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Habitat heterogeneity mediates effects of individual variation on spatial species coexistence

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Abstract

Numerous studies have documented the importance of individual variation (IV) in determining the outcome of competition between species. However, little is known about how the interplay between IV and habitat heterogeneity (i.e. variation and spatial autocorrelation in habitat quality) affects species coexistence at the landscape scale. Here we incorporate habitat heterogeneity into a competition model with IV, in order to explore the mechanism of spatial species coexistence. We find that individual-level variation and habitat heterogeneity interact to promote species coexistence, more obviously at lower levels of dispersal rates. This is in stark contrast to early non-spatial models, which predicted that IV reinforces competitive hierarchies and therefore speeds up species exclusion. In essence, increasing variation in patch quality and/or spatial habitat autocorrelation moderates differences in the competitive ability of species, thereby allowing species to coexist both locally and globally. Overall, our theoretical study offers a mechanistic explanation for emerging empirical evidence that both habitat heterogeneity and IV promote species coexistence and therefore biodiversity maintenance.

Keywords: Beverton-Holt model, spatial competition, habitat heterogeneity, intraspecific variability

1. Introduction

Understanding the underlying mechanism of species coexistence in space and therefore biodiversity maintenance, is a fundamental issue in ecology [1, 2]. Recent developments in spatial competition theory have already advanced our understanding of competitive coexistence in spatially structured habitats [3-7]. In general, coexistence requires species to be different in the way they affect, and are affected by, competitors and available resources, resulting in niche difference or average fitness difference between species [3, 7-11]. Differences in the ecological niches occupied by the species within a community act to stabilize the system, with large differences promoting coexistence [10, 11]. By contrast, differences in the fitness of those species drive competitive exclusion, with large differences suppressing coexistence [8, 9]. As the major forces driving interspecific differences, both individual-level variation and habitat heterogeneity can play a vital role in mediating the demographic characteristics of species, thereby altering population dynamics and species coexistence [11-13].

Recent work, including both theoretical and empirical studies, has begun to highlight the importance of individual-level variation (e.g. life-history processes, functional traits) in determining coexistence outcomes of species [14-19]. Individual variation (IV) can affect species dynamics and community structure through Jensen’s inequality (i.e. variation around the trait mean can alter the average interaction strength if the interaction depends nonlinearly on a species’ trait) [14, 20], increased degree of species interaction (i.e. strength of heterospecific interaction) [21-23], and the Portfolio effect (i.e. intraspecific trait variation can protect populations from extreme temporal fluctuations in population density) [24]. A series of studies found that IV has a positive effect on coexistence when differences in competitive ability among conspecific individuals can break down competitive hierarchies of species, such that intraspecific competition is stronger than interspecific competition [4, 25, 26]. In contrast, other studies predicted that intraspecific variation should increase niche overlap between species and thus suppress coexistence [14, 27]. This discrepancy is probably a result of the fact that almost all studies involving IV are non-spatial, omitting the vital role of spatiality. For instance, species in nature are often spatially structured, and their demographic traits might be strongly selected for by habitat heterogeneity resulting from climate change and anthropogenic disturbance [4, 28, 29]. As such, the effects of individual-level variation on demography are likely to be altered by habitat heterogeneity. Although Uriarte and Menge [4] explored species regional coexistence with IV, they only simulated two different patches (with different species preferring different patches) [4], omitting the potential for variation and spatial autocorrelation in habitat quality.

In recent decades, the importance of habitat heterogeneity for species coexistence has received great attention [30-34]. In spatially heterogeneous landscapes, the demographic characteristics of species (e.g. mortality and fecundity) are likely to vary across environmental gradients, resulting in intra- and inter-specific variation within the community. For instance, empirical evidence showed that the germination rate and per-germinant fecundity of plants might be subject to local habitat suitability (e.g. light, moisture or soil nutrients) [35, 36]. In addition, competitive hierarchies of species might shift in a spatial context due to the effects of biotic and abiotic heterogeneity [5]. In particular, habitat heterogeneity (e.g. resulting from land use change, pollution, over-exploitation and climate change) can have a significant effect on species coexistence for suitable spatial scales, for example, the ‘grain’ of the heterogeneity should be smaller than the ‘extent’ of the community [30, 37].

