Immigration rates and species niche characteristics affect the relationship between species richness and habitat heterogeneity in modeled meta-communities

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The positive relationship between habitat heterogeneity and species richness is a cornerstone of ecology. Recently, it was suggested that this relationship should be unimodal rather than linear due to a tradeoff between environmental heterogeneity and population sizes. Increased environmental heterogeneity will decrease effective habitat sizes, which in turn will increase the rate of local species extinctions. The occurrence of the unimodal richness–heterogeneity relationship at the habitat scale was confirmed in both empirical and theoretical studies. However, it is unclear whether it can occur at broader spatial scales, for meta-communities in diverse and patchy landscapes. Here, I used a spatially explicit meta-community model to quantify the roles of two species–level characteristics, niche width and immigration rates, on the type of the richness–heterogeneity relationship at the landscape scale. I found that both positive and unimodal richness–heterogeneity relationship can occur in meta-communities in patchy landscapes. The type of the relationship was affected by the interactions between inter-patch immigration rates and species' niche widths. Unimodal relationships were prominent in meta-communities comprising species with wide niches but low inter-patch immigration rates. In contrast, meta-communities consisting of species with narrow niches and high immigration rates exhibited positive relationships. Meta-communities comprising generalist species are therefore likely to exhibit unimodal richness-heterogeneity relationships as long as low immigration rates prevent rescue effects and patches are small. The richness-heterogeneity relationship at the landscape scale is dictated by species' niche widths and inter-patch immigration rates. These immigration rates, in turn, depend on the interaction between species dispersal capabilities and habitat connectivity, highlighting the roles of both species traits and landscape structure in generating the richness–heterogeneity relationship at the landscape scale.

2 **Immigration rates and species niche characteristics affect the relationship between species**

3 **richness and habitat heterogeneity in modeled meta-communities**

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8 **Introduction**

9 One of the fundamental ecological concepts is that heterogeneous habitats can support more species,

10 thus there is a positive relationship between species richness and habitat heterogeneity (MacArthur &

11 MacArthur, 1961; Cody, 1981). However, a recent study has challenged the ubiquity of the positive

12 richness–heterogeneity relationship, and suggested that the relationship should in fact be unimodal

13 (Allouche et al., 2012). The reasoning behind this theory, termed the area–heterogeneity tradeoff, is

14 that as habitats become increasingly heterogeneous in finite geographical space, the area comprising a

15 given set of environmental conditions becomes smaller. Consequently, population sizes decrease,

16 eventually leading to an increased prevalence of stochastic extinction events, and subsequently a lower

17 overall species richness (Kadmon & Allouche, 2007). The area-heterogeneity tradeoff, therefore, has

18 three main predictions: [1] there is a negative relationship between population sizes and habitat

19 heterogeneity; [2] there is a positive relationship between habitat heterogeneity and local extinction

20 rates; and therefore [3] there is a unimodal relationship between species richness and habitat

21 heterogeneity. However, in different systems it is possible to find positive, unimodal, or even negative

22 relationships between richness and heterogeneity, depending on the characteristics of the species in

23 those systems, such as their niche widths (Allouche et al., 2012), their fecundity (Kadmon & Allouche,

24 2007), and the rate of immigration into the local community from the regional species pool (Kadmon &

25 Allouche, 2007); as well as the hierarchical scale of the analysis (Bar-Massada & Wood, 2014), the

26 size of the local habitat (Kadmon & Allouche, 2007), and the environmental variable whose

27 heterogeneity is measured (Bar-Massada & Wood, 2014).

28   The original area-heterogeneity tradeoff hypothesis (Kadmon & Allouche, 2007) was

29 developed for communities inhabiting a single island (or habitat patch) in an island-mainland system,

30 based on the unification of niche theory (Hutchinson, 1957) and the theory of island biogeography

31 (MacArthur & Wilson, 1967). The first empirical test of the theory (Allouche et al., 2012) was based

32   on analyses of breeding bird species in geographical units of 100 km^2 in Spain, where elevation range

33   served as a measure of habitat heterogeneity. This study, therefore, did not account for the spatial

34   structure (e.g., patchiness, connectivity) of the geographical regions which served as sampling units.

