Resource competition and coexistence in heterogeneous metacommunities: Many-species coexistence is unlikely to be facilitated by spatial variation in resources

There is little debate of about the potential of environmental heterogeneity to facilitate species diversity. However, attempts to show the relationship between spatial heterogeneity and diversity empirically have given mixed results. One reason for this may be failure to consider how species respond to the factor in the environment that varies. Most models of the heterogeneity-diversity relationship assume heterogeneity in non-resource environmental factors. These models show the potential for spatial heterogeneity to promote many-species coexistence via mainly the spatial storage effect. Here, I present a model of species competition under spatial heterogeneity a resource factor. This model allows for the stable coexistence of only two species. Partitioning the model to quantify the contributions of variation-dependent coexistence mechanisms shows contributions from only one mechanism, growth-density covariance. More notably, it shows the lack of potential for any contribution from the spatial storage effect, the only mechanism that can facilitate stable many-species coexistence. This happens because the spatial storage effect measures the contribution of different species to specializing on different parts of the gradient of the heterogeneous factor. Under simple models of resource competition, in which all species grow best at high resource levels, such specialization is impossible. This analysis suggests that, in the absence of additional mechanisms, spatial heterogeneity in a single resource is unlikely to facilitate many-species coexistence and, more generally, that when evaluating the relationship between heterogeneity and diversity, a distinction should be made between resource and non-resource factors.

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Introduction

18   The potential of spatial heterogeneity to promote plant species coexistence is well

19   documented theoretically (reviewed in Amarasekare 2003), but empirical support documenting

20   the power and scope of its ability to support diverse natural communities is mixed. For example,

21   Lundholm (2009) reviewed 41 observational studies and 11 experimental studies that quantified

22   the relationship between plant species diversity and spatial environmental heterogeneity and

23   found that, while many studies documented positive relationships between the two, the cross-

24   study effect size was not significantly different from zero.

25   One potential reason for the uncertainty observed in the relationship between plant

26   species diversity and spatial environmental heterogeneity is that the strength of the effect

27   depends on what aspect of the environment is varying; specifically whether it is resource or non-

28   resource factors that vary over space. In experiments and observational studies where a non-

29   resource environmental factor (e.g. soil type, pH) varies, positive relationships between spatial

30   heterogeneity and species diversity are often observed (Reynolds et al. 1997, and many more,

31   reviewed in Lundholm 2009). However, there is surprisingly little empirical support for strong

32   positive relationships between the degree of spatial heterogeneity in a limiting resource and plant

33   species diversity at the local scale (Stevens and Carson 2002, Bakker et al. 2003, Reynolds et al.

34   2007, Lundholm 2009). For example, categorizing the factors in the studies reviewed by

35   Lundholm (2009) based upon whether they are resource or non-resources factors, reveals that a

36   significant relationship was found between species diversity and spatial heterogeneity for 71%

37   (49 of 69) of non-resource factors, but only 28.5% (2 of 7) of resource factors[1]. These results

38   suggest an important question: should we expect that resource variation should have the same

39   effect on diversity as non-resource variation?

40   To understand why resource heterogeneity may less effectively facilitate species diversity

41   requires insight into how these factors affect variation dependent species coexistence

42   mechanisms (Chesson 2000a). If plant species are competing for a common resource, then in a

43   uniform environment, the species that can maintain a positive growth rate at the lowest resource

44   concentration (lowest R^* Tilman 1982) is expected to drive all others to extinction. If spatial

45   environmental heterogeneity is to facilitate species coexistence, it must cause variation over

46   space in the identity of the species that has lowest R^* (Amarasekare 2003). For the case of non-

47   resource spatial heterogeneity, Chesson (2000a) has identified the three variation dependent

48   coexistence mechanisms that cause variation in competitive ability over space and thus facilitate

49   coexistence: 1) spatial relative non-linearitiy, which can occur if species have different non-

50   linear responses to a common competitive environment. 2) growth-density covariance, which

51   measures a species ability to concentrate its population in the areas that best promote growth (in

52   the absence of competition), and 3) spatial storage effect, which occurs when different species

53   experience best growth in different areas of the environment. Of these three mechanisms, the

54   storage effect is potentially the most important in that it is evoked by many kinds of trait

55   differences among species (making it potentially common) and has been shown to allow the

56   coexistence of many species (Chesson 1994).

57   While others have shown that spatial variation is resource supply rates can facilitate

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[1] Factors related to water (e.g. soil moisture) were left out of these tallies since they can often act as both resource and non-resource factors.

58   coexistence, a similar partitioning of the mechanisms involved has not been reported. One

59   potential reason for the lack of attention to the difference in resource and non-resource spatial

60   variation is that prominent early theoretical papers made assumptions that minimized the

61   differences between them. For example, Tilman and Pacala (1993) and Abrams (1988) published

62   models that assumed the environment consists of discrete patches containing multiple limiting

63   resources, and that there is no, or only limited dispersal between patches, or that dispersal occurs

64   at a time-scale much slower than that of local competitive exclusion. These assumptions

65   approximate a situation where the spatial scale of heterogeneity is much larger than the

66   characteristic dispersal distances of the species in the community (i.e. most dispersal events

67   occur within patches, few between patches). Under these conditions, spatial heterogeneity creates

68   opportunities for species coexistence if each species is the best competitor at some ratio of

69   resource supply rates represented in a subset of patches (i.e., R^* changes over space). This result

70   is similar to the general result obtained from models of non-resource, environmental

71   heterogeneity based coexistence (Chesson 2000a).

72   Recently however, researchers have begun studying models that assume that competitive

73   exclusion and dispersal occur over similar time-scales (Abrams and Wilson 2004, Golubski et al.

74   2008). This assumption approximates the case where the spatial scale of resource heterogeneity

75   is shorter than typical dispersal distances, and is probably more typical of the systems measured

76   in field studies. These models predict that a poor resource competitor may coexist with a better

77   resource competitor, if the better resource competitor experiences more inter-patch dispersal

78   (Abrams and Wilson 2004). Coexistence in this case is possible because dispersal results in a net

79   loss of individuals from the richest patches which in turn reduces the population's ability to

80   depress resource concentrations in those patches as low as it would in the absence of dispersal;

81 allowing persistence of a competitor that experiences less inter-patch dispersal but has a higher

82 R* (in a uniform environment). However, the identity and relative strength of the coexistence

83 mechanisms involved are yet to be quantified.

84   The assumption that competition and dispersal occur simultaneously increases the

85 complexity of the models, leading most researchers to model systems consisting of only a small

86 number of patches (Abrams and Wilson 2004, Golubski et al. 2008). As a result, these models

87 lack the generality that would allow them to be scaled up to quantify metacommunity-level

88 phenomena such as variation-dependent coexistence mechanisms (i.e. the storage-effect, relative

89 nonlinearity, and growth-density covariance, Chesson 2000a,b). In this article, I derive a simple

90 metacommunity model of plant competition for a single, spatially variable resource. I derive

91 approximate analytical relationships for regional species coexistence from which

92 metacommunity-scale population growth rates may be partitioned into the variation-dependent

93 and variation-independent coexistence mechanisms. These mechanisms are used to argue why

94 spatial variation for resources is less effective than non-resource spatial variation in facilitating

95 coexistence of many species.

96   Model

97   The goal of this model is to answer the questions "how many species can coexist via

98 spatial heterogeneity in resource supply and by what means?" To answer these questions, I

99 define a simple model of plants growing in a spatially heterogeneous environment, and then use

100 the framework developed by Chesson (1994) to partition the regional growth rates implied by the

101 model into contributions from variation-independent and variation-dependent mechanisms.

102   Finally, I use a sequential invasion approach with the mutual invasion criterion to determine how

103   many species each mechanism allows to coexist at equilibrium.

