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1 **Habitat heterogeneity mediates effects of individual variation on spatial species**  
2 **coexistence**

3 Dongdong Chen<sup>1,2,#</sup>, Jinbao Liao<sup>3,#</sup>, Daniel Bearup<sup>4</sup> and Zhenqing Li<sup>1,2\*</sup>

4 <sup>1</sup> State Key Laboratory of Vegetation and Environmental Change, Institute of Botany,  
5 Chinese Academy of Sciences, Beijing 100093, China

6 <sup>2</sup> University of Chinese Academy of Sciences, Beijing 100049, China

7 <sup>3</sup> Ministry of Education's Key Laboratory of Poyang Lake Wetland and Watershed  
8 Research, School of Geography and Environment, Jiangxi Normal University,  
9 Ziyang Road 99, 330022 Nanchang, China

10 <sup>4</sup> University of Kent, School of Mathematics, Statistics and Actuarial Sciences,  
11 Parkwood Road, Canterbury, CT2 7FS, UK

12

13 **\*Author for correspondence:** Prof. Dr. Zhenqing Li, e-mail: lizq@ibcas.ac.cn

14 Address: 20 Nanxincun, Xiangshan, Haidian District, Beijing 100093, China

15 Tel: +86-10-62836956

16 **#Co-first authors with equal contribution**

17 **Abstract**

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

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

35 **1. Introduction**

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

50 Recent work, including both theoretical and empirical studies, has begun to  
51 highlight the importance of individual-level variation (e.g. life-history processes,  
52 functional traits) in determining coexistence outcomes of species [14-19]. Individual  
53 variation (IV) can affect species dynamics and community structure through Jensen's  
54 inequality (i.e. variation around the trait mean can alter the average interaction  
55 strength if the interaction depends nonlinearly on a species' trait) [14, 20], increased

56 degree of species interaction (i.e. strength of heterospecific interaction) [21-23], and  
57 the Portfolio effect (i.e. intraspecific trait variation can protect populations from  
58 extreme temporal fluctuations in population density) [24]. A series of studies found  
59 that IV has a positive effect on coexistence when differences in competitive ability  
60 among conspecific individuals can break down competitive hierarchies of species,  
61 such that intraspecific competition is stronger than interspecific competition [4, 25,  
62 26]. In contrast, other studies predicted that intraspecific variation should increase  
63 niche overlap between species and thus suppress coexistence [14, 27]. This  
64 discrepancy is probably a result of the fact that almost all studies involving IV are  
65 non-spatial, omitting the vital role of spatiality. For instance, species in nature are  
66 often spatially structured, and their demographic traits might be strongly selected for  
67 by habitat heterogeneity resulting from climate change and anthropogenic disturbance  
68 [4, 28, 29]. As such, the effects of individual-level variation on demography are likely  
69 to be altered by habitat heterogeneity. Although Uriarte and Menge [4] explored  
70 species regional coexistence with IV, they only simulated two different patches (with  
71 different species preferring different patches) [4], omitting the potential for variation  
72 and spatial autocorrelation in habitat quality.

73       In recent decades, the importance of habitat heterogeneity for species coexistence  
74 has received great attention [30-34]. In spatially heterogeneous landscapes, the  
75 demographic characteristics of species (e.g. mortality and fecundity) are likely to vary  
76 across environmental gradients, resulting in intra- and inter-specific variation within

77 the community. For instance, empirical evidence showed that the germination rate and  
78 per-germinant fecundity of plants might be subject to local habitat suitability (e.g.  
79 light, moisture or soil nutrients) [35, 36]. In addition, competitive hierarchies of  
80 species might shift in a spatial context due to the effects of biotic and abiotic  
81 heterogeneity [5]. In particular, habitat heterogeneity (e.g. resulting from land use  
82 change, pollution, over-exploitation and climate change) can have a significant effect  
83 on species coexistence for suitable spatial scales, for example, the ‘grain’ of the  
84 heterogeneity should be smaller than the ‘extent’ of the community [30, 37].

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

## 98 2. Modelling description

### 99 2.1 Beverton-Holt model with IV

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

$$105 \quad n_{1,t+1} = g_1 \lambda_1 n_{1,t} / (1 + \alpha_{11} g_1 n_{1,t} + \alpha_{12} g_2 n_{2,t}), \quad (1)$$

106 where  $n_{1,t}$  is the density of seeds of species 1 at time  $t$ ,  $g_1$  is the germination rate of  
107 the seeds,  $\lambda_1$  is the low density fecundity of the germinated seed, and  $\alpha_{11}$  and  $\alpha_{12}$   
108 are the interaction coefficients describing the per-capita effects of conspecifics and  
109 heterospecifics on seed production. The dynamics of the second species are given by  
110 an equation of the same form.