35   Moreover, elevation range, although a popular measure of habitat heterogeneity (Veech & Crist, 2007;

36   Allouche et al., 2012), is a simplistic and indirect measure of actual habitat heterogeneity (Hortal et al.,

37   2013), as species respond and utilize habitat features at much smaller spatial scales (Bar-Massada &

38   Wood, 2014).

39   It is possible, however, to adapt the area-heterogeneity tradeoff theory to a broader-scale,

40   spatially explicit framework, which is more in line with the traditional landscape ecological view of

41   landscapes as comprising patches of different types located within a non-habitat matrix. Consider a

42   landscape consisting of multiple patches of different types. The classic prediction would be that as

43   landscape heterogeneity increases (i.e., there is an increase in patch richness or the number of patch

44   types, and an increase in patch evenness, which corresponds with an increasingly uniform areal

45   distribution of different patch types), species richness increases as well. However, as landscape

46   heterogeneity keeps increasing (by the addition of more and more patches and patch types), the patch

47   size distribution shifts to the left and many patches become smaller, while at the same time edge

48   density increases (Fahrig et al., 2011). Consequently, their ability to support sufficiently large

49   populations of individual species diminishes. Furthermore, with increased landscape heterogeneity,

50   smaller patches may become more isolated, and consequently the landscape becomes more fragmented,

51   with potential detrimental effects on species left in patches. Thus, the intermediate heterogeneity

52   hypothesis (Fahrig et al., 2011) suggests that at extremely high heterogeneity levels, the detrimental

53   effects of fragmentation offset the positive effects of landscape heterogeneity, resulting in decreasing

54   species richness at the landscape scale. Yet species in patchy landscapes often belong to meta-

55   populations, and local communities in patches are part of a meta-community (Leibold et al., 2004). In

56   both meta-populations and meta-communities species persistence at the landscape scale can be

57   maintained by source-sink dynamics and rescue effects (in which populations in small sink patches or

58   patches with suboptimal habitat conditions are maintained by immigration from neighboring source

59   patches; (Brown & Kodric-Brown, 1977); and mass effects (Shmida & Wilson, 1985; Kunin, 1998),

60   through which species can persist in suboptimal habitats by dominating the propagule pool. Indeed,

61   Kadmon and Allouche (2007) showed that higher immigration rates from mainland to island

62   communities promote positive richness-heterogeneity relationships within single communities. In a

63   meta-community / patchy landscape context, the question becomes: do higher immigration rates among

64   patches (regardless of the presence of a mainland) maintain the persistence of species in meta-

65   communities, thus promoting positive richness-heterogeneity relationships across different landscapes?

66   Moreover, species niche widths can affect the number of species that can establish in patches, as

67   species with wider niches can establish in more patch types; if more species establish in a patch, there

68   is less area available for each species (Tilman, 2004). It is possible therefore that niche width can

69   interact with inter-patch immigration rates to affect overall species richness, as well as the type of the

70   richness heterogeneity relationship.

71   Here, I developed a spatially explicit meta-community model, based on existing modeling

72   approaches in community ecology (Gravel et al., 2006; Bar-Massada, Kent & Carmel, 2014; these

73   models were developed to simulate the roles of dispersal and demographic stochasticity in driving

74   species assembly in single communities), to test whether the area-heterogeneity tradeoff can generate a

75   unimodal relationship between species richness and habitat heterogeneity for meta-communities across

76   different landscapes. The model simulates the dynamics of a meta-community residing in a patchy

77   landscape that is characterized by a given level of environmental heterogeneity. Model results reflect

78   the joint operation of three mechanisms that generate species richness gradients along heterogeneity

79   gradients: [1] niche filtering, by assigning patches different environmental conditions, making them

80   suitable for only a subset of species in the meta-community; [2] interspecific competition for space,

81   according to species niche requirements and their relative abundances in the propagule pool; and [3]

82   area-heterogeneity tradeoffs. As patch sizes are finite, any increase in landscape heterogeneity results

83   on a decrease in the area available for each species, leading to smaller population sizes, and an increase

84   in the likelihood of stochastic extinctions.