104   In a set of discrete patches, $x=\{1,2,3,..,N\}$, let $n_{jx}(t)$ be the density of species j in patch x

105   at time t, and let $R_x(t)$ be the resource concentration in patch x. n_{jx} decreases over time at the per

106   capita mortality rate m_j, and increases by reproduction in the current patch, which occurs at the

107   resource-dependent per-capita growth rate $b_j R_x$, plus the contributions of dispersal into patch x

108   from other patches. Let p_j be the proportion of seeds produced by adults of species j in any patch

109   that remain in that patch and assume that the $1-p_j$ seeds that leave natal patches are evenly

110   redistributed among all patches (including the natal patch). Resources are increased in patches at

111   a constant rate S_x and are reduced through the establishment of plants. The resource model is

112   kept intentionally simple to allow analytical treatment. The inclusion of additional loss terms for

113   resources, for example to adult plant maintenance or leaching do not affect the conclusions

114   (Supplemental Appendix S2). The dynamics of this coupled system are described by,

115
$$\frac{dn_{jx}}{dt} = -m_j n_{jx} + b_j R_x \left(p_j n_{jx} + \left(1-p_j\right)\left\langle n_j \right\rangle_x \right)$$
$$\frac{dR_x}{dt} = S_x - \sum_j Q_j b_j R_x \left(p_j n_{jx} + \left(1-p_j\right)\left\langle n_j \right\rangle_x \right)$$
                                   (1a-b)

116   In eqn 1, Q_j is the amount of resource required for establishment; S_x is the patch-specific

117   resource supply rate and $\left\langle \cdot \right\rangle_x$ indicates a mean taken over patches. For a single species, this

118   system has one stable equilibrium point per patch at,

119
$$n_{jx}^* = \frac{S_x}{Q_j m_j}, \quad R_{jx}^{*m} = \frac{m_j S_x}{b_j \left(p_j S_x + \left(1-p_j\right)\left\langle S \right\rangle_x \right)},$$
                                   (2a-b)

120   where the m in R_{jx}^{*m} is used to differentiate this equilibrium concentration of resource from the

121   traditional R^*, that occurs in an uncoupled or homogenous system and is independent of

122   resource supply rate.

123   Eqn.2 shows that, in this model, dispersal has no effect on equilibrium density, n_{jx}^*.

124   However, the equilibrium resource concentration, R_{jx}^{*m} does depend on the amount of dispersal

125   between patches and the resource supply rate in patch x relative to the mean supply rate in the

126   metacommunity. Specifically, if dispersal between patches is high, species j leaves a higher

127   concentration of resources behind in patches with above average supply rates and a lower

128   concentration in patches with below average supply rates than it would in a homogenous

129   environment. This occurs because patches with high supply rates are net exporters of recruits and

130   patches with low supply rates are net importers of potential recruits. The increased concentration

131   of available resources in high supply rate patches allows the invasion and possible coexistence of

132   a species that has a higher R^*, but experiences less inter-patch dispersal (Abrams and Wilson

133   2004)(Fig. 1).

134   *Derivation of variation dependent mechanisms.*

135   One way to measure potential for coexistence is with the mutual invasion criterion. This

136   criterion states that a set of species can coexist with one another if each can invade the

137   equilibrium assemblage of the other species in the set. In practice, one calculates growth rate of

138   a species with inter-specific competition set at the value determined by the competitors at

139   equilibrium and intra-specific competition set to zero. This is called the low-density growth rate

140   of the species. In a spatial context, we are interested in coexistence at the larger scale of the set

141 of all patches, so we calculate what is called the low-density metacommunity scale (or regional)

142 growth rate.

143  Chesson (2000a) has shown how a low density metacommunity-scale growth rate can be

144 calculated an written in terms of variation dependent coexistence mechanisms. First, the local

145 growth rate is decomposed into terms quantifying the direct effects of environmental variation

146 (E), variation in competition (C) and their interaction

147
$$r_{jx} = \mathscr{E}_x - \mathscr{C}_{jx} + \gamma_j \mathscr{E}_x \mathscr{C}_{jx},\qquad(3)$$

148 where $\mathscr{E}_x = G_j\left(E_x, C_j^*\right), \mathscr{C}_{jx} = -G\left(E^*, C\right), \gamma_j = \dfrac{\partial G_j}{\partial \mathscr{E} \partial \mathscr{C}_j}.$

149 The quantities E and C are the population parameters affected by environmental variation and the

150 effect of competition (which is also affected by environmental variation) respectively, G is the

151 growth rate of species j as a function of E and C and the (*) indicates the equilibrium level of the

152 value.

153 The metacommunity-scale growth rate of species $j, \widetilde{r}_j$, in a spatially heterogeneous environment

154 is found by taking the mean of r_{jx} over all individuals in the metapopulation, $\widetilde{r}_j = \dfrac{1}{\sum\limits_x n_{jx}} \sum\limits_x r_{jx} n_{jx}.$

155 It can be written in terms of a spatial mean by defining relative local density as $\nu_{jx} = \dfrac{n_{jx}}{\langle n_j \rangle_x}.$

156 Substituting ν_{jx} into $\widetilde{r}_j$ gives $\widetilde{r}_j = \langle r_j \nu_j \rangle_x$, which can be rewritten as $\widetilde{r}_j = \langle r_j \rangle_x + \mathrm{cov}\left(r_j, \nu_j\right)_x,$

157 where $\mathrm{cov}(.)_x$ indicates a spatial covariance (Chesson 2000a). Plugging eqn 3 into this result

158 gives,

159
$$\tilde{r_j} = \left\langle \mathscr{E} \right\rangle_x - \left\langle \mathscr{C}_j \right\rangle_x + \gamma_j \left\langle \mathscr{E}\mathscr{C}_j \right\rangle_x + \mathrm{cov}(r_j, v_j)_x. \tag{4}$$

160   To argue that any of the terms in eqn 4 contribute to coexistence, the difference between

161   invader's and residents' values must be positive. Because, by definition the metacommunity

162   growth rate of the resident is zero, it can be subtracted from the right side of eqn 4 without

163   changing the left side. Thus, the metacommunity growth rate of the invader, denoted by subscript

164   i, can be rewritten in terms of contributions from multiple coexistence mechanisms by

165   subtracting the metacommunity growth rate of the residents, denoted by subscript r . Subtracting

166   the metacommunity growth rate of the residents gives,

167
$$\tilde{r_i} = \Delta E - \Delta C + \Delta I + \Delta \kappa \tag{5}$$

168   where

169
$$
\begin{aligned}
\Delta E &= \left\langle \mathscr{E}_i \right\rangle_x - q_{ir} \left\langle \mathscr{E}_r \right\rangle_x \\
\Delta C &= \left\langle \mathscr{C}_i \right\rangle_x - q_{ir} \left\langle \mathscr{C}_r \right\rangle_x \\
\Delta I &= \gamma_i \left\langle \mathscr{E}_r \mathscr{C}_i \right\rangle_x - q_{ir}\gamma_r \left\langle \mathscr{E}_r \mathscr{C}_r \right\rangle_x \\
\Delta \kappa &= \mathrm{cov}(r_i, v_i)_x - q_{ir}\, \mathrm{cov}(r_r, v_r)_x
\end{aligned}
\tag{6}
$$

170   and the scaling factor is $q_{ir} = \dfrac{\partial \mathscr{C}_i}{\partial \mathscr{C}_r}$ is chosen to make the resulting expression more biologically

171   interpretable. For example, in this case, it allows ΔC to be expressed as a difference in the R^*

172   values of the species.

