (Levins
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49 114 1969) in a spatially heterogeneous landscape represented by a dispersal network
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51 115 (*Appendix Fig. S1*). We then use this model to investigate how the coexistence of
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54 116 competing species is affected by shared *vs.* unshared networks of varying
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57 117 heterogeneity. In particular, we systematically explore: (i) whether and how
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59 118 competitors can co-occur in shared *vs.* unshared networks when they have the same
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4 119 demographic traits; and (ii) which properties of dispersal network structure can best
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6 120 maintain species diversity.
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10 121 **Methods**

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13 122 *Dispersal networks with heterogeneity*

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16 123 In metapopulation models, the landscape is typically divided into patches (or colony
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18 124 sites) which can be inhabited by a sub-population of a species. In this model, we
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20 125 assume that individuals can move between patches only along a pre-defined set of
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22 126 dispersal pathways (*Appendix* Fig. S1). The result is a network model, with patches
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24 127 and dispersal pathways being represented by network nodes and links respectively.
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30 128 The primary advantage of this approach is that it allows us to make use of the
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32 129 extensive literature that has been developed to describe network structure. In
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34 130 particular, a key feature of network structure is its *degree distribution*. The *degree* of
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36 131 a node is the number of other nodes to which it is connected directly. The degree
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38 132 distribution describes the frequency with which nodes have a particular degree.
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43 133 Dispersal is isotropic or directionally unbiased, relative to the landscape, if the
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45 134 dispersal network is *homogeneous*, i.e. all nodes have the same degree. Anisotropic,
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47 135 directionally biased, dispersal can be represented by a *heterogeneous* network in
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49 136 which the degree of nodes varies. Similar to Gilarranz & Bascompte (2012) and Liao
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51 137 *et al.* (2020), we consider four typical dispersal network structures (illustrated in Fig.
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54 138 1a-d):
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59 139 (i) A homogeneous (or regular) network where all patches have the same degree. For
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4 140 example, Figure 1e shows a completely regular network in which each patch has four
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6 141 links to other patches ($k=4$). This is equivalent to a lattice-structured model with
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8
9 142 nearest neighbour dispersal under periodic boundary conditions (Bascompte & Sole
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11
12 143 1995; Hiebeler 2000).

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15 144 (ii) A randomly structured network with randomly connected patches (Watts &
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18 145 Strogatz 1998). In particular, node degrees are drawn from a Poisson distribution with
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20 146 the variance equal to the mean degree within the network (e.g. $\sigma^2 \approx \bar{k}=4$ in Fig. 1f).
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22
23 147 Thus, all patches have a similar number of connections though there is some variation
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26 148 (heterogeneity) (Erdős & Rényi 1959).

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29 149 (iii) An exponential network constructed based on the generic algorithm of random
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31 150 attachment (Barabási & Albert 1999), which produces an exponential degree
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34 151 distribution. Such networks have a higher variability in degree for a given mean
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36 152 degree than the random network (ii) (e.g. $\bar{k}=4$ and variance $\sigma^2 \approx 5.86$ in Fig. 1g)
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39 153 (Fortuna *et al.* 2006), producing a greater heterogeneity in patch connectivities.

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42 154 (iv) A scale-free network constructed according to the algorithm of Barabási & Albert
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45 155 (1999) with preferential attachment (i.e. increasing the probability that new patches
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48 156 connect to already well-connected patches), which yields a power-law degree
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50 157 distribution. This type of network has a very high variability in degree for a given
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53 158 mean degree (e.g. $\bar{k}=4$ and $\sigma^2 \approx 27.4$ in Fig. 1h). Thus, a few patches are highly
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56 159 connected while most have only few connections.

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59 160 In these networks, all patches are reachable by every species, that is, each patch
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4 161 has at least one link to another patch. Species are assumed to use dispersal links in
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6 162 either direction without preference, i.e. when patches i_1 and i_2 are linked, dispersal can
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9 163 occur from either i_1 to i_2 or vice versa.
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11 12 164 *Competitive dynamics* 13

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15 165 Metapopulation models are typically based on the concept of patch occupancy, i.e.
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17 166 whether a species is present or absent on a patch. Patches are assumed to be of the
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20 167 minimum size required to sustain a viable population of the species studied. In this
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22 168 model, we additionally assume that each patch (or colony site) can either be vacant or
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24 169 host a single species (cf. Tilman 1994), producing competition for available colony
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26 170 sites. Monoculture patches of this sort have been observed in garden plot ecosystems
27
28 171 (Tilman & Wedin 1991; Wedin & Tilman 1993) and insect communities (Hanski
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30 172 1990; Shorrocks 1991). Due to the priority effect, displacing an established
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32 173 population/adult is typically more difficult than colonizing an empty patch (Comins &
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34 174 Noble 1985; Calcagno *et al.* 2006; Fukami 2015). Additionally, ignoring this effect,
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36 175 by permitting a strong competitor to displace weaker species, always leads to
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38 176 monoculture (i.e. only the best competitor survives) when all species have the same
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40 177 demographic traits (*Appendix* Fig. S2). Consequently, we focus on preemptive
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42 178 competition, i.e. species compete only for empty patches, and assume that strong
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44 179 competitors have priority. Thus, a species can colonize an empty patch only if no
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46 180 superior competitor simultaneously colonizes that patch.
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58 181 We consider a system of n species with a strict competitive hierarchy, i.e. species
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4 182 are ranked from the best competitor (species 1) to the poorest (species n). In order to
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6 183 focus on the effect of network structure, we assume that all species have the same
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8 184 demographic traits (colonization and extinction probabilities, c and e respectively).
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10 185 This explicitly precludes the existence of any colonization-competition tradeoff
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12 186 (Tilman 1994).