85   Specifically, I hypothesized that: [1] meta-communities comprising species with higher

86   immigration rates are likely to produce the classical, positive richness–heterogeneity relationship, as

87   species are less likely to go extinct at the landscape scale; [2] low immigration rates preclude rescue

88   effects, making local population extinctions irreversible, and promoting a unimodal richness-

89   heterogeneity relationship at the landscape scale; [3] finally, increasing species' niche width would

90   promote more unimodal relationships, as population sizes in finite-area patches will become smaller,

91   increasing the rate of stochastic extinctions within patches.

92

93   **Methods**

94   *The model*

95   The model simulates the spatiotemporal dynamics of species in a meta-community located on a patchy

96   landscape. The landscape consists of J sites distributed among k patches, with the environment E in

97   each patch being unique. E is a one dimensional variable, which ranges from 1 to 500. Prior to each

98   model simulation, patches are assigned random locations across a two-dimensional landscape spanning

99   100-by-100 arbitrary distance units. Each patch consists of J_p sites having the same environment E, and

100   each site can host a single individual. The value of J_p in each patch is drawn at random from a

101   multinomial distribution with equal probabilities for all patches, while ensuring that the sum of J_p

102   values across the entire landscape equals exactly to J. Consequently, the number of sites can vary

103   slightly across patches.

104   At the first time step of a model simulation, a meta-community of S species and J individuals is

105   allocated across the landscape, with each patch initially having J_p individuals (possibly of multiple

106   species) selected at random from the entire species pool according to the suitability of species to

107   environmental conditions in patches. All species are demographically equivalent (have identical birth

108   and death rates), and birth rates are very high, so that each site receives an influx of propagules. At any

109   subsequent time-step, a proportion d of individuals die and their sites become available for colonization

110   by new individuals. New individuals comprise ones coming from other sites in the same patch, as well

111   as immigrants from other patches in the landscape. Individuals arriving in a patch compete for

112   establishment in available sites according to a lottery process (Chesson & Warner, 1981). The number

113   of establishing individuals from different species is determined according to their relative abundance in

114   the propagule pool coupled with the fit of the environment in the site to their niche requirements:

$$N_{i,t+1} = (1 - d_i)N_{i,t} + \left[\sum_j d_j N_{j,t} \right] \left[\frac{f_i N_{i,t}^*}{\sum_j f_j N_{j,t}^*} \right] \qquad [1]$$

115   where $N_{i,t}$ and $N_{i,t+1}$ are whole numbers (integers) that denote the total abundance of species i in the

116   patch in the current and previous time step, $N_{i,t}^*$ is the total number of propagules of species i

117   competing for establishment in available sites (including immigrants from the meta-community), d_i is

118   mortality rate of species i, the summation terms sums across all possible species, and f_i is a measure of

119   fitness, denoting the suitability of environmental conditions in the patch to the niche requirement of

120   species i (Tilman, 2004; Gravel et al., 2006; Bar-Massada, Kent & Carmel, 2014):

$$f_i = exp \left[-\frac{(e_i - E)^2}{2\sigma^2} \right] \qquad [2]$$

121   where e_i is then niche optimum of species i, E the environmental conditions in the patch, and σ a

122   measure of niche width. The left-hand term in equation [1] denotes the number of individuals that

123   survive to the next time step, the central term denotes the number of sites available for establishment of

124   new individuals, and the right-hand term denotes the proportion of available sites that will be colonized

125   by a given species. To ensure that N_i remains an integer, the right hand term in [1] is used to generate

126   probabilities of establishment for each species. The actual number of establishing individuals per

127   species is then drawn from a multinomial distribution based on the previously calculated probability of

128   establishment, and the number of available sites denoted by the middle term in [1].