173   The quantity ΔE measures differences in the average environment experienced by the

174   invader and resident. The quantity ΔC can contain both the fluctuation independent difference of

175   the average competition experienced by residents and invaders and a measure of the effect of

176   variation in competition. The combination $\Delta E - \Delta C$ is often rewritten to separate it into variation

177   dependent ΔN and variation independent $\tilde{r_i}\,'$ parts, where $\tilde{r_i}\,' = \Delta E - \mathscr{C}_i\,*$ and $\Delta N = \Delta C - \mathscr{C}_i\,*$. The

178   quantity $\mathscr{C}_i\,*$ is the value of competition the invader experiences as a consequence of the resource

179   equilibrium the residents create (Chesson 2000a). The quantity $\tilde{r_i}\,'$ the growth rate the invader

180   would experience in the absence of variation. The quantity ΔN has been called relative-

181   nonlinearity and can facilitate coexistence if species exhibit different non-linear responses in

182   growth rate to variations in competition, specifically if the species with the larger non-linearity in

183   response experiences lower variance in competition. For most models that would describe the

184   growth of plants, this mechanism can only facilitate coexistence of two species (Chesson 1994).

185   The quantity ΔI is the storage effect (Chesson 1994) it measures the covariance between

186   the direct effect of environmental variation and the effect of competition on the growth rate of

187   the invader. This mechanism is potentially very powerful and can facilitate coexistence on many

188   species. An example of many species coexistence via spatial storage effect would where there

189   are many patches and each species is the best competitor in at least one patch (Sears and Chesson

190   2007).

191   The final mechanism, $\Delta \kappa$, is growth-density covariance. It measures the ability of the

192   invader to concentrate its population into patches that are best at supporting growth. The species

193   that is better able to do this will experience an overall boost to metacommunity scale growth rate.

194   This mechanism is most directly related to dispersal.

195   *Derivation of variation dependent mechanisms for spatial resource heterogeneity*

196   Following Chesson (2000), the model (eqns. 1) can be written in terms of variation in

197   environment, E_x (the life history character that varies in space) and competition, C_x. In the case

198   of the present model, where only the supply rate of resources varies over space, environmental

199   variation does not directly affect individuals, it only affects competition; thus $E_x = 0$ and

200    $C_x = -R_x$. Making these substitutions, the model in eqns. 1 can be rewritten as,

$$\frac{dn_{jx}}{dt} = -m_j n_{jx} - b_j C_x \left(p_j n_{jx} + \left(1 - p_j\right)\langle n_j \rangle_x \right)$$
$$\frac{dC_x}{dt} = -S_x + \sum_j Q_j b_j C_x \left(p_j n_{jx} + \left(1 - p_j\right)\langle n_j \rangle_x \right)$$

(7)

202

203   The local growth rate is then, $r_{jx} = -m_j - b_j p_j C_x - \left(1 - p_j\right) b_j \langle C \rangle_x$. Notice that in this case, due to

204   dispersal between patches $r_{jx} \neq \frac{1}{n_{jx}} \frac{dn_{jx}}{dt}$. Instead, r_{jx} is derived by considering the fitness of an

205   individual in patch x (Miller and Chesson 2009). Taking the mean over space, as described in the

206   previous section gives the metacommunity-scale growth rate, $\tilde{r}_i = -\langle \mathscr{C}_i \rangle_x + \mathrm{cov}(r_i, v_i)_x$, where

207    $\langle \mathscr{C}_i \rangle_x = m_i + b_i \langle C \rangle_x$. Assuming a single resident, denoted by subscript r, allows calculation of the

208   various coexistence mechanisms for the case of two species. This is helpful to determining the

209   presence or absence of the various mechanisms implied by this model. Plugging into eqn 6 and

210   scaling by b_i to put the results in the natural time scale of generations instead of an absolute time

211   scale (e.g. months or years) (Chesson 2008) gives (for details see Supplemental Appendix S1),

$$\frac{\Delta E}{b_i} = 0$$

$$\frac{\Delta C}{b_i} = -\frac{m_i}{b_i} + \frac{m_r}{b_r}$$

212

$$\frac{\Delta I}{b_i} = 0$$

(7)

$$\frac{\Delta \kappa}{b_i} \approx \frac{m_r}{b_r}(1 - p_r)^2 \left\langle s^2 \right\rangle_x \left(\frac{p_i}{1 - p_i} - \frac{p_r}{1 - p_r} \right).$$

213   Rewriting $\Delta E - \Delta C$ terms of $\tilde{r}_i{}'$ and ΔN gives,

214

$$\frac{\tilde{r}_i{}'}{b_i} = -R_i^* + R_r^*,$$

(8)

$$\frac{\Delta \kappa}{b_i} \approx \mathrm{var}(s)_x (1 - p_r)^2 R_r^* \left(\frac{p_i}{1 - p_i} - \frac{p_r}{1 - p_r} \right).$$

215   where $\dfrac{m_j}{b_j} = R_j^*$. Notice in this case $\Delta N = 0$ since ΔC contains no variation dependent terms.

216   Biologically, $\tilde{r}_i{}'/ b_i$ is a comparison of abilities to reduce resources in a homogenous

217   environment. Specifically, eqn 9 states that invaders are benefited by the ability to reduce

218   resources to a lower level than the resident in a homogenous environment (Tilman 1982). It also

219   suggests that in the absence of spatial heterogeneity (*var (s)ₓ* = 0) coexistence is impossible

220   because only the species with the lowest *R** would have a positive growth rate as an invader.

221   In addition, eqn. 9 shows that only differences in dispersal can allow coexistence in this

222   model. The storage effect (ΔI) and relative nonlinearity (ΔN) have no effect on invader's

223   metacommunity-scale growth rate and thus do not contribute to coexistence. The effect of

224   growth-density covariance ($\Delta \kappa$) on the growth rate of the invader depends upon R_r^* times the

225   odds of seeds staying in natal patches relative to the resident's. Invaders whose seeds are less

226   widely dispersed than those of the resident species are benefited by growth-density covariance.

227   Thus, this model allows coexistence of species if there is a tradeoff competitive ability ($R*$) and

228   dispersal fraction (p). In addition, coexistence is facilitated by only one variation-dependent

229   mechanism, grow-density covariance.

230   *How many species does growth-density covariance support?*

231   I used a sequential invasion approach based on adaptive dynamics (Geritz et al. 1998) to

232   determine how many species can coexist based on this model. This approach attempts to find the

233   trait values for invaders that allow invasion in a given context. In this case, at each step, I find

234   the values for the trait p_i that allows an invader to have a positive meta-community growth rate

235   (often written as $S(p_i)$ in the adaptive dynamics literature) in an assemblage of n resident species,

236   i.e., $S_{\{p_m\}}(p_i) > 0$. If this species can 1) coexist with the current resident strategies and resist

237   exclusion by similar strategies (i.e. similar values p), then it is added the list of residents. Species

238   are added one at a time until there is no value of p_i that leads to positive metacommunity-scale

239   growth rate. Because the approximated expression for growth-density covariance from eqn. 9

240   assumes small variation in supply rate and has singularities at $p_i=1$ and $p_r=1$, I use simulation of

241   eqn 1 to calculate invasion growth rate. Numerical simulations of the residents were run until

242   they reached a steady state. The resulting value of resource concentration was plugged into the

243   matrix that described each patches' contribution to an invader's low-density growth-rate in patch

244   *x*. The dominant eigenvalue of this matrix is an estimate of the meta-community scale low-

245   density growth rate of the invader. For the simulations, I assumed Log-normal distributed supply

246   rates and trade-offs between R_j^* and p_j of the form $R_j^* - p_j^{\tau} = Z$ where Z is an arbitrary constant

247   and τ affects the shape of the trade-off. The following example considers a linear tradeoff,

248   between competitive ability and dispersal i.e., $\tau = 1$.