Although the individual effects of IV and habitat heterogeneity on species coexistence have been well documented, very few studies have explored their interactive effects on the outcomes of competition at a regional scale. Spatial habitat heterogeneity can be expected to add another axis, in addition to IV, over which species can differ [3]. Consequently, systems incorporating both forms of variation could produce asynchronous community dynamics, as spatial habitat heterogeneity can directly result in individual-level variation among patches. In this study, we incorporate IV into the classical Beverton-Holt model of two competitors [38] with neighbour dispersal in spatially heterogeneous landscapes. With the model, we attempt to answer the following questions. (i) Whether and how IV interacts with habitat heterogeneity to alter competitive outcomes and what is the underlying mechanism? (ii) How does increasing species dispersal rate modulate the interactive effect of IV and habitat heterogeneity on spatial coexistence?

2. Modelling description

2.1 Beverton-Holt model with IV

We base this study on the competition model for two annual plant species developed by Beverton and Holt [38]. This model is well characterized analytically [39] and can describe plant community dynamics in the field [40]. In addition, recently it has been applied to explore the effect of IV on species coexistence [4,15]. In the absence of IV and habitat heterogeneity, the dynamics of the first species are described by

$$n_{1,t+1} = g_1 \lambda_1 n_{1,t} / (1 + \alpha_{11} g_1 n_{1,t} + \alpha_{12} g_2 n_{2,t}), \quad (1)$$

where $n_{1,t}$ is the density of seeds of species 1 at time t, g_1 is the germination rate of the seeds, λ_1 is the low density fecundity of the germinated seed, and α_{11} and α_{12} are the interaction coefficients describing the per-capita effects of conspecifics and heterospecifics on seed production. The dynamics of the second species are given by an equation of the same form.

According to Godoy et al. [41], the interaction coefficient between heterospecifics (α_{12}) can be decomposed into species 1's generic response to competition (competitive sensitivity r_1) and the effect of species 2 on all other species (e_2), i.e. $\alpha_{12} = r_1 e_2$. This simplification can be further applied to diverse communities, as it primarily focuses on the competition between each pair of species (i.e. pairwise interaction), instead of higher-order interactions involving multiple species. In this form, the competitive ability of species 1 becomes a trait of the species independent of the identity of its competitors [41, 42], characterized by

$$(g_1\lambda_1 - 1)/r_1 \quad (2)$$

In the absence of niche difference and IV in the demographic and competitive parameters in eqn 2, the superior competitor can outcompete the inferior species [41].

Recently, Hart et al. ([14] and more detail therein) investigated the effects of IV on local coexistence by incorporating IV into the competitive sensitivity r. In particular, they reformulated eqn 1 as an integro-difference equation

$$n_{1,t+1} = n_{1,t}\int \frac{g_1\lambda_1}{1+r_1(e_1g_1n_{1,t}+e_2g_2n_{2,t})}p_1(r_1)dr_1 \quad (3)$$

where $p_1(r_1)$ is the probability distribution of r_1. Thus the integral represents the mean effect of intra- and inter-specific (with species 2) interactions on species 1. Note that, following previous studies on the effects of variation in species demographic properties on population dynamics [15, 43], the variation in competitive sensitivity *r* is assumed to be constant across generations.

2.2 Spatially structured competition model

Next, we introduce spatial habitat heterogeneity into the above competition model. Specifically, we assume that individuals of the two species with intraspecific variation in *r* compete in a lattice-structured landscape consisting of 10×10 patches with periodic boundary conditions (i.e. acting as a torus). The local patch quality (e.g. nutrients, moisture) was assumed to vary and, thus, to affect species low density fecundity (λ) [35, 44]. This assumption introduces a spatial factor that influences competitive outcomes, since in this model, fecundity affects those outcomes. Following typical assumptions for metacommunity models, we assume that the two species compete only in patches where they co-occur.

The two species were assumed to disperse within the landscape using neighour dispersal. In particular, they were able to colonize patches that share an edge with those in which they were already present (i.e. a von Neumann neighborhood z = 4) [45]. In our framework, we divided habitat heterogeneity into two elements [34]: variation in patch quality and spatial autocorrelation of patch quality (i.e. the clustering degree of patches with similar quality).