129   The abundance of propagules of species i competing for establishment in a given patch ($N_{i,t}^*$ in

130   [1]) is calculated by multiplying the vector of species i abundance in all patches by the probability of

131   propagule arrival in the patch (from both local and neighboring patches).

$$N_{i,t}^* = \Sigma_{j=1}^{k} p_j N_{i,j,t} \qquad [3]$$

132

133   where p_j denotes the probability of propagule arrival in the focal patch from patch j, $N_{i,j,t}$ is the

134   abundance of species i in patch j at time t. Assuming the same dispersal capabilities for all species, in a

135   landscape with k patches the probability of propagules arriving into patch i from patch j ($p_{i,j}$) depends

136   on the distance d_{ij} between them, and is quantified using a negative-exponential dispersal kernel:

$$p_{i,j} = exp\square(-zd_{ij}) \qquad [4]$$

137   where z is the rate coefficient, which denotes the rate of decrease in arrival of propagules with

138   increasing distance (larger values correspond with decreased arrival of propagules from distant

139   patches). In this setting, the value of z serves as a measure of inter-patch immigration rates, with lower

140   values corresponding with increase immigration rates from other patches in the meta-community.

141

142   *Model simulations*

143   I developed, tested, and analyzed the model and its results in R (R Core Team, 2013; R scripts appear

144   in the supplementary material). A flowchart depicting the modelling process appears in Figure S1 in

145   the supplementary material. In each model run, I generated a landscape that consisted of 500 sites,

146   grouped into a randomly assigned number of patches between 2 and 500, with each patch having a

147   unique environmental condition E between 0 and 500. All patches had roughly the same size (barring

148   minor rounding effects), and therefore the diversity of environmental conditions increased together

149   with the number of patches, while the fractional cover of each environmental condition was close to

150   constant when the number of patches was very large. This yielded a complete range of compositional

151   heterogeneity levels (from two large patches with two E values to 500 small patches with 500 different

152   E values, denoting highly homogeneous and highly heterogeneous landscapes, respectively). Given

153   that the fractional cover of each environmental condition was close to (but not completely) constant at

154   maximum heterogeneity (cover type evenness, sensu Fahrig et al. 2011), I used Shannon's index of

155   landscape diversity (Nagendra, 2002) as the measure of compositional environmental heterogeneity

156   (but see Biswas & Wagner, 2012 for a discussion on measures of landscape heterogeneity in the meta-

157   community context). Shannon's index of landscape diversity is denoted by:

$$Shannon's\ diversity = \ -\sum_{E} \frac{J_E}{J} ln\left(\frac{J_E}{J}\right) \qquad [5]$$

158

159   where J_E is the number of sites in all patches of a given type (E value). In addition to Shannon's index,

160   I also quantified heterogeneity using patch richness (the number of unique E values).

161   At the beginning of each simulation, the meta-community consisted of 250 species. Each

162   species was randomly assigned a niche optimum value (E) from the list of E conditions that already

163   existed in patches (to prevent species from having a niche optimum that does not fit conditions in

164   available patches). Species had the same niche width parameter (σ). Death rate d was 0.25 and identical

165   for all species. In all cases, models were run for 1000 time steps, after ensuring that changes in overall

166 species richness were negligible at this stage by comparing them to the results of identical analyses

167 with 250 time steps (supplementary material Figure S2). Landscape scale species richness was

168 calculated at the end of each run.

169 During model simulations, I pre-determined niche width and immigration rates (z in equation 4)

170 to assess their effects on the relationship between meta-community species richness and landscape

171 scale environmental heterogeneity. I tested all possible combinations of $\sigma = 1, 5, 10$, and 50 (from very

172 narrow to wide niches, respectively). To alter immigration rates, I ran the simulations with four

173 different values of z: 0.2, 0.1, 0.05, and 0.025, which correspond with increasing rates of inter-patch

174 immigration, respectively (Figure 1).

175

176 **Results**

177 The type of the richness-heterogeneity relationship at the landscape scale was affected by complex

178 interactions between niche width and inter-patch immigration rates. In general, I found two types of

179 relationships, positive and unimodal. When species had narrow niches, the relationship between

180 richness and heterogeneity was positive regardless of inter-patch immigration rates, and this results

181 was consistent for both heterogeneity metrics (Figure 2A, E). In general, meta-communities with

182 higher immigration rates had lower species richness levels overall (Figure 2). Moreover, the difference

183 in overall species richness among meta-communities with different immigration rates increased with

184 landscape heterogeneity (Figure 2A, E). When heterogeneity was low, richness was very low and all

185 meta-communities had similar species richness levels. In contrast, when heterogeneity was maximal

186 (500 patches, each one having a unique environment E) species richness in meta-communities with low

187 inter-patch immigration rates had at least twice as many species compared to meta-communities with

188 high inter-patch immigration rates (Figure 2A).

