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On the evolution of dispersal via heterogeneity in spatial connectivity

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Dispersal has long been recognized as a mechanism that shapes many observed ecological and evolutionary processes. Thus, understanding the factors that promote its evolution remains a major goal in evolutionary ecology. Landscape connectivity may mediate the trade-off between the forces in favour of dispersal propensity (e.g. kin-competition, local extinction probability) and those against it (e.g. energetic or survival costs of dispersal). It remains, however, an open question how differing degrees of landscape connectivity may select for different dispersal strategies. We implemented an individual-based model to study the evolution of dispersal on landscapes that differed in the variance of connectivity across patches ranging from networks with all patches equally connected to highly heterogeneous networks. The parthenogenetic individuals dispersed based on a flexible logistic function of local abundance. Our results suggest, all else being equal, that landscapes differing in their connectivity patterns will select for different dispersal strategies and that these strategies confer a long-term fitness advantage to individuals at the regional scale. The strength of the selection will, however, vary across network types, being stronger on heterogeneous landscapes compared with the ones where all patches have equal connectivity. Our findings highlight how landscape connectivity can determine the evolution of dispersal strategies, which in turn affects how we think about important ecological dynamics such as metapopulation persistence and range expansion.

1. Introduction

Dispersal is a key factor in both ecology and evolution [1]. From an ecological perspective, dispersal may affect population and community dynamics [2,3], rescue populations from extinction [4], shape species distributions [5] and allow species to track favourable environmental conditions and influence the rate at which species expand their ranges [6]. From an evolutionary perspective, dispersal can produce gene flow and depending on its magnitude, can preclude or promote local adaptation and speciation, increase or decrease local genetic diversity, mitigate the effects of drift in small populations and reduce mutation load [1,7,8]. As such, natural selection is expected to act on traits associated with dispersal [9–12].

Understanding what conditions promote dispersal evolution remains an active research topic in evolutionary ecology through theoretical models [13–15] and empirical studies [9,16,17]. On the one hand, these studies have shown that the evolution of high dispersal rates may be favoured by several mechanisms such as environmental fluctuations (e.g. to cope with temporal variability of resource availability [18–20]), local extinction probability [20] as well as individual and kin competition [9,17,21–23]. On the other hand, the fitness benefits

of dispersing can be reduced by the associated risks such as dispersal costs and mortality [24], thereby promoting the evolution of lower dispersal rates [15,25].

Despite this work, important gaps remain in our understanding of dispersal evolution in realistic landscapes. In natural landscapes, patch connectivity varies as a function of particular features such as topography, patch sizes, habitat types and distribution [26–28]. Such spatial heterogeneity implies that habitat patches across landscapes are seldom equally connected. Empirical evidence suggests that dispersal behaviour may undergo adaptive changes depending on landscape configuration [29–32]. Moreover, heterogeneity in patch connectivity may affect regional persistence and patterns of extinction and colonization [33–35] by promoting asymmetric flows of individuals across patches. In landscapes with heterogeneous levels of connectivity (i.e. some sites really well connected, whereas others weakly connected), more connected patches receive more dispersers than more isolated patches, thus generating spatial variation in abundance and density within landscapes [36]. Therefore, the variance in connectivity across patches has the potential to change the dispersal cost/benefit trade-off through its effect on the spatial variation in population density. Because dispersal evolution is mediated in part by density-dependent intraspecific and kin interactions [23], heterogeneously connected landscapes might yield different selection pressures on dispersal traits than homogeneously connected landscapes.

So far, however, no study has investigated the potential effect of inter-patch variability in connectivity on the evolution of dispersal. Instead, most models have assumed rather simplistic spatial structures, where dispersal is either global [15,21], local (i.e. nearest-neighbour [6,18]) or a simple function of distance [37]. In global dispersal models (i.e. spatially implicit models), all dispersers merge into a global pool from which they are then randomly redistributed among patches. Local dispersal as is classically assumed in spatially explicit models is modelled by creating a regular grid of habitat cells on which dispersers can move only to one, randomly chosen, neighbouring cell with equal probability. Finally, the modelling of dispersal based on dispersal kernels assumes that the probability to disperse from one patch to another is a decreasing function of their distances [38,39]. However, these models are generally based on a torus structure (i.e. no edge effects) and, when averaging the connectivity of each patch to all others, they suffer from the same assumption that all patches have an overall similar connectivity. As such, all these models assume one way or another a homogeneous landscape structure, i.e. all patches have equal connectivity, which is usually not the case in natural landscapes [26,29].

In the present study, we address the following questions: (i) how does spatial structure affect the evolution of dispersal strategies? (ii) does this effect depend on dispersal costs? and (iii) is the evolution of dispersal strategies adaptive? We show that differences in heterogeneity in patch connectivity within landscapes, coupled with density-dependent competition, lead to different evolutionary stable dispersal strategies. We set out to study the influence of landscape structure on the evolution of dispersal using an individual-based model (IBM) in which spatial networks with varying levels of patch connectivity are used to represent different landscape configurations. We assume density-dependent population dynamics and that individuals differ in their dispersal propensity but are otherwise identical. In addition, we also tested if the

adaptation of a metapopulation to one landscape structure generates a specialized coalition of dispersal strategies such that it can resist invasion from metapopulations evolved on other landscape structures. In order to do so, we performed a series of contest simulations akin to reciprocal transplant experiments (see the electronic supplementary material, S1 and S2), where pairs of metapopulations evolved on different landscape types were confronted on their respective landscapes.