249   Figure 2 shows a contour plot for the invasibility of strategy p_i in the presence of resident p_r. The

250   black region of Figure 2 represent negative invader growth rates (i.e. the invasion is

251   unsuccessful), the white regions shows areas of positive growth rates. It shows that any resident

252   strategy $p_r < 1$ can be invaded by $p_i = 1$. However, the strategy $p_r = 1$ is also able to be invaded

253   by any $p_i < 1$. Thus, I set $p_{r1}=1$ and looked for values of p_{r2} that could coexist with p_{r1} and were

254   not excluded by other similar strategies. Figure 3 shows that given $p_{r1}=1$, any resident strategy

255     $p_{r2}>0$ can be invaded by $p_i<p_{r2}$. Thus, since $p_{r2}=0$ can also coexist with $p_{r1}=1$, it was added to the

256   resident list. Figure 3 also suggests that there is no third strategy p_i that can coexist with $p_{r1}=1$

257   and $p_{r2}=0$, since $S_{\{p_{r1=1},p_{r2=0}\}}\left(p_i\right) < 0$ for all possible values of p_i (i.e. a vertical line drawn from

258     $p_{r2}=0$ passes only through the black region of the graph). This suggests that in this model, a

259   tradeoff between competitive ability R_j^* and dispersal p_j, allows coexistence of only two species.

260   To assure these results were robust, I simulated systems of simultaneous competition among

261   many species from along the trade-off manifold (Supplemental Appendix S2).   Those

262   simulations also show an observed maximum of two coexisting species for nonlinear tradeoffs

263   with $\tau < 1$; additional loss terms in the resource equation, and saturating growth responses. For

264   non-linear tradeoffs with $\tau > 1$ no coexistence was possible.

265   Discussion

266   This analysis shows that spatial variation in resources allows for fewer coexistence

267   mechanisms and lower potential species diversity compared to spatial variation in non-resource

268   factors. Although spatial resource variation promotes coexistence if there is a tradeoff between

269 competitive ability and the ability to retain offspring in good patches, this tradeoff allows the

270 coexistence of only a 2 species.

271   Coexistence under spatial resource variation lacks contributions from the spatial storage

272 effect, a powerful mechanism that allows the coexistence of many species. The storage effect is

273 absent because all species grow best in the same patches (high resource patches). As a result,

274 environmental responses and competition are perfectly and equally correlated for all species,

275 allowing no advantages in good patches when a species is rare. In other words, the feedback that

276 organisms have on the resource, make it impossible for any to specialize on a particular supply

277 rate along a gradient.

278   Although the mechanism of resource competition analyzed in this model is simplified,

279 the qualitative results are quite general. For example, the relationship of R^* to the

280 metacommunity-scale coexistence mechanisms described by scale transition theory does not

281 depend on the simplified model of local resource competition presented in eqns 1. If the

282 establishment rate of seeds is a saturating function (e.g. Monod functions with equal half

283 saturation constants) of the amount of resources present, then $\widetilde{r}\,'$ is still a comparison of the

284 (more complicated) R^*s of the invader and resident, and the relative importance of the variation

285 dependent mechanism is the same. The situation is more complex if species growth rates are

286 different non-linear functions of resource concentration, but, even in this case, spatial variation in

287 one only facilitate 2 species coexistence (Supplemental Appendix S2).

288   In this model, competition was for a single resource. Increasing the number of limiting

289 resources can increase the number of species that can coexist at equilibrium. Golubski et al.

290 (2008) found that a maximum of four species could coexist in a system with two resources,

291   heterogeneous supply rates and species that were capable of integrating growth across patches.

292   However, this was only possible with precise arrangement of species trait parameters, and if

293   resource supply rates of the resources were strongly negatively correlated across patches. I

294   presume that, in this case, adding resource factors does not increase the number of mechanisms;

295   the existing mechanism, growth-density covariance, simple works independently for each

296   resource; although this claim should be explored with further analysis.

297   This analysis suggests that spatial resource heterogeneity is not capable of supporting the

298   robust stable coexistence of many plants species that is observed in many natural systems. The

299   reason for this is that the feedback species have on resources concentrations prevents

300   specialization of different species at different supply rates. It is this kind of specialization of

301   different species along different points of a "niche" axis, which is measured by the spatial

302   storage effect, that allows the robust coexistence of many species. The results of this analysis are

303   consistent with the patterns found in the empirical literature, which finds much more support for

304   the relationship between species diversity and nonresource spatial heterogeneity than resource

305   heterogeneity. Taken together, this work suggests that the consideration whether a factor is a

306   resource or not is crucial for those attempting to understand real patterns in species diversity or

307   those interested in managing a habitat for increased species diversity.

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312   References

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Figure 1

R* as a function of dispersal

Concentration of resources left behind at equilibrium (R^{*m}_{jx} *) along a spatial gradient of resource supply rates. The R^{*m}_{jx} of a species depends on the supply rate of the patch and the* amount of interpatch dispersal (Black lines: $R*$ = 0.4, p = 1, solid; p = 0.66, dashed; p = 0.33, dash-dot; p = 0, dotted). As a result, a species with a higher $R*$ may invade the metacommunity if it experiences less interpatch dispersal (Grey line: $R*$ = 0.5; p = 0.9) because it can have a R^{*m}_{jx} lower [i] in patches with the highest supply rates.
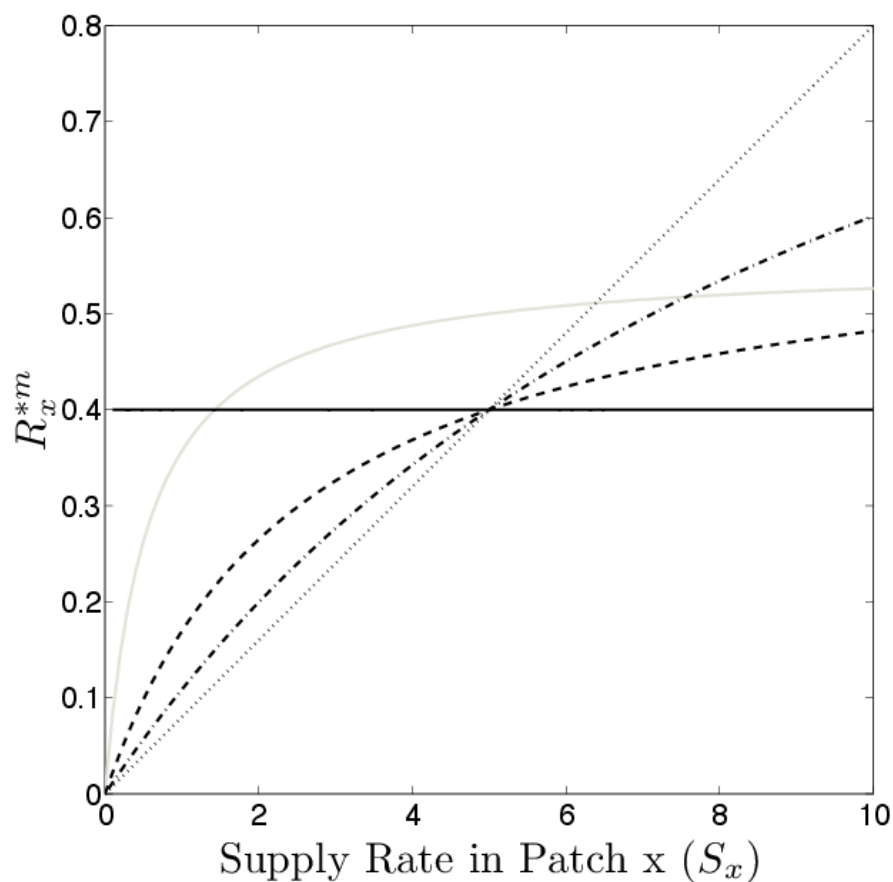
Figure 2