189   As species niche width increased, the dominance of the positive richness–heterogeneity

190   relationship started to diminish, and unimodal richness-heterogeneity relationships emerged in meta-

191   communities with low to intermediate inter-patch immigration rates (Figure 2B-D, F-H). Meta-

192   communities with high immigration rates retained the positive relationship type, but their overall

193   species richness was very low compared to all other meta-communities. In general, meta-communities

194   with low immigration rates had higher levels of species richness compared to those with high

195   immigration rates. To conclude, unimodal richness – heterogeneity relationships at the landscape scale

196   were prominent in meta-communities comprising species with wider niches (more generalists) but low

197   to intermediate inter-patch immigration rates (or more fragmented landscapes). These results were

198   consistent between both heterogeneity metrics, but patch richness exhibited right-skewed unimodal

199   relationships, compared to the left-skewed unimodal relationships which emerged when Shannon's

200   diversity was the heterogeneity measure.

201

202   **Discussion**

203   The results of this analysis highlight the potential coupled roles of species niche characteristics and

204   dispersal capabilities in dictating the type of the richness–heterogeneity relationship for meta-

205   communities. Unimodal relationships emerge when locally extinct populations cannot re-emerge due to

206   the lack of rescue effects from neighboring patches. This results in the eventual extinction of species

207   from the entire meta-community, leading to a decrease in species richness. Species' niche width affects

208   the type of the relationship via controlling the number of species that can establish in a patch. In

209   heterogeneous landscapes where patches differ in environmental conditions, generalist species are able

210   to establish in more patches compared to specialists. Consequently, patch-scale species richness is

211   expected to increase and the area available for populations within patches becomes smaller, increasing

212   the likelihood of stochastic extinction. In patches of finite areas, therefore, mechanisms that initially

213 contribute to increased species richness (i.e., wide niches) are the very same drivers of local extinction,

214 as long as patch isolation prevents rescue effects and patches are relatively small.

215 The effect of niche width on the shape of the richness-heterogeneity relationship are in line with

216 the empirical findings of Carnicer et al. (2013), who re-analyzed the data in Allouche et al. (2012).

217 They reported that assemblages of species with narrow niches exhibited positive linear relationships

218 with habitat heterogeneity, as I found in this study (Figure 2A). Carnicer et al. (2008, 2013) suggest

219 that for species with narrow niches, the traditional niche filtering process is what drives species

220 richness gradients, leading to positive richness-heterogeneity relationships. In line with my other

221 theoretical findings (Figure 2B, C, and D), Carnicer et al. (2013) found that unimodal richness-

222 heterogeneity relationships emerge when species have wide niches. Notice, however, that Allouche et

223 al. (2013) criticized the approach of Carnicer et al. (2013) for not using analogous measures of

224 heterogeneity and niche breadth (i.e., they used habitat preference as a measure of niche width, and

225 elevation range as a measure of heterogeneity). My analysis is robust to this criticism as both niche

226 breadth and environmental heterogeneity were quantified based on the same environmental variable.

227 The finding that species richness is lower when immigration rates are high is in line with the

228 suggestion of Fahrig et al. (2011) (based on Amarasekare, 2008) that reduced inter-patch immigration

229 rates lead to de-coupling of patch dynamics, resulting in meta-community persistence via increased

230 species coexistence. Here, patch-scale species richness is the outcome of the interaction between

231 relative fitness differences among species (Chesson, 2000; Adler, HilleRisLambers & Levine, 2007),

232 which promote the dominance of the best-adapted species; and mass effects (Shmida & Wilson, 1985;

233 Kunin, 1998), which allow less-suitable species to persist since they are abundant in the propagule

234 pool. Presumably, there are two opposite scenarios that describe the effect of immigration rates on this

235 interaction. First, when immigration rates are low and a patch consists of a large population of less-

236 suitable species (versus a small population of a better-suited species), they are able to persist via

237 within-patch mass effects as long as propagules of the better-suited species cannot arrive in the patch.