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17 187 The result is a stochastic model in which the probability that a given empty patch
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19 188 i is colonized by the S -th competitor ($1 \leq S \leq n$) is

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23 189
$$P_i(S) = (1 - c)^{\sum_{j=1}^{S-1} x_j} \cdot [1 - (1 - c)^{x_S}]. \quad (1)$$

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25
26 190 Here x_j (≥ 0) denotes the number of j -patches (occupied by species j) directly linked
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28 191 to the empty patch i , and $(1 - c)^{\sum_{j=1}^{S-1} x_j}$ denotes the probability that the superior
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30 192 competitors (species 1, 2, 3... $S-1$) do not establish a population on this patch. Note
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32 193 that an empty patch can only be colonized from a patch that is directly connected to it.

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37 194 ***Spatially explicit simulations***

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40 195 Initially each patch is occupied by a species randomly sampled from the species pool.
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42 196 When dispersal networks are not shared, we generate a dispersal network for each
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44 197 species with given network properties (e.g. variation in patch degrees). For each time
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46 198 step, we first check whether the population in each occupied patch becomes extinct
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48 199 (with probability e). We then determine whether any empty patches become occupied
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50 200 by the species directly connected to it (see Eq. 1). Finally, we record the patch
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52 201 occupancy for each species at each time step, calculated as its number of occupied
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54 202 patches divided by the network size (i.e. the total number of patches).
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4 203 To reduce the effects of stochasticity (*Appendix* Figs S3-S4), we model patch
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6 204 occupancy dynamics (via Matlab R2018b) using large networks consisting of 1024
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9 205 patches and 2048 undirected links (cf. Gilarranz & Bascompte 2012). As such, all
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11 206 types of network have the same number of patches and links with the same average
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14 207 degree $\bar{k}=4$, allowing us to compare species coexistence in dispersal networks with
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17 208 contrasting levels of heterogeneity. It was observed from simulations that these
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19 209 systems approached steady state after 5000 time steps. We estimated these steady
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21 210 states by simulating a system for 10,000 time steps and then averaging its occupancies
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23 211 over the last 1000 steps. To eliminate effects of specific dispersal network structures,
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25 212 100 replicates were simulated for each case. Each replicate used different, randomly
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27 213 generated, dispersal networks but with the same properties (i.e. the same network size,
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29 214 total links, and degree distribution). The mean steady-state patch occupancy (mean \pm
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31 215 standard deviation SD) was then calculated from these replicates. A broad range of
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33 216 biologically reasonable parameter combinations were explored and found to yield
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35 217 qualitatively similar outcomes (*Appendix* Figs S1-S27), thus allowing us to present
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37 218 our general results in Figs 1-5 by choosing one of those parameter combinations as a
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39 219 reference.

220 **Results**

221 *Two-species system*

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

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4 224 locally. Thus the probability of the superior species A successfully colonizing the
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6 225 empty patch is

$$7 \quad 226 \quad P_i(A) = 1 - (1 - c)^{x_A}, \quad (2)$$

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13 227 with $0 < c < 1$. The inferior species B can colonize the patch only if species A does not.

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16 228 Hence the probability of this event is

$$17 \quad 229 \quad P_i(B) = (1 - c)^{x_A} [1 - (1 - c)^{x_B}]. \quad (3)$$

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22 230 Note that x_A and x_B denote the number of species A and B directly linked to the
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25 231 patch i . We can now determine whether it is possible for the inferior species B to have
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28 232 a greater probability to occupy the focal empty patch i than the superior species A . By
29
30 233 setting $P_i(B) > P_i(A)$, we have

$$31 \quad 234 \quad (1 - c)^{x_A} [1 - (1 - c)^{x_B}] > 1 - (1 - c)^{x_A}. \quad (4)$$

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36 235 As such, the conditions for $P_i(B) > P_i(A)$ can be derived as

$$37 \quad 236 \quad \begin{cases} x_B > \ln[2 - (1 - c)^{-x_A}] / \ln(1 - c) \\ x_A < -\ln 2 / \ln(1 - c) \end{cases}, \quad (5)$$

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44 237 otherwise $P_i(B) < P_i(A)$ (see phase diagram in *Appendix Fig. S5*). Thus, when the
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47 238 inferior species occupies more patches in a given area than the superior species, it is
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50 239 able to overcome its competitive inferiority locally. This indirectly demonstrates that
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52 240 species might coexist regionally if they do not share the same dispersal networks.