Invasion analysis

Contour plot of the growth rate of an invader with dispersal p_i as a function of resident dispersal p_r, assuming a tradeoff between competitive ability (R^*) and dispersal (p). Black regions show areas of negative invader growth rate; white regions, positive. The graph shows that $p_i=1$ can invade a meta-community with a resident with $p_r<1$. It also shows that $p_r=1$ can be invaded by any $p_i<1$, suggesting coexistence with this strategy is possible. Parameter values for this graph are $R_j^*=1-p_j$ in a system of 20 patches and S_x~LogNormal(1,1.5).
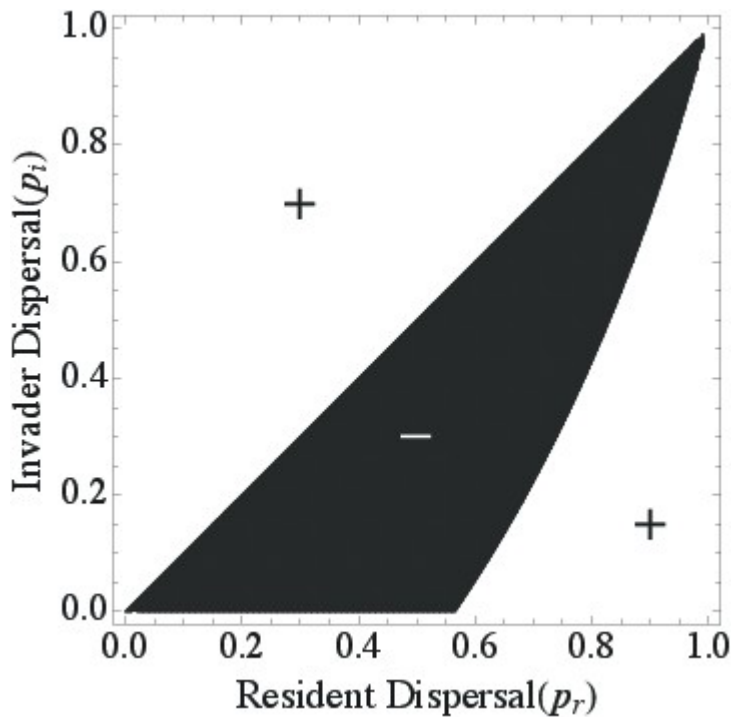
Figure 3

2 Species Invasion Analysis

Contour plot of the growth rate of an invader with dispersal p_i as a function of resident dispersal $p_{r1}=1$, p_{r2}, assuming a tradeoff between competitive ability (R^*) and dispersal (p). Black regions show areas of negative invader growth rate; white regions, positive. The graph shows that given $p_{r1}=1$, $p_{r2}>0$ can be invaded by and excluded by $p_i r$.. Thus, it shows that given $p_{r1}=1$ and $p_{r2}=0$, no third strategy p_i has a positive growth rate; confirming that stable coexistence of only two species is possible. Parameter values for this graph are $R_j^{\;*}=1-p_j$ in a system of 20 patches and S_x~LogNormal(1,1.5).

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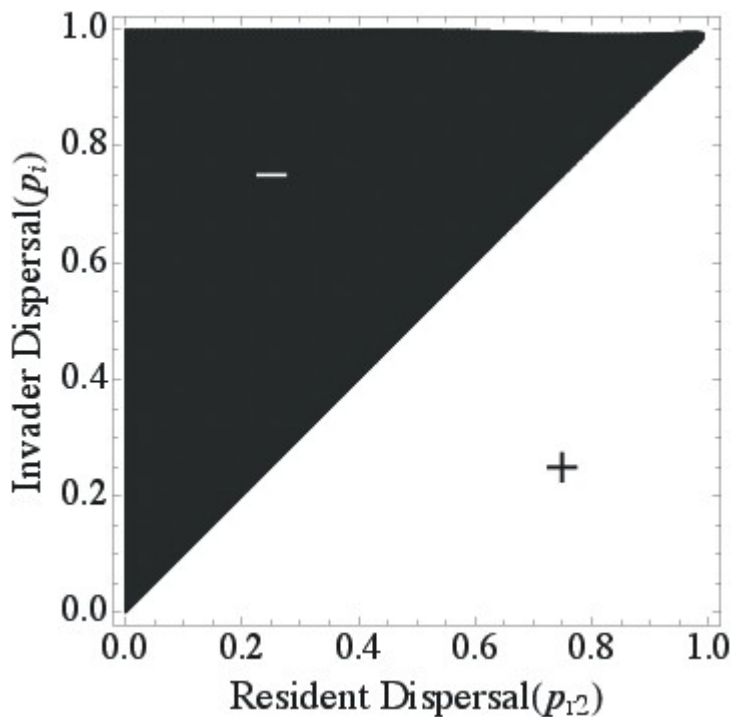
16   Equation Chapter 1 Section 1

17   Introduction

18   The potential of spatial heterogeneity to promote plant species coexistence is well

19   documented theoretically (reviewed in Amarasekare 2003), but empirical support documenting

20   the power and scope of its ability to support diverse natural communities is mixed. For example,

21   Lundholm (2009) reviewed 41 observational studies and 11 experimental studies that quantified

22   the relationship between plant species diversity and spatial environmental heterogeneity and

23   found that, while many studies documented positive relationships between the two, the

24   cross-study effect size was not significantly different from zero.

25   One potential reason for the uncertainty observed in the relationship between plant

26   species diversity and spatial environmental heterogeneity is that the strength of the effect

27   depends on what aspect of the environment is varying; specifically whether it is resource or

28   non-resource factors that vary over space. In experiments and observational studies where a

29   non-resource environmental factor (e.g. soil type, pH) varies, positive relationships between

30   spatial heterogeneity and species diversity are often observed (Reynolds et al. 1997, and many

31   more, reviewed in Lundholm 2009). However, there is surprisingly little empirical support for

32   strong positive relationships between the degree of spatial heterogeneity in a limiting resource

33   and plant species diversity at the local scale (Stevens and Carson 2002, Bakker et al. 2003,

34   Reynolds et al. 2007, Lundholm 2009). For example, categorizing the factors in the studies

35   reviewed by Lundholm (2009) based upon whether they are resource or non-resources factors,

36   reveals that a significant relationship was found between species diversity and spatial

37   heterogeneity for 71% (49 of 69) of non-resource factors, but only 28.5% (2 of 7) of resource

38 factors[1]. These results suggest an important question: should we expect that resource variation

39 should have the same effect on diversity as non-resource variation?

40   To understand why resource heterogeneity may less effectively facilitate species diversity

41 requires insight into how these factors affect variation dependent species coexistence

42 mechanisms (Chesson 2000a). If plant species are competing for a common resource, then in a

43 uniform environment, the species that can maintain a positive growth rate at the lowest resource

44 concentration (lowest R^* Tilman 1982) is expected to drive all others to extinction. If spatial

45 environmental heterogeneity is to facilitate species coexistence, it must cause variation over

46 space in the identity of the species that has lowest R^* (Amarasekare 2003). For the case of

47 non-resource spatial heterogeneity, Chesson (2000a) has identified the three variation dependent

48 coexistence mechanisms that cause variation in competitive ability over space and thus facilitate

49 coexistence: 1) spatial relative non-linearitiy, which can occur if species have different non-linear

50 responses to a common competitive environment. 2) growth-density covariance, which measures

51 a species ability to concentrate its population in the areas that best promote growth (in the

52 absence of competition), and 3) spatial storage effect, which occurs when different species

53 experience best growth in different areas of the environment. Of these three mechanisms, the

54 storage effect is potentially the most important in that it is evoked by many kinds of trait

55 differences among species (making it potentially common) and has been shown to allow the

56 coexistence of many species (Chesson 1994).

57   While others have shown that spatial variation is resource supply rates can facilitate

58 coexistence, a similar partitioning of the mechanisms involved has not been reported. One

---

1 1 Factors related to water (e.g. soil moisture) were left out of these tallies since they can often act
2 as both resource and non-resource factors.