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

119 
$$(g_1\lambda_1 - 1)/r_1 \tag{2}$$

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

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

125 
$$n_{1,t+1} = n_{1,t} \int \frac{g_1\lambda_1}{1+r_1(e_1g_1n_{1,t}+e_2g_2n_{2,t})} p_1(r_1) dr_1 \tag{3}$$

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

131 **2.2 Spatially structured competition model**

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



140 species compete only in patches where they co-occur.

141 The two species were assumed to disperse within the landscape using neighbour  
142 dispersal. In particular, they were able to colonize patches that share an edge with  
143 those in which they were already present (i.e. a von Neumann neighborhood  $z = 4$ )  
144 [45]. In our framework, we divided habitat heterogeneity into two elements [34]:  
145 variation in patch quality and spatial autocorrelation of patch quality (i.e. the  
146 clustering degree of patches with similar quality).

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

$$154 \quad n_{1,t+1,i} = \left( (1 - \sum_j m_{1,i \rightarrow j}) L_{1,t,i} + \sum_j m_{1,j \rightarrow i} L_{1,t,j} \right) \quad (4a)$$

$$155 \quad L_{1,t,i} = \int \frac{g_{1,i} \lambda_{1,i} n_{1,t,i}}{1+r_1(e_{1,i} g_{1,i} n_{1,t,i} + e_{2,i} g_{2,i} n_{2,t,i})} p_1(r_1) dr_1 \quad (4b)$$

$$156 \quad L_{1,t,j} = \int \frac{g_{1,j} \lambda_{1,j} n_{1,t,j}}{1+r_1(e_{1,j} g_{1,j} n_{1,t,j} + e_{2,j} g_{2,j} n_{2,t,j})} p_1(r_1) dr_1 \quad (4c)$$

157 where  $m_{1,i \rightarrow j}$  is the proportion of species 1's seeds dispersing from patch  $i$  to patch  $j$ .

158  $L_{1,t,i}$  is the seed number of species 1 in patch  $i$ , while  $L_{1,t,j}$  is the seed number of

159 species 1 in patch  $j$ . The dynamics of the two species within any patch can be

160 expressed with equations of the form eqn 4a-c with appropriate changes in subscripts.

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

166 We simulate the lattice-structured landscape with periodic boundaries, consisting  
167 of 10×10 patches (cells) of varying habitat quality and spatial habitat autocorrelation  
168 (figure 1a, b). Variation in patch quality ( $h_i$ ) is characterized using a probability  
169 distribution (uniform or gamma) with the mean  $\bar{h}$  and the variance  $\sigma_h^2$  ( $\sigma_h^2 = 0$   
170 representing the homogeneous landscape). We assume the low-density fecundity  $\lambda_i$   
171 of individuals inhabiting a patch  $i$  is positively correlated to the local patch quality (i.e.  
172  $\lambda_{i1} = ah_i$ ,  $\lambda_{i2} = bh_i$ ). Equation 2 demonstrates that both greater  $\lambda$  and lower  $r$  have  
173 a positive effect on competitive ability [41]. As such, we assume that there exists a  
174 tradeoff between  $\lambda$  and  $r$  for both competitors (i.e. higher fecundity implies greater  
175 sensitivity to competition and vice versa). This is implemented by assuming that  $a >$   
176  $b > 0$  and  $\bar{r}_1 > \bar{r}_2$ . To make our results comparable to Hart et al. [14], we set  $\bar{r}_1 =$   
177  $0.012$  and  $\bar{r}_2 = 0.011$ . In our study, two types of landscape are considered by  
178 generating spatially correlated random fields based on variogram models [46]  
179 (electronic supplementary material, appendix A and figure S1 in appendix C):  
180 randomly structured (Moran's  $I = 0$ ) and spatially autocorrelated (Moran's  $I = 0.75$ )  
181 landscapes (e.g. figure 1a, b). Additional simulations with intermediate Moran's  $I =$

182 0.5 are provided in figures S2-S4 (electronic supplementary material, appendix C).

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

203 one of these parameter combinations as a representative reference parameter set  
204 throughout.