2. Material and methods

(a) Landscape structure

The landscape structure of our IBM was modelled as four different types of networks (figure 1) of increasing heterogeneity: regular, random, exponential and scale-free [35] (note that landscape and network are used interchangeably). To understand the effects of network heterogeneity, all networks were set with the same number of nodes ($n_p = 1024$ patches), edges ($n_c = 4096$ connections) and average degree (eight connections per patch). The only factor manipulated across network types was the degree of heterogeneity (variance) in patch connectivity. Connections among patches are undirected, i.e. individuals may disperse both ways with equal probabilities between two connected patches. These four types of networks provide a gradient in terms of the variance in connectivity across patches. Regular networks (figure 1a) consisted of a simple regular grid where each patch was connected to its eight closest neighbours, representing a Moore neighbourhood in traditional spatially explicit models (e.g. [6,18]). Regular networks were wrapped into a torus to avoid edge effects. Random networks (figure 1b) were generated based on the Erdős & Rényi [40] random graph model: patches were connected at random, with equal probability, until the desired average number of connections per patch (degree = 8) was reached. This algorithm created variation in patch degree, so that the degree was Poisson distributed. Exponential networks (figure 1c) were generated after Barabási & Albert [41] but with an average degree of 8 rather than 2 as in their original framework. They were built by connecting five patches randomly and then adding new patches to the network one at a time and connecting them to one of the existing patches with equal probability until the maximum number of patches (1024) is reached. Finally, an average of eight connections per patch was generated by repeating the second step three times. The exponential model creates asymmetry in patches' connectivity because initial patches will naturally have a higher degree and thus the network will exhibit an exponential degree distribution (see the electronic supplementary material, S3). Finally, scale-free networks (figure 1d) were also created by connecting five patches at random as in the case of exponential networks. However, in this case, new patches were added to the network with preferential attachment instead of equal probability until the desired number of patches was reached. Preferential attachment is a process by which the probability to be connected to any existing patch is proportional to its degree [41]. Therefore, more connected patches were more likely to become even more connected. Finally, an average of eight connections per patch was built by adding connections one at a time between random pairs of nodes, with preferential attachment. Scale-free networks are the most heterogeneous landscapes due to preferential attachment, creating a degree distribution that follows a power law ([41]; see also the electronic supplementary material, S3).

(b) Population dynamics

All patches were initially populated with a number of individuals equal to their equilibrium density (K). Individuals are haploid, asexually reproducing and characterized by three dispersal traits (see *Density-dependent dispersal* section). For each individual, the

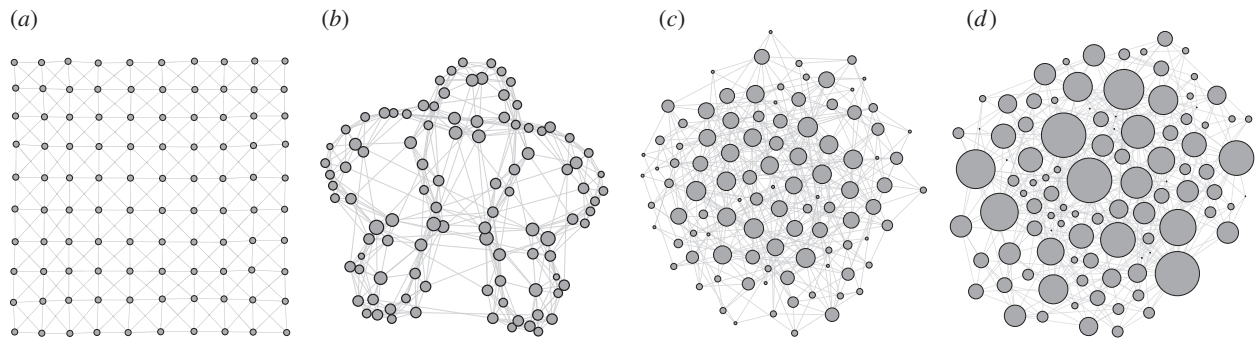


Figure 1. The four different spatial structures used for the simulations, from the most homogeneous to the most heterogeneous. Node size is proportional to its degree. (a) Regular network, (b) random network, (c) exponential network, and (d) scale-free network. All networks were built with 1024 patches and included 4096 connections among patches, with an average of eight connections per patch. The networks differ in terms of their degree variance and the average degree variance across the 200 replicates for each network is: (a) 0, (b) 0.14, (c) 19.42 and (d) 48.70.

three dispersal traits were initially generated by drawing random values from a uniform distribution, hence assuring that a broad mix of genotypes were distributed across all network types at the start of each simulation and that the final outcome of the model would not depend on initial conditions. Genetic variation in traits important for dispersal has been documented [8], such as evidence for additive genetic variation in morphological (e.g. body size, wing length [42]), behavioural (e.g. propensity to initiate dispersal, duration of dispersal [43]) and physiological traits (e.g. enzymes associates directly with locomotion [44]). As the genetic determinism of condition-dependent dispersal traits is poorly known, we used the classical one locus per trait approach. Each time step of the simulation was then generated by the following sequence of events: density-dependent reproduction, death of adults (i.e. individuals are semelparous) and offspring dispersal (i.e. natal dispersal); therefore, we assumed no overlap between generations.