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55 241 We then simulate the coexistence of two competitors with the same demography
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58 242 (i.e. identical colonization and extinction rate) on shared vs. unshared dispersal
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4 243 networks with contrasting heterogeneities, including (from most homogeneous to
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6 244 most heterogeneous) regular, random, exponential and scale-free networks (Fig. 1).
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9 245 For shared networks, we find that the two species cannot coexist regardless of the
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11 246 level of heterogeneity in the dispersal network, as the superior species eventually
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14 247 excludes the inferior species (Fig. 1I-IV). However, for unshared dispersal networks
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17 248 (with the same heterogeneity), stable coexistence becomes possible (Fig. 1VI-VIII;
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19 249 see coexistence pattern in *Appendix* Fig. S6), with the exception of regular networks
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22 250 (Fig. 1V). Interestingly, increasing the degree of dispersal network heterogeneity
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25 251 causes the long-term species occupancies to converge (Fig. 1VI-VIII), i.e. the
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28 252 competitive advantage of the superior species is reduced.

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30 253 The coexistence patterns described above can, however, be altered by varying the
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33 254 species' relative extinction and colonization rates (Fig. 2; *Appendix* Figs S7-S15) or
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36 255 the average patch degree (*Appendix* Fig. S16). Again, no coexistence is possible when
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39 256 the species share the same dispersal network (*Appendix* Fig. S17I-IV), as the superior
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41 257 competitor excludes the inferior species. However, when dispersal networks are
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44 258 unshared, a coexistence (grey) region exists (Fig. 2II-IV & VI-VIII), except in regular
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47 259 networks (Fig. 2I & V). As expected, the global occupancy of both species declines as
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49 260 the relative extinction rate (e/c) increases (Fig. 2I-IV). This typically results in the
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52 261 weaker competitor becoming extinct first (Fig. 2I-IV; *Appendix* Fig. S17). However,
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55 262 species coexistence is maintained at much higher e/c -ratios if dispersal networks are
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57 263 unshared and the network heterogeneity is high.

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60 264 By contrast, increasing the relative colonization rate (c/e) produces a quite different

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4 265 pattern (Fig. 2V-VIII). The abundance of the superior species increases monotonically
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6 266 with increasing relative colonization rate regardless of other factors, but tends to
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9 267 saturate at high c/e -ratios. On shared networks, the inferior species is simply excluded
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11 268 (*Appendix Fig. S17V-VIII*). However, on unshared heterogeneous networks, there is
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14 269 an intermediate range (grey) in which the species coexist, which expands as the
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17 270 networks become more heterogeneous (Fig. 2V-VIII). In particular, the patch
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19 271 occupancy of the inferior species initially increases with the relative colonization rate
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22 272 before declining to extinction at high c/e -ratios. Intermediate levels of c/e thus
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25 273 maximize the inferior species' occupancy and consequently promote species
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27 274 coexistence, as opposed to lower or higher colonization rate which would speed up
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30 275 species exclusion (a unimodal response). This outcome is similar to the case where
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33 276 the average patch degree is increased (*Appendix Fig. S16*) and follows directly from
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36 277 the observation that increasing c reduces the area of parameter space in which the
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38 278 inferior species can locally outcompete the superior species (*Appendix Fig. S5*).

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41 279 Finally, for this two-species system, we explore how coexistence is affected when
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44 280 the species utilize differing dispersal modes, corresponding to the dispersal networks
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47 281 with different heterogeneities (Fig. 3). When the inferior species has a longer
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49 282 dispersal range (i.e. it disperses on a non-local network, including random,
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52 283 exponential and scale-free networks), it can exclude a locally dispersing superior
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54 284 species (Fig. 3I-III). By contrast, when the inferior competitor uses local dispersal (i.e.
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57 285 a regular dispersal network), it is always outcompeted by the superior competitor (Fig.
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59 286 3IV-VI). Thus, non-local dispersal modes can compensate for competitive

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4 287 disadvantage and overturn the competitive outcome. In other cases, where both
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6 288 competitors use non-local dispersal modes, we observe that the species can coexist
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9 289 stably (Fig. 3VII-XII) and that species abundances are very similar when the inferior
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12 290 competitor disperses on the network with highest heterogeneity (Fig. 3X & XI).

15 291 *Multispecies system*

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18 292 We now extend this investigation to a multi-species system (Fig. 4; *Appendix* Figs
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21 293 S18-S20) showing that the behaviours described above transfer well to this more
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23
24 294 complex case. Again, increasing the relative extinction rate (e/c) reduces species
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26 295 richness on both shared and unshared dispersal networks. Furthermore, on shared
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29 296 networks, only the best competitor survives (*Appendix* Fig. S18a), while on unshared
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32 297 networks, coexisting sub-communities are possible (Fig. 4a). Greater degrees of
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34 298 dispersal network heterogeneity promote species diversity. Similarly when the relative
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36 299 colonization rate (c/e) is varied, we find that, only the best competitor can survive on
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39 300 shared networks (*Appendix* Fig. S18b). Moreover, on unshared networks, the greatest
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42 301 community diversity is attained at intermediate levels of c/e (a unimodal response,
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44 302 similar to the effect on patch degree; see *Appendix* Fig. S21). Again, increasing
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47 303 dispersal network heterogeneity increases community diversity.