We assume that competitive sensitivity is not heritable but rather a population level variation, thus in each generation seeds mature into plants with sensitivity drawn from the sensitivity distribution for their species r_i. However, the fecundity of mature plants is determined by the quality of the patch in which they reside, and so, in particular, the number of seeds L they produce varies by patch. These seeds can either be dispersed into neighbouring patches or stay in the natal patch. Thus we derive the following equations for the dynamics of species 1 in a given patch i

$$n_{1,t+1,i} = \left(\left(1 - \sum_j m_{1,i\to j}\right) L_{1,t,i} + \sum_j m_{1,j\to i} L_{1,t,j}\right) \tag{4a}$$

$$L_{1,t,i} = \int \frac{g_{1,i}\lambda_{1,i}n_{1,t,i}}{1+r_1\left(e_{1,i}g_{1,i}n_{1,t,i}+e_{2,i}g_{2,i}n_{2,t,i}\right)} p_1(r_1)dr_1 \tag{4b}$$

$$L_{1,t,j} = \int \frac{g_{1,j}\lambda_{1,j}n_{1,t,j}}{1+r_1\left(e_{1,j}g_{1,j}n_{1,t,j}+e_{2,j}g_{2,j}n_{2,t,j}\right)} p_1(r_1)dr_1 \tag{4c}$$

where $m_{1,i\to j}$ is the proportion of species 1’s seeds dispersing from patch i to patch j. $L_{1,t,i}$ is the seed number of species 1 in patch i, while $L_{1,t,j}$ is the seed number of species 1 in patch j. The dynamics of the two species within any patch can be expressed with equations of the form eqn 4a-c with appropriate changes in subscripts.

Following Hart et al. [14] and Uriarte et al. [4], we consider individual variation in competitive sensitivity (r) and assume it obeys a four-parameter beta distribution (characterized by the mean $\bar{r}$, variance σ_r^2, the maximum and the minimum), regardless of patch quality. The variance σ_r^2 can reflect the magnitude of IV, with IV at $\sigma_r^2 > 0$ but no IV if $\sigma_r^2 = 0$.

We simulate the lattice-structured landscape with periodic boundaries, consisting of 10×10 patches (cells) of varying habitat quality and spatial habitat autocorrelation (figure 1a, b). Variation in patch quality (h_i) is characterized using a probability distribution (uniform or gamma) with the mean $\bar{h}$ and the variance σ_h^2 ($\sigma_h^2 = 0$ representing the homogeneous landscape). We assume the low-density fecundity λ_i of individuals inhabiting a patch *i* is positively correlated to the local patch quality (i.e. $\lambda_{i1} = ah_i,\ \lambda_{i2} = bh_i$). Equation 2 demonstrates that both greater λ and lower *r* have a positive effect on competitive ability [41]. As such, we assume that there exists a tradeoff between λ and *r* for both competitors (i.e. higher fecundity implies greater sensitivity to competition and vice versa). This is implemented by assuming that $a > b > 0$ and $\bar{r}_1 > \bar{r}_2$. To make our results comparable to Hart et al. [14], we set $\bar{r}_1 = 0.012$ and $\bar{r}_2 = 0.011$. In our study, two types of landscape are considered by generating spatially correlated random fields based on variogram models [46] (electronic supplementary material, appendix A and figure S1 in appendix C): randomly structured (Moran's I = 0) and spatially autocorrelated (Moran's I = 0.75) landscapes (e.g. figure 1a, b). Additional simulations with intermediate Moran's I =

0.5 are provided in figures S2-S4 (electronic supplementary material, appendix C).

Using R [47], we simulate three scenarios (see Table 1): (i) the separate effect of habitat heterogeneity and IV on the coexistence of two competitors; (ii) the interactive effect of IV and landscape heterogeneity on competitive coexistence; and (iii) the effect of dispersal rates on spatial competition.. Specifically, we study spatial coexistence by modelling invasion dynamics, i.e. an exotic species (greater fecundity or lower competitive sensitivity) with low initial density invades into the patches housing a resident species until the system reaches the equilibrium state [14]. However, for display purposes, we show competitive dynamics by initially assigning an intermediate density to each species in each patch (see figure 1 and sensitivity anlaysis in electronic supplementary material, figures S5-S6 in appendix C). We run simulations up to 1000 timesteps (sufficient for the system to reach its equilibrium state) with 50 replicates for each scenario (varying IV, habitat heterogeneity, spatial autocorrelation, or dispersal rate), and quantify the competition dynamics over the landscape (population densities of the two species across space and time). A new landscape was generated for each simulation run, by randomly drawing the habitat quality of each patch from a normal distribution with a given variance. These patch properties determined the fecundity of each species within that patch for the duration of the run. A broad range of biologically reasonable parameter combinations were explored and found to yield qualitatively consistent competitive patterns (see electronic supplementary material, figures S2-S10 in appendix C). As such, we use one of these parameter combinations as a representative reference parameter set throughout.