Local population dynamics were based on a density-dependent reproduction function [45], which is commonly used in simulation studies that evaluate density-dependent dispersal evolution [6,15,18,46] and has been successfully fitted to the dynamics of insect populations [45,47]. In order to introduce demographic stochasticity into the model, every individual gave birth to a number of offspring drawn randomly from a Poisson distribution with mean μ , defined as

$$\mu = \lambda(1 + aN_i)^{-b},$$

where λ is the *per capita* rate of growth, a is related to patch quality (see below), b describes the shape of the density-dependent competition affecting patches and N_i is the local population density in the patch. In the present study, we used $b = 1$, which describes a contest competition [6]; note, however, that this parameter has little influence on dispersal evolution [15]. The parameter a represents patch quality and is calculated as follows:

$$a = \frac{\lambda^{1/b} - 1}{K},$$

so that the equilibrium population density is K for all patches across the landscape and therefore the environment is homogeneous. For all simulations, K was set to 20. It should be noted that the reproduction (μ) varies only across patches due to local density (N_i). All other parameters were fixed and there was no genotype (i.e. trait) that could confer differential lifetime reproductive success, assuring that all individuals within a patch had the same fitness. As such, we assume equal strength for kin and intraspecific competition.

(c) Density-dependent dispersal

After reproduction, all parents die and offspring disperse. The probability that an individual disperses d is controlled by three

individual traits (D_0 , α and β) and depends on the local population density. This dispersal model represents organisms that can actively assess information about the quality of their natal patch in order to make dispersal decisions [29] and does not apply to passively dispersing organisms (e.g. wind-dispersed trees). However, the model assumes that movement is costly enough to preclude information gathering on the quality and number of potential target patches. Thus, dispersal decision depends solely on natal patch condition. Each dispersal trait is inherited by the offspring from its parent with a mutation probability $m = 10^{-4}$, and the magnitude was drawn randomly from a uniform distribution (D_0 [−0.1–0.1], α [−0.5–0.5], β [−5.0–5.0]) after Travis *et al.* [6]. The probability of dispersal is obtained from the sigmoid logistic function

$$d = \frac{D_0}{1 + \exp[-(N_i - \beta)\alpha]},$$

where D_0 (range values: [0–1]) represents the maximum dispersal probability, β [0– ∞] is the population density at which the dispersal probability reaches half of its maximum and α [0–10] describes the sharpness of the variation in dispersal probability at this inflection point (IP). Note that we chose this flexible logistic function rather than simple single-parameter functions in order to introduce as few constraints as possible on the type of dispersal strategies that can evolve (figure 2), given the increasing evidence that dispersal strategies are highly variable within a species [48,49]. The cost of dispersal is represented by a fixed-mortality probability c when dispersing between patches. It accounts for the risks of dispersal (e.g. predation) and implicitly accounts for the energetic expense and other deferred fitness costs of dispersal [24]. This scenario would apply when connectivity between patches is controlled by natural or anthropogenic obstacles rather than pure inter-patch distances and it was chosen to estimate the effects of connectivity independent of dispersal costs. However, in order to test if an interaction between mortality and connectivity could affect our initial results, we performed a second set of simulations that assumed a greater weight to the cost of dispersing from a less connected patch. This situation applies when individuals are dispersing randomly in all directions; as such, leaving a less connected patch would be riskier (i.e. less neighbouring patches) than leaving a highly connected patch. Individuals that survive the dispersal process ($1 - c$) enter one randomly chosen patch connected to the natal patch. Once all individuals have dispersed, they become adults and the next time-step begins.

(d) Simulations

We performed 200 replicates for each network structure assuming three levels of dispersal cost for the fixed-mortality scenario: no