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50 304 Finally, we examine the effect of network size on biodiversity (i.e. the species-area
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53 305 curve) in shared (*Appendix* Fig. S22) and unshared dispersal networks (Fig. 5). In
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56 306 shared networks, only the best competitor survives regardless of network size and
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59 307 heterogeneity (*Appendix* Fig. S22). By contrast, increasing the network size in
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4 308 unshared networks leads to a monotonic increase in species richness, with greater
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6 309 species richness on more heterogeneous dispersal networks (Fig. 5a). Additionally,
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9 310 we observe that patches which are highly connected within the dispersal network of a
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11 311 particular species are normally occupied by that species (Fig. 5b-d; *Appendix Fig.*
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14 312 S23).

17 313 **Discussion**

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21 314 The key innovation of our model is to place metapopulation dynamics on an irregular
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23 315 dispersal network. Existing theoretical studies of the mechanisms controlling
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26 316 community diversity are based on models which assume regular connections between
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28 317 landscape patches. However, in natural systems such connections can be far from
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31 318 regular (Hanski & Ovaskainen 2000; Fortuna *et al.* 2006; McIntire *et al.* 2007). Our
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34 319 study demonstrates that such heterogeneity can allow species with differing dispersal
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36 320 connections (i.e. species-specific dispersal networks) to coexist, thereby promoting
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38 321 community diversity. Thus, previous patch-dynamic models focusing only on shared
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41 322 regular networks, might have largely underestimated species diversity, as species in
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44 323 natural communities often exhibit diverse dispersal patterns with more or less
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47 324 heterogeneity.

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49 325 When dispersal networks are shared, all species have the same ability to access any
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52 326 given colony site. Consequently, the outcome of competition events is not influenced
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55 327 by this spatial structure. By contrast, when each species disperses differently (i.e. on a
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57 328 different dispersal network), any given species will have greater access to some areas
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60 329 of the landscape than others. This creates refuges for inferior competitors within the

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4 330 landscape, i.e. areas which the superior competitors have limited access to, allowing
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7 331 the inferior competitor to outcompete them locally.
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9 332 This explanation is confirmed by comparing the spatial distribution of each species
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12 333 to its dispersal network (*Appendix* Figs S6 & S23), where we observe that species
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15 334 form self-organized clusters of occupied patches with the most connected patches at
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18 335 the core. This mechanism can be explored further by relating the incidence of a
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21 336 species upon a patch (i.e. the proportion of time steps that a patch is occupied by that
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24 337 species) to the degree of that patch and the mean degree of patches it is connected to
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27 338 (*Appendix* Figs S24-S27). Species incidence on a patch increases with the patch
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30 339 degree (*Appendix* Figs S24-S25) and with the mean degree of the connected patches
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33 340 (*Appendix* Figs S26-S27). This can be explained by the observation that a patch is
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36 341 more likely to be recolonized by a species, if it is adjacent to a large number of sites
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39 342 occupied by that species (Eq. 1). In turn, if a patch is likely to be occupied by a
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42 343 specific species, it is more likely that the patches connected to it will be colonized by
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45 344 that species. This creates a positive feedback between highly connected patches and
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48 345 those that connect to them. The result is a segregation-aggregation process (*sensu*
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51 346 Pacala 1997; Murrell *et al.* 2001; Holyoak & Loreau 2006), which permits species to
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54 347 coexist on the landscape scale; although single species dominate in any given region.
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57 348 Thus, our study shows that unshared dispersal networks offer a mechanism for the
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60 349 emergence of landscape scale community diversity (γ -diversity).

350 It is well known that a dispersal range advantage can compensate for a
351 disadvantage in direct competition or permit coexistence of competitors (e.g. Liao *et*

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4 352 *al.* 2013a). We observe exactly the same trends when competing species disperse on
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6 353 networks with differing levels of heterogeneity (Fig. 3). This can be explained by the
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9 354 observation that a higher level of heterogeneity within a dispersal network permits
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11 355 longer-range dispersal. In particular, if we regard the regular network as representing
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14 356 the physical arrangement of the habitat (i.e. a regular lattice), it describes short range
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17 357 dispersal (dispersal only between “nearest neighbours”). However, when the degree
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19 358 distribution is heterogeneous, some patches have more connections than the mean. In
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22 359 the context of the physical arrangement described above, this means they must
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25 360 connect to more than only their “nearest neighbours” (in that lattice), allowing longer
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28 361 range dispersal. As the level of heterogeneity increases, the number of connections
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30 362 possessed by highly connected patches increases, allowing a species occupying such a
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33 363 site to access a greater proportion of the total sites. This corresponds to increasing
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36 364 dispersal range. Interestingly, these patterns have been observed empirically by
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38 365 Yeaton & Bond (1991), where two competing shrub species with dispersal differences
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40 366 (one with ant-dispersed seeds and another with wind-dispersed seeds) can co-occur
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43 367 stably.