3. Results

Firstly, we undertook a systematic comparison of competitive dynamics in random vs. autocorrelated landscapes (Figure 1). In both landscapes, only the combination of IV and patch-quality variation results in species coexistence (blue lines in figure 1c, d), while other cases lead to the exclusion of the inferior species. In particular, the cases without IV result in rapid species exclusion, regardless of habitat heterogeneity (red and black lines in figure 1c, d). In the homogeneous landscape including IV (all patches with the same quality) slows down species exclusion (green lines in figure 1c, d) but does not prevent it. We find that there is little difference between random and auto-correlated landscapes, with the coexistence (or exclusion) patterns remaining the same and very small changes in equilibrium population levels.

Here the combined effects of IV in r and variation in habitat quality facilitate species coexistence because the negative, concave-up relationship between competitive sensitivity (r) and seed production (L) can alter the dominance of the superior species in heterogeneous landscapes (figure 2). Specifically, if the low density fecundities (λ) of the two species are the same (e.g. for homogeneous landscapes), it is clear that the relationship between r and L is also the same. Thus, IV in r speeds up competitive exclusion and species 2 (with lower mean r) wins (figure 2a). In the heterogeneous landscape, variation in habitat quality induces differences in fecundity between patches. Thus, the nonlinear relationship between *r* and *L* is not only species-specific but also patch-specific, and the degree of dominance of the superior species in one patch might decline in another (figure 2b). For instance, for two neighbouring patches *i* and *j* with variation in patch quality, the mean seed production of species 1 in patch *j* can be greater than that of species 2 in patch *i*. This allows dispersal of species 1 from patch *j* to compensate for species 1’s higher sensitivity to competition, ultimately allowing it to dominate patch *i*. Thus, regional coexistence can occur. The underlying mechanism can be thought of the interplay of nonlinear averaging and source-sink dynamics.

Secondly, we evaluated the effect of individual variation on competitive outcomes through varying IV in *r* between species in random and autocorrelated landscapes (figure 3a, b). For limited dispersal rates ($m = 0.01$), the species with larger IV dominates in either landscape type. If the difference in IV between two species is too small, then IV fosters species coexistence. Furthermore, the coexistence region expands in autocorrelated landscapes relative to random landscapes, reducing the region where species 2 dominates. This indicates that spatial autocorrelation in habitat quality weakens the competitive ability of species 2.

The degree of variation in patch quality also has significant effects on species coexistence (figure 3c). In the homogeneous landscape ($\sigma_h^2 = 0$) or landscapes with small variation in patch quality, the dominant species 1 (with greater fecundity) outcompetes species 2 (with lower competitive sensitivity). However, increasing variation in patch quality creates high quality patches which favour species 2’s lower competitive sensitivity. This allows the two species to co-occur regionally. At high variation in patch quality, the population density of species 2 exceeds species 1, and thus the dominance shifts from species 1 to species 2.

Thirdly, since individual dispersal can alter population dynamics in heterogeneous landscapes, we systematically investigated the effects of dispersal rate on species coexistence. At zero dispersal rate, species can coexist, with species 2 having a higher final population density (figure 4a). At low dispersal rates, the dominance of species 2 increases with dispersal rate. However, this trend reverses at high dispersal rates with species 1 becoming dominant and excluding species 2. When the dispersal rate varies between species, large differences in dispersal rate result in competitive exclusion, and the species with the lower dispersal rate wins in both random and autocorrelated landscapes (figure 4b, c). Coexistence occurs when the difference in dispersal rates of both species is relatively small. Spatial autocorrelation in patch quality produces a wider coexistence region than the random landscapes (figure 4c). Note that without IV, the coexistence region decreases rapidly due to competitively exclusion of species 2 (electronic supplementary material, figure S10 in appendix C).