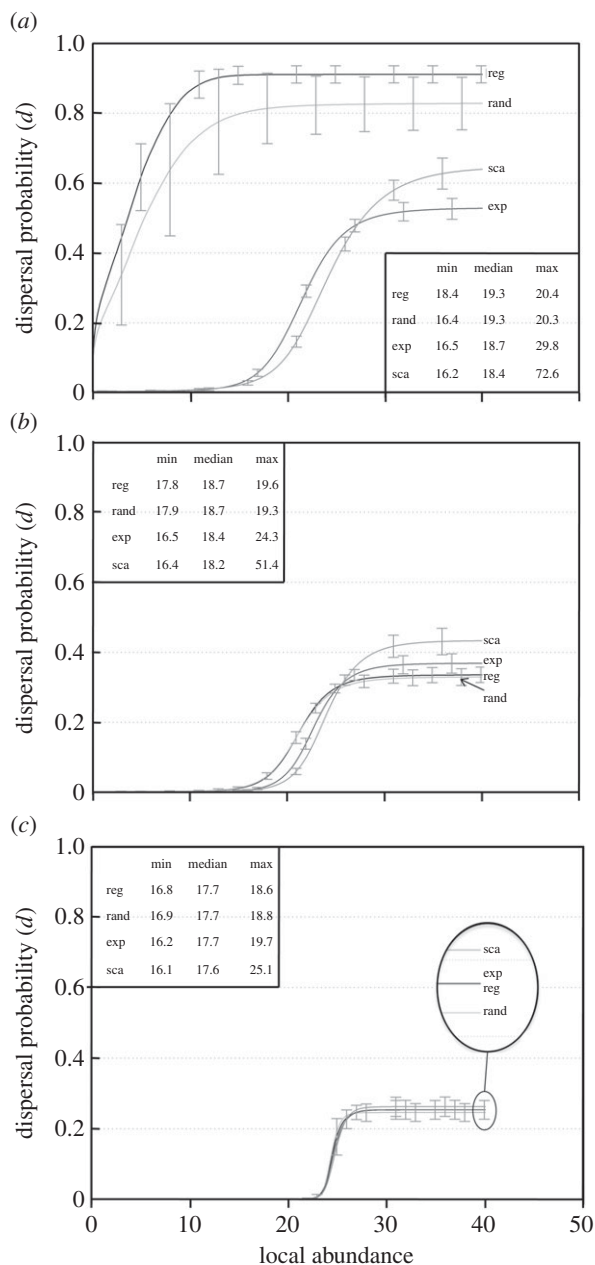


Figure 2. Average dispersal functions built from the three dispersal traits of all individuals at the last generation across the 200 replicates from simulations with (a) 0%, (b) 10%, and (c) 50% dispersal mortality. These logistic functions represent the average dispersal strategy selected in each network and stand for the potential dispersal rates. Average abundances of sites on the last time step were calculated across the 200 replicates for each network in order to evaluate the realized dispersal rates. Horizontal bars represent the standard deviation of the dispersal strategies across 200 replicates. The numbers within the squares are the minimum, median and maximum abundances across sites in each network computed on the last time step. Reg, regular network; rand, random network; exp, exponential network and sca, scale-free network.

mortality (0%), low mortality (10%) and extreme mortality (50%), resulting in $n = 200 \times 4 \times 3 = 2400$ simulations. In addition, 200 replicates for each network ($n = 200 \times 4 = 800$) were performed for the connectivity-dependent mortality scenario, which was estimated using a modified version of the connectivity metric from [50]:

$$c = \omega D^{-\delta},$$

where the dispersal mortality c is a rational function of the degree (D) of the site from which the individual is emigrating, ω controls

Table 1. Initial parameter values used across simulations.

parameter	definition	value
λ	per capita rate of growth	1.5
B	competition parameter	1
K	equilibrium density	20
M	mutation probability	0.001
C	fixed dispersal cost	0.0, 0.1, 0.5
D_0	maximum dispersal probability	[0.0–1.0]
β	IP	[0.0– ∞]
α	sharpness of the curve at the IP	[0.0–10.0]

the average mortality of the function and δ parameter is the effect of connectivity on the function and controls the shape of the kernel. Specific results and parameter values used on the connectivity-dependent dispersal mortality scenario are presented in the electronic supplementary material, S4 and S5.

The values used for all other parameters are presented in table 1. Note that except for the regular network, in which connectivity for all sites is fixed, a different network for each replicate was generated for the other three types following their respective generation rules described earlier (i.e. random, exponential and scale-free networks). The evolutionary dynamics of the dispersal traits were tracked for 40 000 generations (i.e. time steps), which allowed sufficient time for the metapopulation to attain an equilibrium strategy regardless of the initial conditions (see the electronic supplementary material, S6). During the simulation, data on trait values of all individuals across all sites were saved every 50 generations. In order to compare the evolutionary dynamics of different network structures and dispersal cost, we calculated for each replicate the mean of the three dispersal parameters across all patches at each generation. Afterwards, we computed the average and standard deviation of these means across the 200 replicates of each network–dispersal cost combination. In order to test the effects of network structure and dispersal costs (c), we used a two-way ANOVA using both these factors as fixed predictors and the average values from the 200 replicates of each trait at the last time-step as the response variable. Further, if ANOVAs showed significant differences owing to network structures, we applied post hoc Tukey–Kramer tests to evaluate which types of networks and dispersal mortality treatments differed significantly in trait values. In order to explore the parameter space and the robustness of our results, we conducted a sensitivity analysis following Kubisch *et al.* [18].

Finally, in order to assess if a dispersal strategy selected in a particular network structure represented a regional adaptation to the landscape type in which they evolved, we tested if resident metapopulations could resist an invasion from metapopulations evolved on different networks. All the details and results from this set of simulations are presented in the electronic supplementary material, S1 and S2. All simulations and statistical analyses were performed in MATLAB (Mathworks 2010).

3. Results

Both spatial structure and dispersal mortality had a significant effect on the evolutionary dynamics and optima of the three dispersal traits. Figure 2 shows the average dispersal strategy selected in each network for each dispersal cost scenario as well as the range of abundances of sites within networks, which represents the realized dispersal rates of their

metapopulations. It was only in the last scenario ($c = 0.5$) that the realized dispersal rates were below the potential dispersal rates because the local abundances were, except for the most connected patches in scale-free networks, below the threshold density (β) for dispersal propensity (figure 2c). Two-way ANOVAs performed on the last time step across the 200 replicates of each structure indicated significant effects of network (regular, random, exponential and scale-free) and dispersal mortality (i.e. $c = 0, 0.1$ or 0.5) as well as their interaction for all three traits (see the electronic supplementary material, S7 and S8). Post hoc Tukey–Kramer tests indicated that differences among all networks were significant for all traits, except between regular and random networks and exponential and scale-free networks for the trait α (sharpness of the curve at the IP; see the electronic supplementary material, S9). Pairwise comparison of dispersal mortality treatments indicated significant differences across all traits (see the electronic supplementary material, S10). Finally, post hoc Tukey–Kramer test in the interaction term showed that most were significantly different from one another (electronic supplementary material, S11), with the following exceptions: network effects in the extreme dispersal mortality scenario ($c = 0.5$) and some comparisons of the interactions affecting the α trait (steepness of the curve at the IP).