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45 368 In order for these mechanisms to operate, colonization success rates cannot be too
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48 369 high. In particular, we find a unimodal biodiversity response to colonization success
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51 370 rate (Figs 2 & 4). This follows from the observation that, if the colonization success
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54 371 rate is high, the best competitors will almost always successfully colonize any
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57 372 unoccupied patch which they can access. Consequently, even large aggregations of an
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59 373 inferior competitor are not able to resist invasion. For similar reasons, we also find a
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4 374 unimodal biodiversity response to average patch degree (*Appendix* Figs S16 & S21).

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6 375 The aggregation-segregation mechanism relies on inferior competitors forming
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9 376 relatively isolated clusters (*Appendix* Figs S6 & S23). As landscape connectivity
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11 377 increases, all patches become more accessible and such isolated clusters become
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14 378 harder to form.

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17 379 A final observation is that increasing network size monotonically increases species
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19 380 richness in unshared networks and that the strength of this response increases with
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21 381 dispersal network heterogeneity (Fig. 5). Essentially, as network (or landscape) size
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23 382 increases, the chance that each species can achieve local competitive dominance
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25 383 within a specific region of the landscape increases. The resulting monotonically
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27 384 increasing species-area curves refute the previous view that the number of species
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29 385 coexisting cannot exceed the number of limiting resources (Levin 1970; Tilman 1982).
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31 386 Instead, we theoretically demonstrate that, when there are species-specific differences
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33 387 in dispersal networks, many more species than the number of limiting resources
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35 388 should be able to coexist, as empirically observed in several natural systems (Tilman
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37 389 1982; Kotler & Brown 1988; Wellborn *et al.* 1996). Previously, coexistence of an
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39 390 unlimited number of species in a spatial context was ascribed to the
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41 391 colonization-competition tradeoff (Tilman 1994) rather than to differences in the
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43 392 dispersal opportunities available to individual species (Adler & Mosquera 2000). Our
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45 393 model provides an alternative explanation; i.e. if the landscape is large enough,
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47 394 unshared heterogeneous dispersal networks can support the coexistence of many more
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49 395 species than expected, due to a segregation-aggregation mechanism.
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4 396 By demonstrating that the structure of dispersal networks strongly governs species
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6 397 coexistence, mediated by species life-history attributes, our work helps fill the gap
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9 398 between landscape structure and spatial competition. We find that incorporating
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11 399 species-specific dispersal networks into the traditional hierarchical competitive
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14 400 systems can greatly promote regional coexistence owing to the formation of
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17 401 self-organized clusters. This implies that traditional shared lattice- or
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20 402 randomly-structured models might have severely underestimated biodiversity
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22 403 maintenance. More importantly, the model suggests significant implications for
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25 404 biodiversity conservation and management. For instance, as different species often
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27 405 display diverse patterns of patch connectivity based on their dispersal traits (e.g.
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30 406 wind-dispersed vs. bird-dispersed seeds; walking vs. flying species), it is essential to
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32 407 characterize the dispersal networks of species of interest. We could then overlay or
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35 408 intersect these networks to find hub locations, so as to design multispecies
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38 409 conservation plans (e.g. Bunn *et al.* 2000; Urban & Keitt 2001; Nicholson &
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40 410 Possingham 2006; Bearup *et al.* 2013).

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43 411 Furthermore, the unimodal diversity response to an increase of species colonization
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45 412 rate or average patch degree observed in our model (Figs 2 & 4; *Appendix* Figs S16 &
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47 413 S21), indirectly supports the intermediate heterogeneity hypothesis (cf. Duelli 1997;
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49 414 Tschardtke *et al.* 2005; Sirami *et al.* 2019). In particular, we find that intermediate
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52 415 levels of patch connectivity (inversely related to habitat fragmentation) maximize
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55 416 species coexistence as predicted. This contradicts existing strategy for biodiversity
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58 417 conservation, which calls for increasing habitat connectivity (e.g. constructing
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4 418 ecological corridors) as much as possible (reviews in Fahrig 2002, 2003; Ewers &
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6 419 Didham 2006; Fischer & Lindenmayer 2007). Such interventions might lead to more
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9 420 species losses because of increasing competitive exclusion. Thus, we suggest that
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11 421 several small reserves would conserve more species than a single large reserve (see
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13 422 SLOSS debate in Ovaskainen 2002), if the patch size meets the minimum area
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16 423 required for a viable population. This conclusion has been supported by empirical
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19 424 studies (Fahrig 2003, 2017), which found that habitat fragmentation generally
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22 425 enhanced species diversity though the effects were small. However, we make the
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25 426 additional point that local aggregation of weaker competitors can prevent invasions.
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27 427 This suggests a complementary strategy for species conservation, i.e. establishing
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30 428 enclaves of species endangered by non-native invaders and limiting access to them.
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33 429 Similar concepts have, in fact, been applied to the problem of red squirrel
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35 430 conservation in the UK (Parrott *et al.* 2009).