Finally, we determined the spatial distribution of the coexisting species in spatially heterogeneous landscapes (electronic supplementary material, figure S8). In both random and autocorrelated landscapes, individuals of species 2 are more likely to inhabit high-quality patches due to their lower mean competitive sensitivity. In contrast, individuals of species 1 are more likely to be found in low-quality patches where their higher fecundity rate compensates for this poorer habitat. Although species have different habitat preferences, species can coexist locally and regionally when dispersal rates are low.

4. Discussion

Early non-spatial models of species competition found that, due to the negative, concave-up relationship between competitive sensitivity and population growth, IV in competitive sensitivity reinforced competitive hierarchies, thereby promoting exclusion of weaker competitors from the community [14]. However, we found that spatial heterogeneity in habitat quality reverses this outcome. Variation in patch quality altered the strength of the nonlinear competitive relationship and reduced species differences in competitive ability (figure 2b), allowing them to co-occur on both local and regional scales. In addition, with short-range dispersal, conspecifics aggregated while heterospecifics segregated in spatially autocorrelated landscapes according to the spatial distribution of the coexisting species (electronic supplementary material, figure S8 in appendix C). This further decreases the intensity of interspecific interaction and thus reduces the probability of competitive exclusion, as intraspecific, rather than inter-specific, interactions dominate the population dynamics. Consequently, the probability of regional coexistence of species was higher in auto-correlated landscapes compared to those with random structure (figures 3b &

4c). Therefore, habitat heterogeneity promotes species coexistence through two key mechanisms, the direct effect of variation in habitat quality and, additionally, the effect of spatial autocorrelation in local habitat quality.

These effects of habitat heterogeneity depend on the rate at which the species disperse within the landscape. In particular, for species with similar dispersal rates, habitat heterogeneity promoted coexistence when these rates were low, but as rates increased, one species came to dominate and eventually excluded the other. This phenomenon follows naturally from the observation that the effect of increasing dispersal rate is approximately the same as that of increasing dispersal range or, equivalently, increasing the characteristic size of a habitat patch [48]. Thus, for a fast dispersing species, the landscape can be regarded as being composed of a smaller number of larger “patches” (each made up of several of lattice cells) with a habitat quality equal to the average quality in those constituent cells. As a result, the variation in habitat quality experienced by a fast dispersing species is lower than that experienced by a slow dispersing species, thus the effect of habitat heterogeneity declines with dispersal rate. This emergent property of the model can be interpreted ecologically as increasing dispersal rates causing waste of resources on poorer habitats [49] and the destruction of refuges for weaker competitors.

Furthermore, large differences in dispersal rate between species promote competitive exclusion, with the slower dispersing species winning. This is initially a counter-intuitive result, in that greater dispersal rate is typically an advantage.

However, it can, again, be understood in terms of the connection between dispersal rate and effective patch size. In particular, whereas a fast dispersing species experiences a landscape of large patches of similar quality, a slow dispersing species can distinguish between patches of high quality and those of low quality. In ecological terms, a fast dispersing species wastes a significant proportion of the seeds it produces on poorer habitats, while the slow dispersing species does not and thus selectively colonizes high quality habitats [49]. Thus, the optimal dispersal strategy for a species may depend on the scale of heterogeneity within the landscape it inhabits. This can be expected to shape the dispersal strategies of resident species through natural selection [50].

Previous studies have classified the mechanisms by which species can coexist in spatially heterogeneous landscapes as: a spatial relative nonlinearity, a spatial storage effect, and growth-density covariance [7, 8]. In these terms, species coexistence emerges in our model as a result of the simultaneous operation of a spatial relative nonlinearity and a spatial storage effect (electronic supplementary material, appendix B). On the one hand, a spatial relative nonlinearity is created by the interplay between habitat heterogeneity and the nonlinear relationship between competitive sensitivity and population growth, which is not only patch-specific but also species-specific [3]. This landscape scale variation in the strength of the interaction between the species creates variation in the relative competitive strength of the two species, providing the equalising mechanism needed for coexistence [51]. On the other hand, a spatial storage effect arises when a species response to local patch quality varies in space (positive relationship between fecundity and local quality in our model), thereby generating a covariance between habitat quality and competitive ability (i.e. the interaction between the effects of environment and competition in determining population growth rate [1, 8]; see derivation in electronic supplementary material, appendix B). For species with IV in competitive sensitivity (as the first niche axis), habitat heterogeneity acts as a second niche axis, creating a broader range of niches for the species to fill and thus promoting coexistence. In addition, relatively low dispersal rates among patches further facilitate species coexistence both locally and regionally by maximizing the species' experience of habitat heterogeneity, a fundamental component of the mechanisms outlined above.