238 In contrast, when immigration rates are high, a small population of a less-suitable species can persist in

239 a patch even as it is dominated by a superior species as long as a sufficient flux of its propagules keeps

240 arriving in the patch, promoting a rescue effect (Brown & Kodric-Brown, 1977; Leibold et al., 2004).

241 However, in my model all species had the same dispersal rates and demographic parameters, thus the

242 overall effect of unlimited immigration between patches is the arrival of the competitively-optimal

243 species to every suitable patch. In the absence of temporal variation in patch condition or species

244 demographical traits (i.e., birth and death rates), the eventual outcome of any lottery-type competition

245 between species is the dominance of the most-suitable species, with all other species driven to local

246 extinction (Chesson, 2000; Gravel, Guichard & Hochberg, 2011). Therefore, when there is no inter-

247 patch immigration overall species richness at the meta-community scale will converge towards the

248 number of patches types (i.e., patch richness), as long as for each patch type there is a species whose

249 niche requirements fit the conditions in the patch better than all other species.

250   I caution that model results should be interpreted in the context of the scale of the analysis,

251 coupled with richness of the regional species pool. The outcome of the area-heterogeneity tradeoff is

252 more likely to be detected in empirical studies when species are sampled in small (and area-limited)

253 habitat patches. As habitat patches become larger, so does the number of potential species they can

254 host without portraying the limiting factor of habitat area. Thus the type of the richness-heterogeneity

255 relationship is likely to be affected by the size of the regional species pool compared to the area

256 available in local patches and landscapes. The relationship will also be affected by the ability of

257 populations to persist in small patches. Communities comprising species that cannot persist in small

258 patches are likely to exhibit the unimodal relationship, while communities comprising species that can

259 are likely to portray positive richness-heterogeneity relationships.

260   In general, the results of this model (and the empirical findings of Bar-Massada and Wood,

261   2014) raise an intriguing question about the length of the heterogeneity gradient in actual landscapes:

262   to reach truly low levels of species richness that are caused by increased extinctions at very high

263   heterogeneity levels, how heterogeneous should a real landscape be? Obviously, the conditions used in

264   this study to represent the extreme end of the heterogeneity gradient (500 patches of different types,

265   each comprising a single site) are unrealistic. Yet the richness-heterogeneity relationship became

266   negative at much lower levels of heterogeneity than the theoretical maximum. Understanding its

267   drivers and predicting the tipping point of the richness-heterogeneity relationship in actual landscapes

268   is an intriguing question for future studies, which may offer useful insights for conservation planning.

269

270   **Conclusions**

271   The ongoing debate about the predominant type of the richness–heterogeneity relationship may be

272   overcome if we better understand the processes that drive this relationship for different taxa, habitats,

273   and spatial scales. This study, although based solely on a theoretical model, suggests that at broad

274   spatial scales the type of this relationship may be driven by an interaction between species niche

275   characteristics and their dispersal capabilities. Ultimately, if we were able to better understand the

276   mechanisms that drive the richness-heterogeneity relationship, including those caused by human

277   activity (Seiferling, Proulx & Wirth, 2014), it would add invaluable insight for conservation

278   management and planning, by informing about the level of heterogeneity that may support maximum

279   levels of biodiversity in a given landscape.