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38 431 Two caveats should be addressed when applying our model to terrestrial
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41 432 ecosystems. Firstly, although there have been a large number of studies on scale-free
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43 433 graphs (Barabási & Albert 1999), actual patch mosaics seem to not quite fit the
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46 434 definitions of such well-studied networks so that they tend to not include the
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49 435 extremely connected patches that characterize scale-free networks (Urban *et al.* 2009).
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51 436 Secondly, it may be inappropriate to apply a graph representation for some landscapes
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54 437 if habitat patches are poorly resolved spatially (Urban & Keitt 2001). For example,
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57 438 habitat quality varies continuously and subtly over the landscape, thus aggregating
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59 439 this variability into discrete patches may be inappropriate (e.g. Liao *et al.* 2013b).
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4 440 However, our modelling predictions could be further validated by both controlled
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6 441 micro- or mesocosms and field observations. For example, by manipulating habitat
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9 442 connectivity in protist/microarthropod experiments (e.g. Violle *et al.* 2010; Staddon *et*
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11 443 *al.* 2010; Chischolm *et al.* 2011; Carrara *et al.* 2012, 2014), it would be possible to
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14 444 test spatial coexistence of hierarchical competitors with different dispersal patterns.
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17 445 For mesocosms, it would be possible to perform long-term competition experiments
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20 446 for glass plants in gardens by controlling species dispersal between plots, e.g. via
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22 447 addition of propagules of plant species (Tilman & Wedin 1991; Wedin & Tilman
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25 448 1993). Furthermore, open field experiments, such as those performed by Ding *et al.*
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28 449 (2013) and Wang *et al.* (2015) on dispersal of forest birds in Thousand Island Lake,
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31 450 China, could be extended to explore the effect of variation in dispersal pathways on
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33 451 their coexistence. Overall, by integrating both network and metapopulation
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35 452 approaches, our modelling study provides a new way to understand the coexistence
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38 453 mechanism of spatial dispersal heterogeneity, thereby strengthening our
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41 454 comprehension of biodiversity maintenance in hierarchical competitive communities.
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4 456 **Acknowledgements**
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7 457 This study was supported by the National Science Foundation of China (No.
8
9 458 31760172 & 31901175) and the Key Joint Youth Project of Jiangxi Province (No.
10
11 459 20192ACBL21029). Comments from two reviewers greatly improved this
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15 460 manuscript.
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18 461 **Competing interests:** The author declares no competing interests.
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21 462 **Supplementary Information** is available for this paper.
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For Review Only

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4 **640 Figure legends**

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6 **641 Figure 1.** Patch dynamics of two competing species in shared (I-IV) vs. unshared
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9 **642 (V-VIII)** dispersal networks. Panels (a-d): Examples of networks for each level of
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11 **643** heterogeneity with 256 patches (red nodes) with 512 links (green lines). Variation in
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13 **644** patch degree (proportional to node size) increases from left to right. Panels (c-h):
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16 **645** Degree distributions for networks of each type with 1024 patches and 2048 links,
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19 **646** again with variation in degree increasing from left to right. Panels (I-IV): The species
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21 **647** share the same dispersal network. The superior competitor always excludes the
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23 **648** inferior competitor regardless of network heterogeneity. Panels (V-VIII): The species
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25 **649** disperse on separate dispersal networks with the same level of heterogeneity. They are
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27 **650** able to coexist except on regular networks. Parameter values are the same for both
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29 **651** species: colonization rate $c=0.05$ and extinction rate $e=0.05$.

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35 **652 Figure 2.** Effects of relative extinction (I-IV: e/c at fixed $c=0.05$) and colonization
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37 **653** rate (V-VIII: c/e at fixed $e=0.05$) on patch occupancy of both inferior and superior
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39 **654** competitors at steady state (mean \pm SD of 100 replicates) in unshared networks but
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41 **655** with the same levels of heterogeneity. The coexistence region (grey) expands as the
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43 **656** level of heterogeneity increases in the dispersal networks. Panels (I-IV): Both species
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45 **657** show a monotonic decline in patch occupancy as e/c increases, but with the inferior
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47 **658** species becoming extinct first. Panels (V-VIII): Increasing c/e leads to a monotonic
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49 **659** increase in patch occupancy of the superior competitor, while the occupancy of the
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51 **660** inferior species initially increases but later declines to zero.

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4 662 **Figure 3.** Patch dynamics of both inferior and superior competitors with different
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6 663 heterogeneous networks. Panels (I-III): The inferior competitor, which disperses on a
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8 664 network with higher heterogeneity, excludes the superior competitor which only has
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10 665 access to a regular dispersal network (i.e. local dispersal), in contrast to panels
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12 666 (IV-VI). Panels (VII-XII): both competitors can coexist when their dispersal networks
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14 667 have different levels of heterogeneity. Parameter values for both species are the same:
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19 668 $c=e=0.05$.