The interactions between habitat heterogeneity and individual variation have clear implications for future empirical studies. In particular, while there is substantial experimental evidence for the existence of habitat heterogeneity and IV in ecological systems, there has been little work exploring their combined effects. Instead, experimental studies have focused on predicting competitive outcomes by measuring the variation of functional traits within and between species [28]. Additionally, the interplay of IV and habitat heterogeneity can reinforce the effects of spatial nonlinearity and spatial storage effects. Recent empirical studies have found that in spatially heterogeneous landscapes, species responses to local patch quality (with variation in soil nutrients) result in an increase in population density as variation in patch quality increases, suggesting that more species and more individuals could co-occur [52, 53]. Thus, integrating individual-level variation in species traits with spatial habitat heterogeneity into statistical analysis of experimental data could offer new insights into the mechanism of spatial competitive coexistence.

Our study demonstrates the critical role of habitat heterogeneity for species coexistence in a spatial competition model with IV. In particular, habitat heterogeneity promotes spatial coexistence in a two-competitor system if both species have: (1) similar degrees of IV and a negative, concave-up relationship between competitive sensitivity and per-capita growth, (2) a low dispersal rate relative to the scale of habitat variability, and (3) a life-history trade-off between competitive sensitivity and fecundity. Our model suggests that previous non-spatial models might underestimate species coexistence and thus biodiversity in spatially realistic landscapes. Note that, IV is constant in our model, but we might expect a strong selective pressure on IV if its degree is insufficient to maintain species coexistence from an evolutionary perspective. This type of selection occurs rapidly when there is only a small change in the relative abundance of existing genotypes in the population. As such, we strongly recommend that future models could further explore this process in the context of species range boundaries by tracking both demography and the evolution of a quantitative trait in a population that is continuously distributed in space [54-56]. Further studies could also extend this theoretical framework to multispecies systems, but care needs to be taken in inferring that our current outcomes can be applied to diverse communities, as there may be some differences in the behaviours of two vs. multispecies models [57]. Overall, we demonstrate the importance of the combination of habitat heterogeneity and IV for outcomes of competition between species, offering new insights into the mechanisms of spatial coexistence at both local and regional scales.

Code accessibility: The R source code supporting this article is available at https://github.com/dongdongc/habitat-heterogeneity-and-IV.

Authors' contributions: DC conceived of the study and did the simulations, DC and ZL built the model, DC and JL draft the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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Tables

Table 1. Three cases of spatial competition simulation. Abbreviations: $n_{1,t}$ – seed density of species 1 at time *t*; g – seed germination rate; λ – low-density fecundity of the germinated seed; α_{ij} – per-capita effects of conspecifics (*i*=*j*) or heterospecifics (*i*≠*j*) on seed production; *r* – competitive sensitivity; *e* – species competitive effect; $m_{1,i\rightarrow j}$ - proportion of species 1's seeds from patch *i* dispersing into patch *j*; $L_{1,t,i}$ - seed production of species 1 in patch *i* at time *t*; σ_r^2 - magnitude of IV in *r*; h_i - quality of patch *i*; and σ_h^2 - variation in patch quality.

Simulation case	Landscape heterogeneity		Individual variation (IV) in *r*		Dispersal rate (m)	Figures
	Spatial autocorrelation (Moran's I)	Variation in patch quality (σ_h^2)	Mean ($\bar{r}$)	Variance (σ_r^2)		
1	0,0.5,0.75	0,8.3	$\bar{r}_1$= 0.012,$\bar{r}_2$= 0.011	5e-5	0.01	1,2,S2
2	0,0.5,0.75	0,0.2,0.4,…10	$\bar{r}_1$= 0.012,$\bar{r}_2$= 0.011	0.5e-5,1e-5, …10e-5	0.01	3,S3
3	0,0.5,0.75	0,8.3	$\bar{r}_1$= 0.012,$\bar{r}_2$= 0.011	5e-5	0,0.01,…0.2	4,S4,S8