59   potential reason for the lack of attention to the difference in resource and non-resource spatial

60   variation is that prominent early theoretical papers made assumptions that minimized the

61   differences between them. For example, Tilman and Pacala (1993) and Abrams (1988) published

62   models that assumed the environment consists of discrete patches containing multiple limiting

63   resources, and that there is no, or only limited dispersal between patches, or that dispersal occurs

64   at a time-scale much slower than that of local competitive exclusion. These assumptions

65   approximate a situation where the spatial scale of heterogeneity is much larger than the

66   characteristic dispersal distances of the species in the community (i.e. most dispersal events

67   occur within patches, few between patches). Under these conditions, spatial heterogeneity creates

68   opportunities for species coexistence if each species is the best competitor at some ratio of

69   resource supply rates represented in a subset of patches (i.e., R^* changes over space). This result

70   is similar to the general result obtained from models of non-resource, environmental

71   heterogeneity based coexistence (Chesson 2000a).

72   Recently however, researchers have begun studying models that assume that competitive

73   exclusion and dispersal occur over similar time-scales (Abrams and Wilson 2004, Golubski et al.

74   2008). This assumption approximates the case where the spatial scale of resource heterogeneity

75   is shorter than typical dispersal distances, and is probably more typical of the systems measured

76   in field studies. These models predict that a poor resource competitor may coexist with a better

77   resource competitor, if the better resource competitor experiences more inter-patch dispersal

78   (Abrams and Wilson 2004). Coexistence in this case is possible because dispersal results in a net

79   loss of individuals from the richest patches which in turn reduces the population's ability to

80   depress resource concentrations in those patches as low as it would in the absence of dispersal;

81   allowing persistence of a competitor that experiences less inter-patch dispersal but has a higher

82   R* (in a uniform environment). However, the identity and relative strength of the coexistence

83   mechanisms involved are yet to be quantified.

84   The assumption that competition and dispersal occur simultaneously increases the

85   complexity of the models, leading most researchers to model systems consisting of only a small

86   number of patches (Abrams and Wilson 2004, Golubski et al. 2008). As a result, these models

87   lack the generality that would allow them to be scaled up to quantify metacommunity-level

88   phenomena such as variation-dependent coexistence mechanisms (i.e. the storage-effect, relative

89   nonlinearity, and growth-density covariance, Chesson 2000a,b). In this article, I derive a simple

90   metacommunity model of plant competition for a single, spatially variable resource. I derive

91   approximate analytical relationships for regional species coexistence from which

92   metacommunity-scale population growth rates may be partitioned into the variation-dependent

93   and variation-independent coexistence mechanisms. These mechanisms are used to argue why

94   spatial variation for resources is less effective than non-resource spatial variation in facilitating

95   coexistence of many species.

96   Model

97   The goal of this model is to answer the questions "how many species can coexist via

98   spatial heterogeneity in resource supply and by what means?" To answer these questions, I define

99   a simple model of plants growing in a spatially heterogeneous environment, and then use the

100   framework developed by Chesson (1994) to partition the regional growth rates implied by the

101   model into contributions from variation-independent and variation-dependent mechanisms.

102   Finally, I use a sequential invasion approach with the mutual invasion criterion to determine how

103   many species each mechanism allows to coexist at equilibrium.

104   In a set of discrete patches, $x=\{1,2,3,..,N\}$, let $n_{jx}(t)$ be the density of species j in patch x at

105   time t, and let $R_x(t)$ be the resource concentration in patch x. n_{jx} decreases over time at the per

106   capita mortality rate m_j, and increases by reproduction in the current patch, which occurs at the

107   resource-dependent per-capita growth rate b_jR_x, plus the contributions of dispersal into patch x

108   from other patches. Let p_j be the proportion of seeds produced by adults of species j in any patch

109   that remain in that patch and assume that the $1-p_j$ seeds that leave natal patches are evenly

110   redistributed among all patches (including the natal patch). Resources are increased in patches at

111   a constant rate S_x and are reduced through the establishment of plants. The resource model is kept

112   intentionally simple to allow analytical treatment. The inclusion of additional loss terms for

113   resources, for example to adult plant maintenance or leaching do not affect the conclusions

114   (Supplemental Appendix S2). The dynamics of this coupled system are described by,

$$\frac{dn_{jx}}{dt} = -m_j n_{jx} + b_j R_x \left(p_j n_{jx} + \left(1-p_j\right)\left\langle n_j \right\rangle_x \right)$$
$$\frac{dR_x}{dt} = S_x - \sum_j Q_j b_j R_x \left(p_j n_{jx} + \left(1-p_j\right)\left\langle n_j \right\rangle_x \right)$$

115   .* MERGEFORMAT (a-b)

116   In eqn 1, Q_j is the amount of resource required for establishment; S_x is the patch-specific

117   resource supply rate and $\left\langle \cdot \right\rangle_x$ indicates a mean taken over patches. For a single species, this

118   system has one stable equilibrium point per patch at,

$$n_{jx}^* = \frac{S_x}{Q_j m_j}, \quad R_{jx}^{*m} = \frac{m_j S_x}{b_j \left(p_j S_x + \left(1-p_j\right)\left\langle S \right\rangle_x \right)}$$

119   ,* MERGEFORMAT (a-b)

120 where the m in R_{jx}^{*m} is used to differentiate this equilibrium concentration of resource from the

121 traditional R^*, that occurs in an uncoupled or homogenous system and is independent of

122 resource supply rate.

123   Eqn.2 shows that, in this model, dispersal has no effect on equilibrium density, n_{jx}^*.

124 However, the equilibrium resource concentration, R_{jx}^{*m} does depend on the amount of dispersal

125 between patches and the resource supply rate in patch x relative to the mean supply rate in the

126 metacommunity. Specifically, if dispersal between patches is high, species j leaves a higher

127 concentration of resources behind in patches with above average supply rates and a lower

128 concentration in patches with below average supply rates than it would in a homogenous

129 environment. This occurs because patches with high supply rates are net exporters of recruits and

130 patches with low supply rates are net importers of potential recruits. The increased concentration

131 of available resources in high supply rate patches allows the invasion and possible coexistence of

132 a species that has a higher R^*, but experiences less inter-patch dispersal (Abrams and Wilson

133 2004)(Fig. 1).

134 *Derivation of variation dependent mechanisms.*

135   One way to measure potential for coexistence is with the mutual invasion criterion. This

136 criterion states that a set of species can coexist with one another if each can invade the

137 equilibrium assemblage of the other species in the set. In practice, one calculates growth rate of

138 a species with inter-specific competition set at the value determined by the competitors at

139 equilibrium and intra-specific competition set to zero. This is called the low-density growth rate

140   of the species. In a spatial context, we are interested in coexistence at the larger scale of the set

141   of all patches, so we calculate what is called the low-density metacommunity scale (or regional)

142   growth rate.

143   Chesson (2000a) has shown how a low density metacommunity-scale growth rate can be

144   calculated an written in terms of variation dependent coexistence mechanisms. First, the local

145   growth rate is decomposed into terms quantifying the direct effects of environmental variation

146   (E), variation in competition (C) and their interaction

$$r_{jx} = \mathcal{E}_x - \mathcal{C}_{jx} + \gamma_j \mathcal{E}_x \mathcal{C}_{jx}$$

147   ,   * MERGEFORMAT ()

148   where $\mathcal{E}_x = G_j\left(E_x, C_j^*\right)$, $\mathcal{C}_{jx} = -G\left(E^*, C\right)$ $\gamma_j = \dfrac{\partial G_j}{\partial \mathcal{E} \partial \mathcal{C}_j}$.