In all cases, differences in trait values were greater between homogeneously connected landscapes (random and regular) and heterogeneously connected landscapes (exponential and scale-free). This difference was due to the spatial variation in fitness (measured by the number of potential offspring μ) that occurred in heterogeneous networks (negative correlation between patch connectivity (i.e. degree) and μ ; figure 3) but not in regular and random networks owing to their null or low variance in patch degree, respectively (results not shown). In simulations with 10% dispersal mortality, selection favoured IP (β) values close to the equilibrium density (K) in random and regular networks, while in more heterogeneous landscapes (exponential and scale-free), selection favoured higher β -values (figure 2b). For all networks, the α trait had the largest variability across replicates compared with the other dispersal parameters (see the electronic supplementary material, S6). Finally, the trait that controlled the asymptote of the curve (D_0) was rapidly selected (see the electronic supplementary material, S6) and presented higher values in heterogeneous landscapes in contrast to more homogeneous spatial structures (figure 2b). The average dispersal function from the last generation across replicates clearly shows that different dispersal strategies were selected in each spatial structure (figure 2b). Overall, metapopulations from regular and random networks had more similar dispersal strategies, whereas metapopulations from exponential and scale-free networks were slightly different from each other and clearly different from the strategies selected in homogeneous landscapes (figure 2b). As expected, when we increased dispersal mortality to 50%, all metapopulations adopted fairly similar dispersal strategies irrespective of landscape structure (low D_0 and high β -values; i.e. low dispersal probability triggered only at high densities; figure 2c). The set of simulations with connectivity-dependent dispersal mortality shows that the results from our main simulation are robust and remain when we relaxed the assumption of fixed dispersal mortality (see the electronic supplementary material, S4). Indeed, the dispersal strategies selected in these simulations

are fairly similar to the one with 10% dispersal mortality (see the electronic supplementary material, S5).

In simulations without dispersal costs ($c = 0$), the dispersal strategies selected in regular and random networks changed drastically in relation to the simulations with dispersal costs (figure 2a); by contrast, exponential and scale-free networks remained fairly similar, except for the selection of higher maximum dispersal probability (D_0) values. The α trait increased sharply in homogeneously connected landscapes, resulting in individual dispersal probability increasing at a slightly faster rate once the population threshold was reached in the patches of these landscapes. Moreover, β -values decreased to ≈ 5 , selecting for a highly dispersive strategy where individuals migrated even when patches were empty. Again, the dispersal strategies selected in this set of simulations showed clear differences between homogeneously (regular and random) and heterogeneously (exponential and scale-free) connected landscapes (figure 2a).

Although there was one dispersal strategy clearly favoured by selection in each network structure, there were always multiple dispersal strategies at any one point in time that were maintained by a mutation–selection–drift balance. This was true regardless of dispersal mortality (figure 4). Nevertheless, there were some differences in the magnitude of this variability. For instance, α had much greater variation across homogeneous networks in simulations without dispersal cost (figure 4c) or very high cost (figure 4i) compared with the ones with moderate cost (figure 4c). In heterogeneous networks, the variability of this trait was slightly higher in simulations with moderate or high dispersal cost (figure 4c,i).

Results from the contest experiment between metapopulations evolved in different network types (see the electronic supplementary material, S1 and S2) showed that, in general, the fitness advantage conferred by dispersal strategies of resident metapopulations was sufficient to resist invasion from individuals evolved in non-resident metapopulations. Note, however, that these performance differences were more evident when comparing dispersal strategies adopted in metapopulations from homogeneously against heterogeneously connected landscapes. Moreover, the variation in dispersal traits within landscapes (figure 4) was important in the contest simulations because, in some cases, it allowed the adaptation of invaders to a different selection pressure (i.e. different spatial structure) before being eliminated by the residents.

The sensitivity analysis showed that under all tested scenarios, the results were robust to parameter changes (see the electronic supplementary material, S12 and S13). The dispersal strategy adopted in each network across tested scenarios was fairly similar to the ones adopted in the original simulation with 10% dispersal cost.

4. Discussion

There is an increasing recognition that the spatial structure of landscapes influences evolutionary processes [29,30,38,51]. Indeed, the application of spatially explicit as opposed to spatially implicit models has shown that the spatial geometry between patches matters for dispersal evolution [52], especially when the environment is heterogeneous [25,38,53]. However, these models assume that patches are equally connected, which is not the case in natural landscapes [29,54]. To our knowledge, this is the first study showing that variation in