Figure captions

Figure 1. Dynamics of two competitors in (a) random (Moran's I = 0) *vs.* (b) autocorrelated (Moran's I=0.75) landscapes, where each cell represents a patch with different quality (described using uniform distributions). The landscape is homogeneous when σ_h^2 = 0, i.e. all patches have the same quality (not shown). Graphs (c & d): Population dynamics of species 1 (short dashed lines) and species 2 (dashed lines) in both random and autocorrelated landscapes with/without IV and variation in patch quality. Parameter values: $\bar{h}$ = 5.5, σ_h^2 = 8.3, m = 0.01, $\lambda_{i1} = h_i$, λ_{i2}= 0.77h_i, $e_1 = e_2$ = 1, $g_1 = g_2$ = 1, $\bar{r}_1$ = 0.012, $\bar{r}_2$ = 0.011, $n_{1,1,i}$= $n_{2,1,i}$ = 175, max/min values for beta distribution: $\bar{r}_1 \pm$ 0.0109, $\bar{r}_2 \pm$ 0.0109.

Figure 2. Effects of IV in *r* on species coexistence in homogeneous *vs.* heterogeneous landscapes, with IV being constant across species and patches. (a) The nonlinear relationship between *r* and *L* for two competitors is identical in the homogeneous landscape, with IV accelerating competition exclusion. (b) In the heterogeneous landscape with variation in patch quality, IV can facilitate coexistence or switch which species is dominant. For visualisation, results are illustrated using a Gaussian distribution for *r*. Note that, the straight lines perpendicular to the coordinate axes represent the case without IV. Parameter values: $\bar{r}_1$ = 0.015, $\bar{r}_2$ = 0.01, σ_r^2 = 0.001, m = 0.01, $e_1 = e_2$ = 1, $g_1 = g_2$ = 1, $n_1 = n_2$ =165. In (a): h = 3, $\bar{\lambda}_1 = \bar{\lambda}_2 = \bar{h}$; (b): h_i = 3 h_j = 5, $\bar{\lambda}_1$ = 1.25$\bar{h}$, $\bar{\lambda}_2 = \bar{h}$.

Figure 3. Interactive effects of IV and landscape heterogeneity (spatial autocorrelation and variation in patch quality) on species coexistence. IV varies across species in both (a) random and (b) autocorrelated landscapes. (c) Effect of variation in patch quality (σ_h^2) on species final populaion density with 95% confidence interval. Graphs (a & b): patch quality is uniformly distributed with σ_h^2 = 8.3; and graph (c): patch quality follows the gamma distribution with σ_r^2 = 5e-5. Graphs (a & c): Moran's I = 0; and graph (b): Moran's I = 0.75. Other parameters: $\bar{h}$ = 5.5, *m* = 0.01, $\lambda_{i1} = h_i$, λ_{i2}= $0.77h_i$, $e_1 = e_2$ = 1, $g_1 = g_2$ = 1, $\bar{r}_1$ = 0.012, $\bar{r}_2$ = 0.011, max/min values for beta distribution: $\bar{r}_1 \pm$ 0.0109, $\bar{r}_2 \pm$ 0.0109. Standard derivations of 50 replicates of graphs (a & b) are shown in figure S7 (appendix C).

Figure 4. Effect of dispersal rate on the competitive outcomes in both random vs. heterogeneous landscapes. Graph (a): the effect of dispersal rate on final population density with two competitors having the same dispersal rate. Dispersal rates vary across species in (b) random and (c) autocorrelated landscapes. Patch quality is uniformly distributed with σ_h^2= 8.3. Graphs (a & b): Moran's I = 0; and graph (c): Moran's I=0.75. Other parameters: $\bar{h}$ = 5.5, *m* = 0.01, $\lambda_{i1} = h_i$, λ_{i2}= $0.77h_i$, $e_1 = e_2$ = 1, $g_1 = g_2$ = 1, $\bar{r}_1$ = 0.012, $\bar{r}_2$ = 0.011, σ_r^2 = 5e-5, max/min values for beta distribution: $\bar{r}_1 \pm$ 0.0109, $\bar{r}_2 \pm$ 0.0109. Standard derivations (SDs) of 50 replicates of (a) are omitted for clarity as they are very small (<7), while SDs for graphs (b & c) are shown in figure S7 (appendix C).