149   The quantities E and C are the population parameters affected by environmental variation and the

150   effect of competition (which is also affected by environmental variation) respectively, G is the

151   growth rate of species j as a function of E and C and the (*) indicates the equilibrium level of the

152   value.

153   The metacommunity-scale growth rate of species j, $\mathring{r}_j$, in a spatially heterogeneous environment

154   is found by taking the mean of r_{jx} over all individuals in the metapopulation, $\mathring{r}_j = \dfrac{1}{\sum\limits_x n_{jx}} \sum\limits_x r_{jx} n_{jx}$.

$$v_{jx} = \frac{n_{jx}}{\langle n_j \rangle_x}$$

155 It can be written in terms of a spatial mean by defining relative local density as   .

156 Substituting v_{jx} into $\mathring{r}_j$ gives $\mathring{r}_j = \langle r_j v_j \rangle_x$, which can be rewritten as $\mathring{r}_j = \langle r_j \rangle_x + \text{cov}(r_j, v_j)_x$,

157 where cov(.)$_x$ indicates a spatial covariance (Chesson 2000a). Plugging eqn 3 into this result

158 gives,

$$\mathring{r}_j = \langle \mathcal{E} \rangle_x - \langle \mathcal{C}_j \rangle_x + \gamma_j \langle \mathcal{E}\mathcal{C}_j \rangle_x + \text{cov}(r_j, v_j)_x$$

159   .* MERGEFORMAT ()

160   To argue that any of the terms in eqn 4 contribute to coexistence, the difference between

161 invader's and residents' values must be positive. Because, by definition the metacommunity

162 growth rate of the resident is zero, it can be subtracted from the right side of eqn 4 without

163 changing the left side. Thus, the metacommunity growth rate of the invader, denoted by subscript

164 *i*, can be rewritten in terms of contributions from multiple coexistence mechanisms by

165 subtracting the metacommunity growth rate of the residents, denoted by subscript *r* . Subtracting

166 the metacommunity growth rate of the residents gives,

$$\tilde{r}_i = \Delta E - \Delta C + \Delta I + \Delta \kappa$$

167   * MERGEFORMAT ()

168 where

$$\Delta E = \langle \mathcal{E}_i \rangle_x - q_{ir} \langle \mathcal{E}_r \rangle_x$$
$$\Delta C = \langle \mathcal{C}_i \rangle_x - q_{ir} \langle \mathcal{C}_r \rangle_x$$
$$\Delta I = \gamma_i \langle \mathcal{E}\mathcal{C}_i \rangle_x - q_{ir} \gamma_r \langle \mathcal{E}\mathcal{C}_r \rangle_x$$
$$\Delta \kappa = \text{cov}(r_i, v_i)_x - q_{ir} \text{cov}(r_r, v_r)_x$$

169   * MERGEFORMAT ()

$$q_{ir} = \frac{\partial C_i}{\partial C_r}$$

170   and the scaling factor is   is chosen to make the resulting expression more biologically

171   interpretable. For example, in this case, it allows ΔC to be expressed as a difference in the R^*

172   values of the species.

173   The quantity ΔE measures differences in the average environment experienced by the

174   invader and resident. The quantity ΔC can contain both the fluctuation independent difference of

175   the average competition experienced by residents and invaders and a measure of the effect of

176   variation in competition. The combination $\Delta E - \Delta C$ is often rewritten to separate it into variation

177   dependent ΔN and variation independent $\tilde{r}_i'$ parts, where $\tilde{r}_i' = \Delta E - C_i*$ and $\Delta N = \Delta C - C_i*$. The

178   quantity C_i* is the value of competition the invader experiences as a consequence of the resource

179   equilibrium the residents create (Chesson 2000a). The quantity $\tilde{r}_i'$ the growth rate the invader

180   would experience in the absence of variation. The quantity ΔN has been called

181   relative-nonlinearity and can facilitate coexistence if species exhibit different non-linear

182   responses in growth rate to variations in competition, specifically if the species with the larger

183   non-linearity in response experiences lower variance in competition. For most models that

184 would describe the growth of plants, this mechanism can only facilitate coexistence of two

185 species (Chesson 1994).

186   The quantity ΔI is the storage effect (Chesson 1994) it measures the covariance between

187 the direct effect of environmental variation and the effect of competition on the growth rate of

188 the invader. This mechanism is potentially very powerful and can facilitate coexistence on many

189 species. An example of many species coexistence via spatial storage effect would where there

190 are many patches and each species is the best competitor in at least one patch (Sears and Chesson

191 2007).

192   The final mechanism, $\Delta \kappa$, is growth-density covariance. It measures the ability of the

193 invader to concentrate its population into patches that are best at supporting growth. The species

194 that is better able to do this will experience an overall boost to metacommunity scale growth rate.

195 This mechanism is most directly related to dispersal.

196 *Derivation of variation dependent mechanisms for spatial resource heterogeneity*

197   Following Chesson (2000), the model (eqns. 1) can be written in terms of variation in

198 environment, E_x (the life history character that varies in space) and competition, C_x. In the case

199 of the present model, where only the supply rate of resources varies over space, environmental

200 variation does not directly affect individuals, it only affects competition; thus $E_x = 0$ and

201 $C_x = -R_x$. Making these substitutions, the model in eqns. 1can be rewritten as,

$$\frac{dn_{jx}}{dt} = -m_j n_{jx} - b_j C_x \left(p_j n_{jx} + \left(1 - p_j\right) \left\langle n_j \right\rangle_x \right)$$

$$\frac{dC_x}{dt} = -S_x + \sum_j Q_j b_j C_x \left(p_j n_{jx} + \left(1 - p_j\right) \left\langle n_j \right\rangle_x \right)$$

202 $\hspace{10cm}$ (7)

203

$$r_{jx} = -m_j - b_j p_j C_x - \left(1 - p_j\right) b_j \left\langle C \right\rangle_x$$

204 The local growth rate is then, $\hspace{5cm}$. Notice that in this case, due to

$$r_{jx} \neq \frac{1}{n_{jx}} \frac{dn_{jx}}{dt}$$

205 dispersal between patches $\hspace{3cm}$. Instead, r_{jx} is derived by considering the fitness of an

206 individual in patch x (Miller and Chesson 2009). Taking the mean over space, as described in the

$$\tilde{r}_i = -\left\langle C_i \right\rangle_x + \mathrm{cov}(r_i, v_i)_x$$

207 previous section gives the metacommunity-scale growth rate, $\hspace{2cm}$, where

$$\left\langle C_i \right\rangle_x = m_i + b_i \left\langle C \right\rangle_x$$

208 $\hspace{4cm}$. Assuming a single resident, denoted by subscript r, allows calculation of the

209 various coexistence mechanisms for the case of two species. This is helpful to determining the

210 presence or absence of the various mechanisms implied by this model. Plugging into eqn 6 and

211 scaling by b_i to put the results in the natural time scale of generations instead of an absolute time

212 scale (e.g. months or years) (Chesson 2008) gives (for details see Supplemental Appendix S1),

$$\frac{\Delta E}{b_i} = 0$$

$$\frac{\Delta C}{b_i} = -\frac{m_i}{b_i} + \frac{m_r}{b_r}$$

$$\frac{\Delta I}{b_i} = 0$$

$$\frac{\Delta \kappa}{b_i} \approx \frac{m_r}{b_r}(1-p_r)^2 \left\langle s^2 \right\rangle_x \left(\frac{p_i}{1-p_i} - \frac{p_r}{1-p_r} \right)$$

213   * MERGEFORMAT ()

214   Rewriting $\Delta E - \Delta C$ terms of $\tilde{r}_i{}'$ and ΔN gives,

$$\frac{\tilde{r}_i{}'}{b_i} = -R_i^* + R_r^*,$$

$$\frac{\Delta \kappa}{b_i} \approx \mathrm{var}(s)_x (1-p_r)^2 R_r^* \left(\frac{p_i}{1-p_i} - \frac{p_r}{1-p_r} \right)$$

215   * MERGEFORMAT ()

216   where $\frac{m_j}{b_j} = R_j^*$. Notice in this case $\Delta N = 0$ since ΔC contains no variation dependent terms.