### 205 **3. Results**

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

216 Here the combined effects of IV in  $r$  and variation in habitat quality facilitate  
217 species coexistence because the negative, concave-up relationship between  
218 competitive sensitivity ( $r$ ) and seed production ( $L$ ) can alter the dominance of the  
219 superior species in heterogeneous landscapes (figure 2). Specifically, if the low  
220 density fecundities ( $\lambda$ ) of the two species are the same (e.g. for homogeneous  
221 landscapes), it is clear that the relationship between  $r$  and  $L$  is also the same. Thus, IV  
222 in  $r$  speeds up competitive exclusion and species 2 (with lower mean  $r$ ) wins (figure  
223 2a). In the heterogeneous landscape, variation in habitat quality induces differences in

224 fecundity between patches. Thus, the nonlinear relationship between  $r$  and  $L$  is not  
225 only species-specific but also patch-specific, and the degree of dominance of the  
226 superior species in one patch might decline in another (figure 2b). For instance, for  
227 two neighbouring patches  $i$  and  $j$  with variation in patch quality, the mean seed  
228 production of species 1 in patch  $j$  can be greater than that of species 2 in patch  $i$ . This  
229 allows dispersal of species 1 from patch  $j$  to compensate for species 1's higher  
230 sensitivity to competition, ultimately allowing it to dominate patch  $i$ . Thus, regional  
231 coexistence can occur. The underlying mechanism can be thought of the interplay of  
232 nonlinear averaging and source-sink dynamics.

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

241       The degree of variation in patch quality also has significant effects on species  
242 coexistence (figure 3c). In the homogeneous landscape ( $\sigma_h^2 = 0$ ) or landscapes with  
243 small variation in patch quality, the dominant species 1 (with greater fecundity)  
244 outcompetes species 2 (with lower competitive sensitivity). However, increasing

245 variation in patch quality creates high quality patches which favour species 2's lower  
246 competitive sensitivity. This allows the two species to co-occur regionally. At high  
247 variation in patch quality, the population density of species 2 exceeds species 1, and  
248 thus the dominance shifts from species 1 to species 2.

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

263 Finally, we determined the spatial distribution of the coexisting species in  
264 spatially heterogeneous landscapes (electronic supplementary material, figure S8). In  
265 both random and autocorrelated landscapes, individuals of species 2 are more likely to

266 inhabit high-quality patches due to their lower mean competitive sensitivity. In  
267 contrast, individuals of species 1 are more likely to be found in low-quality patches  
268 where their higher fecundity rate compensates for this poorer habitat. Although  
269 species have different habitat preferences, species can coexist locally and regionally  
270 when dispersal rates are low.

#### 271 **4. Discussion**

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

287 4c). Therefore, habitat heterogeneity promotes species coexistence through two key  
288 mechanisms, the direct effect of variation in habitat quality and, additionally, the  
289 effect of spatial autocorrelation in local habitat quality.

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

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



308 However, it can, again, be understood in terms of the connection between dispersal  
309 rate and effective patch size. In particular, whereas a fast dispersing species  
310 experiences a landscape of large patches of similar quality, a slow dispersing species  
311 can distinguish between patches of high quality and those of low quality. In ecological  
312 terms, a fast dispersing species wastes a significant proportion of the seeds it produces  
313 on poorer habitats, while the slow dispersing species does not and thus selectively  
314 colonizes high quality habitats [49]. Thus, the optimal dispersal strategy for a species  
315 may depend on the scale of heterogeneity within the landscape it inhabits. This can be  
316 expected to shape the dispersal strategies of resident species through natural selection  
317 [50].

318 Previous studies have classified the mechanisms by which species can coexist in  
319 spatially heterogeneous landscapes as: a spatial relative nonlinearity, a spatial storage  
320 effect, and growth-density covariance [7, 8]. In these terms, species coexistence  
321 emerges in our model as a result of the simultaneous operation of a spatial relative  
322 nonlinearity and a spatial storage effect (electronic supplementary material, appendix  
323 B). On the one hand, a spatial relative nonlinearity is created by the interplay between  
324 habitat heterogeneity and the nonlinear relationship between competitive sensitivity  
325 and population growth, which is not only patch-specific but also species-specific [3].  
326 This landscape scale variation in the strength of the interaction between the species  
327 creates variation in the relative competitive strength of the two species, providing the  
328 equalising mechanism needed for coexistence [51]. On the other hand, a spatial

329 storage effect arises when a species response to local patch quality varies in space  
330 (positive relationship between fecundity and local quality in our model), thereby  
331 generating a covariance between habitat quality and competitive ability (i.e. the  
332 interaction between the effects of environment and competition in determining  
333 population growth rate [1, 8]; see derivation in electronic supplementary material,  
334 appendix B). For species with IV in competitive sensitivity (as the first niche axis),  
335 habitat heterogeneity acts as a second niche axis, creating a broader range of niches  
336 for the species to fill and thus promoting coexistence. In addition, relatively low  
337 dispersal rates among patches further facilitate species coexistence both locally and  
338 regionally by maximizing the species' experience of habitat heterogeneity, a  
339 fundamental component of the mechanisms outlined above.