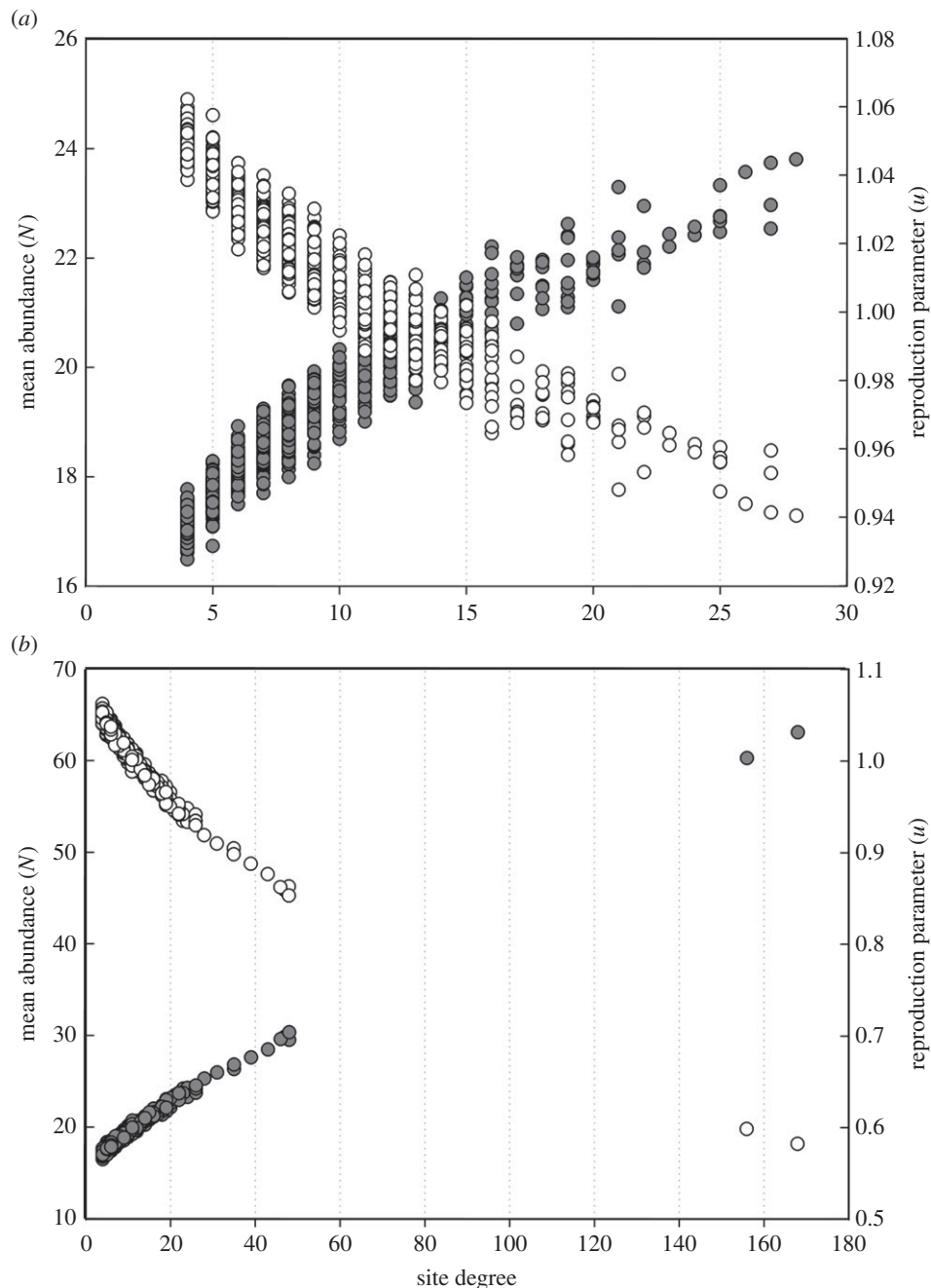


Figure 3. Relationship between site degree with the mean local abundance (grey circles) or the mean reproduction parameter (white circles) across the 40 000 generations. The graphs represent one replicate from the (a) exponential network and one from the (b) scale-free networks in the 10% fixed dispersal mortality scenario. In general, patches with high degree support higher local abundance and produce lower mean fitness.

connectivity across patches also has important implications for dispersal evolution. Our results clearly indicate the possibility that landscape structure selects for different strategies (figure 2) depending on the costs of dispersing.

Under extreme dispersal mortality (50%), selection favoured extremely sedentary individuals, which has been shown by previous studies [15,20,46]. The high rate of dispersal mortality eclipsed the indirect costs of spatial variation in fitness on heterogeneous networks thus promoting dispersal strategies that were similar across all networks (figure 2c). By contrast, different dispersal strategies were selected under low (10%) or zero dispersal mortality and we focus our analysis below on contrasting homogeneously and heterogeneously connected landscapes under these dispersal costs. Note that the conclusions taken from the model with a fixed 10% dispersal

mortality are also valid for the connectivity-dependent dispersal mortality simulation as similar dispersal strategies evolved in both scenarios (see the electronic supplementary material, S4 and S5).

In regular and random networks, under low dispersal mortality, selection favoured the evolution of somewhat sedentary individuals, which dispersed mostly once local abundance reached the equilibrium density ($\beta \approx K = 20$) and, even then, with a somewhat low probability ($D_0 < 0.35$; figure 2b). This is in agreement with other theoretical models, which have shown that if dispersal is a function of local density, almost no dispersal occurs when abundances are below the equilibrium density ($N < K$) in stationary populations [6,15,46]. Alternatively, when there was no dispersal cost ($c = 0$), selection favoured the evolution of highly dispersive