217   Biologically, $\tilde{r}_i{}'/b_i$ is a comparison of abilities to reduce resources in a homogenous

218   environment. Specifically, eqn 9 states that invaders are benefited by the ability to reduce

219   resources to a lower level than the resident in a homogenous environment (Tilman 1982). It also

220   suggests that in the absence of spatial heterogeneity (*var (s)$_x$* = 0) coexistence is impossible

221   because only the species with the lowest R^* would have a positive growth rate as an invader.

222   In addition, eqn. 9 shows that only differences in dispersal can allow coexistence in this

223   model. The storage effect (ΔI) and relative nonlinearity (ΔN) have no effect on invader's

224   metacommunity-scale growth rate and thus do not contribute to coexistence. The effect of

225   growth-density covariance ($\Delta\kappa$) on the growth rate of the invader depends upon R_r^* times the

226   odds of seeds staying in natal patches relative to the resident's. Invaders whose seeds are less

227   widely dispersed than those of the resident species are benefited by growth-density covariance.

228   Thus, this model allows coexistence of species if there is a tradeoff competitive ability (*R**) and

229   dispersal fraction (*p*). In addition, coexistence is facilitated by only one variation-dependent

230   mechanism, grow-density covariance.

231   *How many species does growth-density covariance support?*

232   I used a sequential invasion approach based on adaptive dynamics (Geritz et al. 1998) to

233   determine how many species can coexist based on this model. This approach attempts to find the

234   trait values for invaders that allow invasion in a given context. In this case, at each step, I find

235   the values for the trait p_i that allows an invader to have a positive meta-community growth rate

236   (often written as *S(p_i)* in the adaptive dynamics literature) in an assemblage of *n* resident species,

237   i.e., $S_{\{P_{rn}\}}\left(p_i \right) > 0$. If this species can 1) coexist with the current resident strategies and resist

238   exclusion by similar strategies (i.e. similar values *p),* then it is added the list of residents. Species

239   are added one at a time until there is no value of p_i that leads to positive metacommunity-scale

240   growth rate. Because the approximated expression for growth-density covariance from eqn. 9

241   assumes small variation in supply rate and has singularities at *p_i=1* and *p_r =1*, I use simulation of

242   eqn 1 to calculate invasion growth rate. Numerical simulations of the residents were run until

243   they reached a steady state. The resulting value of resource concentration was plugged into the

244 matrix that described each patches' contribution to an invader's low-density growth-rate in patch

245 x. The dominant eigenvalue of this matrix is an estimate of the meta-community scale

246 low-density growth rate of the invader. For the simulations, I assumed Log-normal distributed

247 supply rates and trade-offs between R_j^* and p_j of the form $R_j^* - p_j^\tau = Z$ where Z is an arbitrary

248 constant and τ affects the shape of the trade-off. The following example considers a linear

249 tradeoff, between competitive ability and dispersal i.e., $\tau = 1$.

250 Figure 2 shows a contour plot for the invasibility of strategy p_i in the presence of resident p_r. The

251 black region of Figure 2 represent negative invader growth rates (i.e. the invasion is

252 unsuccessful), the white regions shows areas of positive growth rates. It shows that any resident

253 strategy $p_r < 1$ can be invaded by $p_i = 1$. However, the strategy $p_r = 1$ is also able to be invaded

254 by any $p_i < 1$. Thus, I set $p_{r1}=1$ and looked for values of p_{r2} that could coexist with p_{r1} and were

255 not excluded by other similar strategies. Figure 3 shows that given $p_{r1}=1$, any resident strategy

256 $p_{r2}>0$ can be invaded by $p_i<p_{r2}$. Thus, since $p_{r2}=0$ can also coexist with $p_{r1}=1$, it was added to the

257 resident list. Figure 3 also suggests that there is no third strategy p_i that can coexist with $p_{r1}=1$

258 and $p_{r2}=0$, since $S_{\{p_{r1=1},p_{r2=0}\}}(p_i) < 0$ for all possible values of p_i (i.e. a vertical line drawn from

259 $p_{r2}=0$ passes only through the black region of the graph). This suggests that in this model, a

260 tradeoff between competitive ability R_j^* and dispersal p_j, allows coexistence of only two species.

261 To assure these results were robust, I simulated systems of simultaneous competition among

262 many species from along the trade-off manifold (Supplemental Appendix S2).   Those

263 simulations also show an observed maximum of two coexisting species for nonlinear tradeoffs

264 with $\tau < 1$; additional loss terms in the resource equation, and saturating growth responses. For

265 non-linear tradeoffs with $\tau > 1$ no coexistence was possible.

266   Discussion

267   This analysis shows that spatial variation in resources allows for fewer coexistence

268 mechanisms and lower potential species diversity compared to spatial variation in non-resource

269 factors. Although spatial resource variation promotes coexistence if there is a tradeoff between

270 competitive ability and the ability to retain offspring in good patches, this tradeoff allows the

271 coexistence of only a 2 species.

272   Coexistence under spatial resource variation lacks contributions from the spatial storage

273 effect, a powerful mechanism that allows the coexistence of many species. The storage effect is

274 absent because all species grow best in the same patches (high resource patches). As a result,

275 environmental responses and competition are perfectly and equally correlated for all species,

276 allowing no advantages in good patches when a species is rare. In other words, the feedback that

277 organisms have on the resource, make it impossible for any to specialize on a particular supply

278 rate along a gradient.

279   Although the mechanism of resource competition analyzed in this model is simplified,

280   the qualitative results are quite general. For example, the relationship of R^* to the

281   metacommunity-scale coexistence mechanisms described by scale transition theory does not

282   depend on the simplified model of local resource competition presented in eqns 1. If the

283   establishment rate of seeds is a saturating function (e.g. Monod functions with equal half

284   saturation constants) of the amount of resources present, then $\hat{r}'$ is still a comparison of the (more

285   complicated) R^*s of the invader and resident, and the relative importance of the variation

286   dependent mechanism is the same. The situation is more complex if species growth rates are

287   different non-linear functions of resource concentration, but, even in this case, spatial variation in

288   one only facilitate 2 species coexistence (Supplemental Appendix S2).

289   In this model, competition was for a single resource. Increasing the number of limiting

290   resources can increase the number of species that can coexist at equilibrium. Golubski et al.

291   (2008) found that a maximum of four species could coexist in a system with two resources,

292   heterogeneous supply rates and species that were capable of integrating growth across patches.

293   However, this was only possible with precise arrangement of species trait parameters, and if

294   resource supply rates of the resources were strongly negatively correlated across patches. I

295   presume that, in this case, adding resource factors does not increase the number of mechanisms;

296   the existing mechanism, growth-density covariance, simple works independently for each

297   resource; although this claim should be explored with further analysis.

298   This analysis suggests that spatial resource heterogeneity is not capable of supporting the

299   robust stable coexistence of many plants species that is observed in many natural systems. The

300   reason for this is that the feedback species have on resources concentrations prevents

301 specialization of different species at different supply rates. It is this kind of specialization of

302 different species along different points of a "niche" axis, which is measured by the spatial

303 storage effect, that allows the robust coexistence of many species. The results of this analysis are

304 consistent with the patterns found in the empirical literature, which finds much more support for

305 the relationship between species diversity and nonresource spatial heterogeneity than resource

306 heterogeneity. Taken together, this work suggests that the consideration whether a factor is a

307 resource or not is crucial for those attempting to understand real patterns in species diversity or

308 those interested in managing a habitat for increased species diversity.

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