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23 669 **Figure 4.** Effects of relative extinction (a: e/c at fixed $c=0.05$) and colonization rate (b:
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25 670 c/e at fixed $e=0.05$) on the number of coexisting species at steady state (mean \pm SD of
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27 671 100 replicates) on unshared networks with the same levels of heterogeneity. As shown
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29 672 in graphs (a & b), species diversity decreases monotonically with increasing e/c , while
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31 673 intermediate levels of c/e maximize species richness except in regular networks.
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36 674 **Figure 5.** Panel (a): Species-area relationship between network size (i.e. total number
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38 675 of patches) and the number of coexisting species at steady state (mean \pm SD of 100
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40 676 replicates) on unshared networks with the same levels of heterogeneity, by fixing
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42 677 average patch degree at $\bar{k}=4$. As shown, increasing network size leads to a monotonic
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44 678 increase in species richness except in regular networks. Panels (b-d): Examples of
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47 679 species coexistence patterns at steady state on small heterogeneous networks with 256
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49 680 patches (black nodes – empty patches, and nodes in other colors – patches occupied
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51 681 by other species). Node size is proportional to its degree. Parameter values for all
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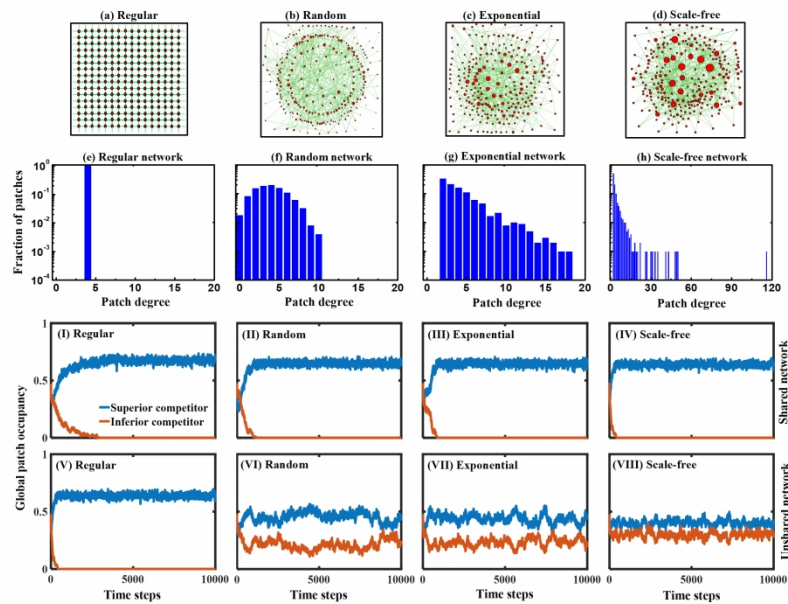


Figure 1. Patch dynamics of two competing species in shared (I-IV) vs. unshared (V-VIII) dispersal networks. Panels (a-d): Examples of networks for each level of heterogeneity with 256 patches (red nodes) with 512 links (green lines). Variation in patch degree (proportional to node size) increases from left to right. Panels (e-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 $e=0.05$.

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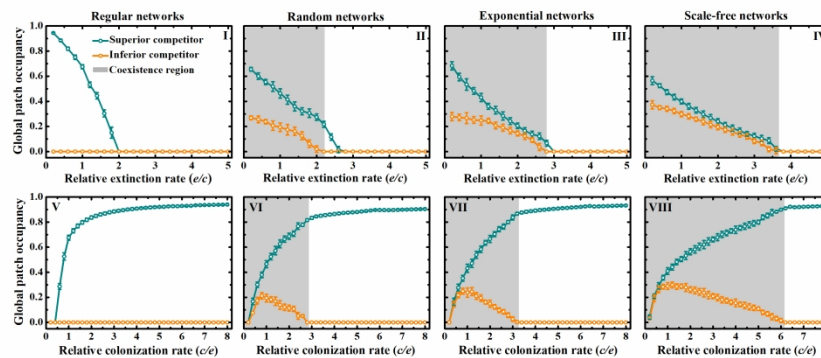


Figure 2. Effects of relative extinction (I-IV: e/c at fixed $c=0.05$) and colonization rate (V-VIII: c/e at fixed $e=0.05$) on patch occupancy of both inferior and superior competitors at steady state (mean \pm SD of 100 replicates) in unshared networks but with the same levels of heterogeneity. The 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.