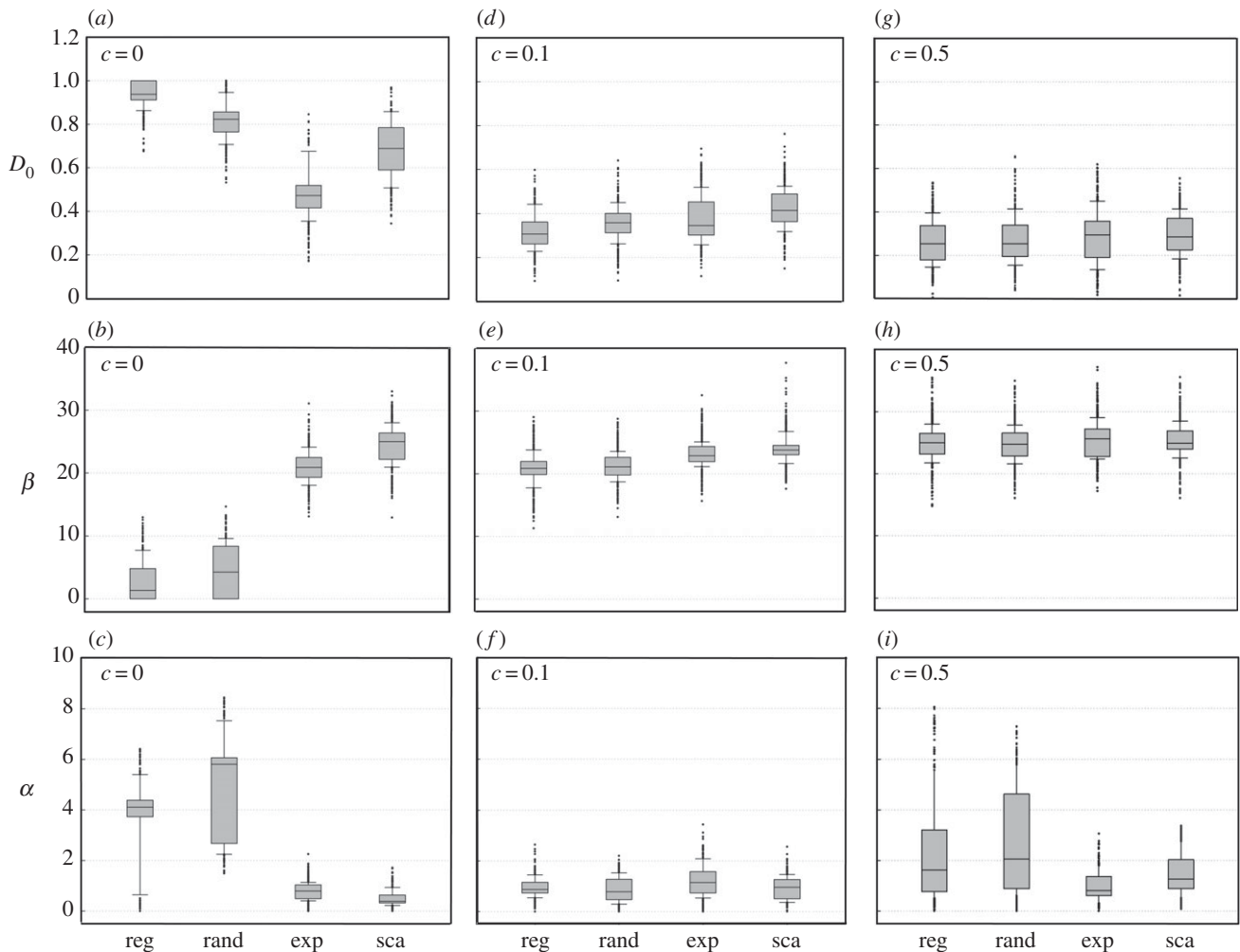


Figure 4. Box plots representing the distributions for the three dispersal parameters at equilibrium in the last generation. The bottom and top boundary of the box plots represent the 25% and 75% percentiles, respectively, while the line within the box plots represents the median. Bottom and top whiskers outside box plots represent 10% and 90% percentiles. Data comes from one replicate of each network type. Columns represent, from left to right, simulations with no mortality ($c = 0$), simulations with 10% dispersal mortality ($c = 0.1$) and simulations with 50% dispersal mortality ($c = 0.5$). (a,d,g) D_0 = maximum dispersal probability; (b,e,h) β = IP; (c,f,i) α = steepness of the curve at the IP. Reg, regular network; rand, random network; exp, exponential network and sca, scale-free network.

individuals ($D_0 \approx 0.8$ – 0.9 ; $\beta \approx 5$; figure 2a). These results were due to the fact that spatial variation in abundances (the only parameter influencing reproduction) was low in homogeneously connected landscapes as they all received, on average, a similar number of individuals from other patches. Therefore, the probability of dispersing into a better patch with lower abundances is similar to dispersing into an unfavourable patch. Consequently, when $c = 0.1$, the dispersal cost outweighs the small potential benefit of dispersing. By contrast, when there is no dispersal mortality, these homogeneously connected landscapes select for highly dispersive strategies owing to the lack of both direct and indirect cost to dispersal (figure 2a).

The novelty of the present study comes from networks with high variance in patch connectivity (i.e. exponential and scale-free), an aspect of landscape structure that has not been considered in previous studies, which clearly showed the potential for selection of alternative dispersal strategies. For instance, the importance of low dispersal mortality as a selective force in dispersal traits is drastically reduced within heterogeneously connected landscapes. The strategy adopted by individuals in these networks was fairly similar between simulations with low dispersal cost ($c = 0.1$) and without

it, differing only in the magnitude of maximum dispersal probability (D_0 ; figure 2a,b). Within such networks, highly connected patches receive a much greater number of immigrants than poorly connected ones. This asymmetric flow of individuals creates considerable variability in abundances (figure 3), which in turn generates variability in density-dependent competition across patches. For instance, the most and least connected patches in the scale-free network have an average abundance over time of 65 and 16, respectively (figure 3b). Therefore, individuals in isolated patches will only disperse when populations exceed their equilibrium density ($N > K$; $\beta \approx 22$ or $\beta \approx 24$ in exponential and scale-free networks, respectively; figure 2a,b) because there is a high probability to disperse into a highly connected and crowded patch (i.e. most patches are linked to them). Such a dispersal strategy incurs an additional cost to fitness compared with individuals that disperse at the equilibrium density. Therefore, the former are more likely to disperse (i.e. higher D_0) when the patch reaches the threshold density (β) in contrast to individuals from homogeneously connected landscapes if there is a direct cost to dispersal (figure 2b). However, in the absence of dispersal mortality ($c = 0$), individuals from heterogeneously connected landscapes have a lower D_0 than those in

homogeneous networks (figure 2a), because the former still suffer an indirect cost by potentially immigrating into an unfavourable patch.