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346

Figure 1(on next page)

Effect of inter-patch distance on the probability of propagule arrival into a patch

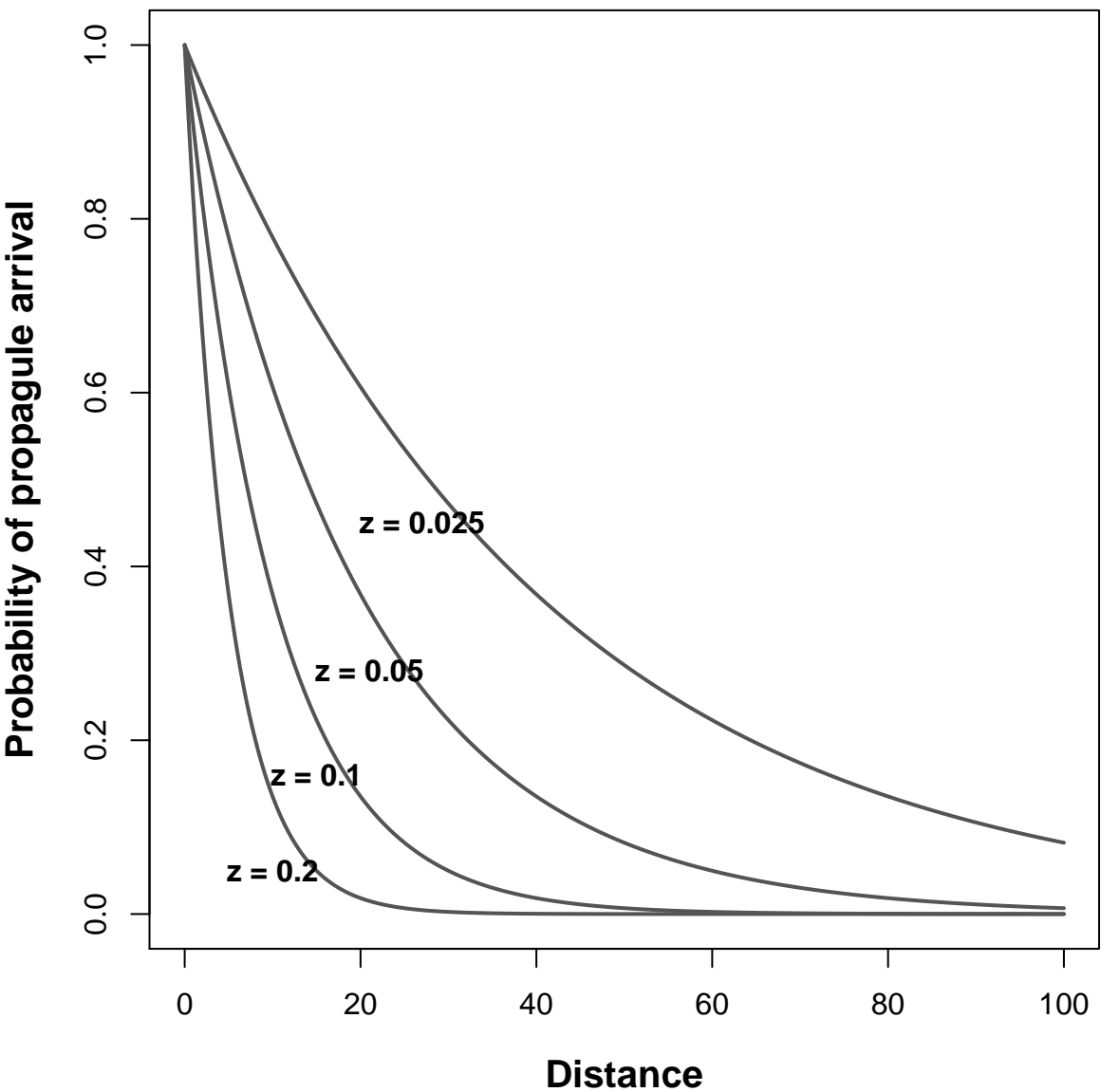Each curve is based on a different z parameter (Equation 4).

Figure 2 (on next page)

Relationships between species richness and landscape heterogeneity for modeled meta-communities

Panels correspond with different species niche widths (A, E - very narrow, B, F – narrow, C, G-intermediate, and D, H - wide). Curves denote inter-patch immigration rates, with circle colors depicting the value of the z parameter (0.2 – black, 0.1 – blue, 0.05 – green, and 0.025 – white, reflecting increasing levels of inter-patch immigration rates). The top row is based on Shannon's measure of heterogeneity, while the bottom row uses patch richness as the heterogeneity measure.