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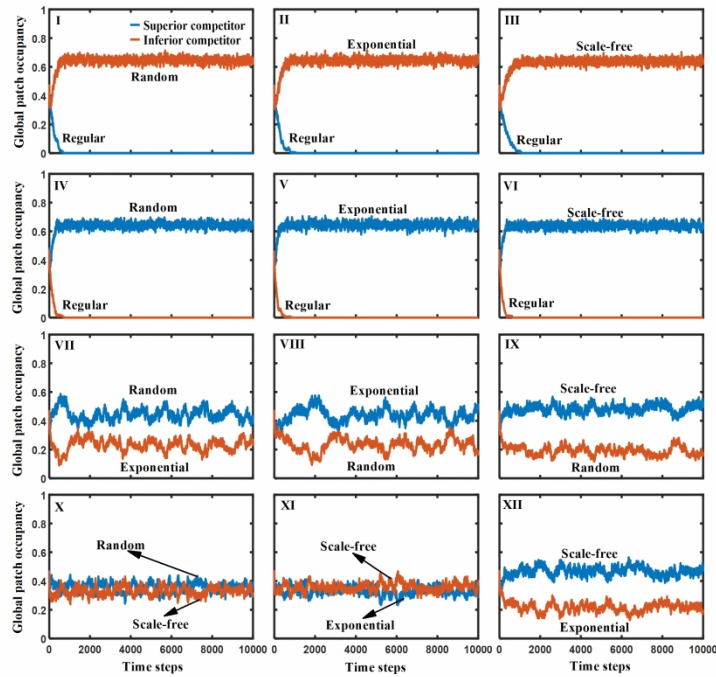


Figure 3. Patch dynamics of both inferior and superior competitors with different heterogeneous networks. Panels (I-III): The inferior competitor, which disperses on a network with higher heterogeneity, excludes the superior competitor which only has access to a regular dispersal network (i.e. local 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: $c=e=0.05$.

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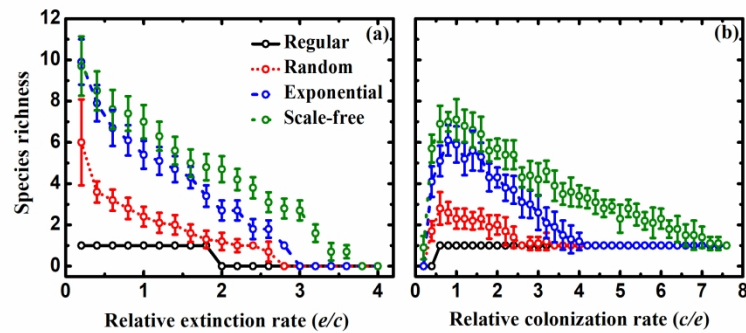


Figure 4. Effects of relative extinction (a: e/c at fixed $c=0.05$) and colonization rate (b: c/e at fixed $e=0.05$) on the number of coexisting species at steady state (mean \pm SD of 100 replicates) on unshared networks with the same levels of heterogeneity. As shown in graphs (a & b), species diversity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

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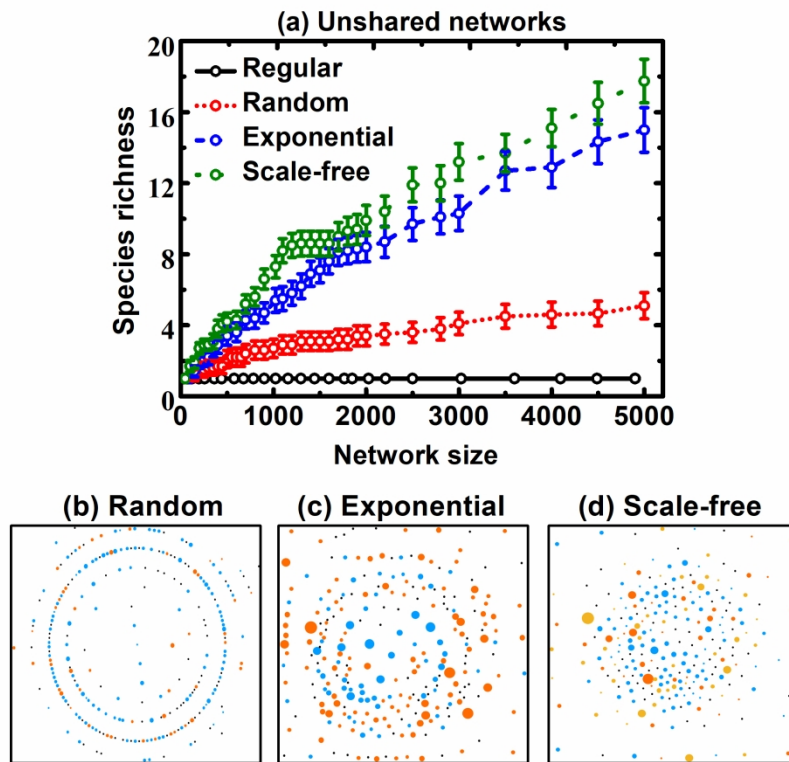


Figure 5. Panel (a): Species-area relationship between network size (i.e. total number of patches) and the number of coexisting species at steady state (mean \pm SD of 100 replicates) on unshared networks with the same levels of heterogeneity, by fixing average patch degree at $k = 4$. As shown, increasing 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: $c=e=0.05$.

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