Dispersal strategies can be considered as regional adaptations [51], because they give a long-term fitness advantage to individuals at the landscape scale (i.e. network) while not having any adaptive value at the local scale (i.e. patch) [55]. Indeed, the results obtained in the contest simulations reinforce the idea of a selective effect promoted by the landscape structure on dispersal strategies (electronic supplementary material, S1 and S2). Resident populations from homogeneous landscapes, where the selective pressure is lower, were more likely to be invaded than resident populations evolved in heterogeneous landscapes, which exert a stronger selection pressure. In these landscapes, invading populations from regular or random networks were, on average, not able to adapt their dispersal strategy fast enough and were maintained at a lower relative abundance compared with the resident populations. Note, however, that they did outperform the heterogeneous landscapes in a few replicates, highlighting the importance of the variability in dispersal strategies across individuals (figure 4).

The potential to adapt dispersal strategies to novel landscapes with different spatial arrangement of habitats should be relevant for species shifting their geographical ranges in response to climate change as well as invasive species extending their ranges to non-native regions [56]. Most species do not live in a continuous homogeneous habitat, thus their ranges are constrained by dispersal dynamics (e.g. colonization and extinction) that are regulated by the availability of suitable habitat patches, their quality (e.g. size, resource abundance) and the connectivity among them [57]. Successfully predicting if species will be able to shift (or expand) their ranges is contingent on how they move across landscapes with different spatial configurations [58]. Populations at the core of the species' range most likely inhabit landscapes with low variance in connectivity among patches because more suitable habitats are available for them, while populations at the edge should be coping with sparsely distributed habitat patches that potentially have a higher variance in connectivity. Thus, it is possible that different dispersal strategies are being selected between these populations [6].

Empirical evidence indicates that landscape spatial properties can exert selection on dispersal traits [59,60]. For instance, an increase in the degree of fragmentation across landscapes was significantly related to a monotonic reduction in dispersal propensity of *Boloria eunomia* butterflies [31]. However, butterflies in highly fragmented landscapes that did disperse were more likely to survive than migrants from more connected ones, indicating that an adaptive behaviour was adopted in order to reduce the costs of dispersing [31]. Other studies demonstrated that the degree of connectivity between patches affect the dispersal propensity in spiders [30] and lizards [59]. Moreover, Merckx *et al.* [61] showed experimentally that the dispersal propensity of speckled wood butterflies (*Pararge aegeria*) was higher or lower depending on whether the individuals were born from parents sampled in woodland (less fragmented) or agricultural landscapes (more fragmented), respectively, suggesting that differences in dispersal propensity might have a genetic basis.

It should be noted that the results of our model are based on the assumption that dispersal propensity responds positively to density, which is commonly found in nature [9,62]. However, many species exhibit no or a negative relationship between dispersal propensity and local density. Examples for these cases are rare sexual species where mate availability is an important factor for dispersal decisions [63], invasive species at the edge of their ranges [64] or cooperative species. These species may suffer from Allee effect and thus have a fitness disadvantage in low-density sites. In these cases, the sigmoid dispersal function used in our study should be inverted, where the asymptote of the curve (D_0) would occur at low densities and dispersal propensity would decrease as density increases. For instance, in the case of a rare sexual species, we may predict that heterogeneous landscapes would select for low dispersal rates (low D_0 and high β) owing to the uneven distribution of individuals across patches. After colonizing highly connected patches, individuals would not emigrate from them to avoid suffering from Allee effects in isolated low-density patches. These high-connectivity patches would behave like oceanic islands, in which losses of dispersal ability in colonist populations have been extensively documented due to the high risk of emigrating from them [65]. Conversely, in homogeneously connected landscapes, individuals should be spread more evenly across patches. In this case, it would become advantageous to disperse to find potential mates and one would expect selection to favour higher dispersal rates (higher D_0 and lower β).

5. Conclusion

In summary, we have shown that landscape connectivity can promote the evolution of dispersal strategies and, more importantly, that these strategies provide a long-term fitness advantage to the individuals at the regional scale. Our results highlight the importance of integrating the spatial context of habitat patches in order to predict how evolution affects the spread of species [28] and thus suggest important implications for the study of species invasiveness and range shift under climate change. Results also suggest the potential for the evolution of dispersal to influence metapopulation and metacommunity dynamics by altering the connectivity depending on regional landscape heterogeneity. We acknowledge that empirical dispersal data are difficult to obtain [29]; however, we hope that experimental facilities designed to study dispersal such as the *Metatron* [66] and recent developments in spatial networks, least-cost-path analysis and other indirect methods to quantify dispersal and connectivity might address this issue (reviewed in [27,54]) and allow tests of the theoretical predictions demonstrated here.

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