340       The interactions between habitat heterogeneity and individual variation have clear  
341 implications for future empirical studies. In particular, while there is substantial  
342 experimental evidence for the existence of habitat heterogeneity and IV in ecological  
343 systems, there has been little work exploring their combined effects. Instead,  
344 experimental studies have focused on predicting competitive outcomes by measuring  
345 the variation of functional traits within and between species [28]. Additionally, the  
346 interplay of IV and habitat heterogeneity can reinforce the effects of spatial  
347 nonlinearity and spatial storage effects. Recent empirical studies have found that in  
348 spatially heterogeneous landscapes, species responses to local patch quality (with  
349 variation in soil nutrients) result in an increase in population density as variation in

350 patch quality increases, suggesting that more species and more individuals could  
351 co-occur [52, 53]. Thus, integrating individual-level variation in species traits with  
352 spatial habitat heterogeneity into statistical analysis of experimental data could offer  
353 new insights into the mechanism of spatial competitive coexistence.

354 Our study demonstrates the critical role of habitat heterogeneity for species  
355 coexistence in a spatial competition model with IV. In particular, habitat heterogeneity  
356 promotes spatial coexistence in a two-competitor system if both species have: (1)  
357 similar degrees of IV and a negative, concave-up relationship between competitive  
358 sensitivity and per-capita growth, (2) a low dispersal rate relative to the scale of  
359 habitat variability, and (3) a life-history trade-off between competitive sensitivity and  
360 fecundity. Our model suggests that previous non-spatial models might underestimate  
361 species coexistence and thus biodiversity in spatially realistic landscapes. Note that,  
362 IV is constant in our model, but we might expect a strong selective pressure on IV if  
363 its degree is insufficient to maintain species coexistence from an evolutionary  
364 perspective. This type of selection occurs rapidly when there is only a small change in  
365 the relative abundance of existing genotypes in the population. As such, we strongly  
366 recommend that future models could further explore this process in the context of  
367 species range boundaries by tracking both demography and the evolution of a  
368 quantitative trait in a population that is continuously distributed in space [54-56].  
369 Further studies could also extend this theoretical framework to multispecies systems,  
370 but care needs to be taken in inferring that our current outcomes can be applied to

371 diverse communities, as there may be some differences in the behaviours of two vs.  
372 multispecies models [57]. Overall, we demonstrate the importance of the combination  
373 of habitat heterogeneity and IV for outcomes of competition between species, offering  
374 new insights into the mechanisms of spatial coexistence at both local and regional  
375 scales.

376 **Code accessibility:** The R source code supporting this article is available at

377 <https://github.com/dongdongc/habitat-heterogeneity-and-IV>.

378 **Authors' contributions:** DC conceived of the study and did the simulations, DC and

379 ZL built the model, DC and JL draft the manuscript. All authors gave final approval

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387

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545 **Tables**

546 **Table 1.** Three cases of spatial competition simulation. Abbreviations:  $n_{1,t}$  – seed density of species 1 at time  $t$ ;  $g$  – seed germination rate;  $\lambda$   
 547 – low-density fecundity of the germinated seed;  $\alpha_{ij}$  – per-capita effects of conspecifics ( $i=j$ ) or heterospecifics ( $i \neq j$ ) on seed production;  $r$  –  
 548 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  
 549 production of species 1 in patch  $i$  at time  $t$ ;  $\sigma_r^2$  - magnitude of IV in  $r$ ;  $h_i$  - quality of patch  $i$ ; and  $\sigma_h^2$  - 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 ( $\sigma_h^2$ )	Mean ( $\bar{r}$ )	Variance ( $\sigma_r^2$ )		
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

550 **Figure captions**

551 **Figure 1.** Dynamics of two competitors in (a) random (Moran's  $I = 0$ ) vs. (b)  
552 autocorrelated (Moran's  $I=0.75$ ) landscapes, where each cell represents a patch with  
553 different quality (described using uniform distributions). The landscape is  
554 homogeneous when  $\sigma_h^2 = 0$ , i.e. all patches have the same quality (not shown).  
555 Graphs (c & d): Population dynamics of species 1 (short dashed lines) and species 2  
556 (dashed lines) in both random and autocorrelated landscapes with/without IV and  
557 variation in patch quality. Parameter values:  $\bar{h} = 5.5$ ,  $\sigma_h^2 = 8.3$ ,  $m = 0.01$ ,  $\lambda_{i1} = h_i$ ,  
558  $\lambda_{i2} = 0.77h_i$ ,  $e_1 = e_2 = 1$ ,  $g_1 = g_2 = 1$ ,  $\bar{r}_1 = 0.012$ ,  $\bar{r}_2 = 0.011$ ,  $n_{1,1,i} = n_{2,1,i} =$   
559  $175$ , max/min values for beta distribution:  $\bar{r}_1 \pm 0.0109$ ,  $\bar{r}_2 \pm 0.0109$ .

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

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

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