1   DISPERSAL STOCHASTICITY MEDIATES SPECIES RICHNESS

2   IN SOURCE-SINK METACOMMUNITIES

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19   **Summary**

20   Although it is well-known that dispersal of organisms within a metacommunity will

21   influence patterns of coexistence and richness, theoretical and experimental studies generally

22   assume that dispersal rates are constant through time. However, dispersal is often a highly variable

23   process that can vary seasonally and/or when stochastic events (e.g., wind storms, droughts, floods)

24   occur. Using a well-known source-sink metacommunity model, we present novel predictions for

25   local and regional species richness when stochasticity in dispersal is expressly considered. We

26   demonstrate that dispersal stochasticity alters some of the predictions obtained with constant

27   dispersal; the peak of the predicted hump-shaped relationship between dispersal and local species

28   richness is diminished and shifted towards higher values of dispersal. Dispersal stochasticity

29   increases extinction probabilities of inferior competitor species particularly in metacommunities

30   subjected to severe isolation events (i.e. decreases of dispersal) or homogenization events (i.e.

31   sudden increases of dispersal). Our results emphasize how incorporating dispersal stochasticity into

32   theoretical predictions will broaden our understanding of metacommunities dynamics and their

33   responses to natural and human-related disturbances.

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35   Keywords: dispersal, stochasticity, extinction, metacommunity, source-sink

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37

37   **Introduction**

38   The structure of local communities (e.g., the numbers and types of species) was historically

39   thought to be primarily influenced by an interaction between local environmental (e.g.,

40   productivity, disturbance) and biotic (e.g., competition, predation) factors, whereas more recent

41   advances have emphasized the importance of regional processes such as dispersal and habitat

42   heterogeneity (e.g. Leibold *et al.* 2004, Massol *et al.* 2011). The formalization of the idea that

43   variation in dispersal can influence local community structure dates at least as far back as the theory

44   of island biogeography (e.g., MacArthur and Wilson 1963, 1967), and has been an important

45   consideration for issues of biodiversity conservation in the face of increased habitat isolation (and

46   thus lower dispersal) that occurs with anthropogenic habitat fragmentation (e.g., Gonzalez *et al.*

47   1998, Fahrig 2003, Damschen *et al.* 2008).

48   Understanding the role of dispersal as driver of patterns of species diversity in among and

49   within communities is a main focus of metacommunity theory (e.g., Leibold *et al.* 2004, Chase *et*

50   *al.* 2005, Holyoak *et al.* 2005). The effects of dispersal on patterns of species richness can depend

51   on the underlying model assumptions that influence coexistence (reviewed in Chase *et al.* 2005).

52   For example, when coexistence is achieved by a regional balance of competitive abilities across

53   heterogeneous sites, dispersal rates can influence patterns of diversity in a source-sink

54   metacommunity whereby sustained fluxes of immigrants can override local competitive hierarchies

55   and promote local coexistence (Mouquet and Loreau 2002, Leibold et al. 2004). At high levels,

56   however, dispersal can be detrimental for local coexistence by creating conditions allowing the

57   dominance of a single best regional competitor (Mouquet and Loreau 2002, Mouquet et al. 2002).

58   While empirical studies have generally found an increase in local species richness (albeit variable)

59   with increased dispersal (reviewed in Myers and Harms 2009), there is some circumstantial meta-

60   analytical evidence for the predicted (Mouquet and Loreau 2003) hump-shaped dispersal-diversity

61   pattern in experiments that carefully controlled dispersal of organisms among localities (Cadotte

62   2006, Logue *et al.* 2011).

63   Dispersal in theoretical models and in controlled experimentation is typically implemented

64   as a constant. In theoretical models, a fixed proportion of individuals disperse from one habitat to

65   another (or immigrate from a mainland) in each unit of time (e.g., MacArthur and Wilson 1967,

66   Loreau and Mouquet 1999, Mouquet and Loreau 2003). Experimental investigations have either

67   emulated this relative constancy in dispersal (reviewed in Cadotte 2006), or simply added species

68   from the regional species pool once (or a few times) near the beginning of the experiment (reviewed

69   in Myers and Harms 2009). Natural communities, however, more likely experience dispersal that is

70   variable through time. This variability can either result from seasonality, where organisms typically

71   disperse in one part of the season, but not others (reviewed in Nathan *et al.* 2000, Levin *et al.* 2003),

72   or simply due to the stochastic vagaries of weather conditions or other environmental and

73   demographic factors (e.g., Engen *et al.* 2005, Grotan *et al.* 2005). Furthermore, it is becoming well

74   accepted that climate change is not only altering the average of environmental conditions (e.g.,

75   Schar *et al.* 2004), but more likely, is changing the variability in those conditions, leading to more

76   extreme temperatures and precipitation events (Karl and Easterling 1999). This increased climatic

77   variability may also increase the stochasticity in dispersal dynamics among communities (e.g., more

78   frequent/intense droughts, floods, storms).

79   In this manuscript, we address how dispersal stochasticity can influence patterns of species

80   coexistence and diversity in source-sink metacommunities. We extended a previous modelling

81   framework of a source sink metacommunity (2002, 2003, see also Mouquet et al. 2006) to illustrate

82   how dispersal stochasticity influences the coexistence among species and overall diversity in a

83   metacommunity. That is, we examine how temporally variable dispersal (e.g., very high during

84   some time periods, and very low during others) might alter the interactions among species, and

85   likelihood for coexistence, differently than if dispersal was the average of low and high dispersal

86   events. This modelling framework has been widely discussed and was therefore considered

87   appropriate to conduct a theoretical examination of the effects of temporally variable dispersal on

88   metacommunities (reviewed in Leibold et al. 2004, Logue et al. 2011, Massol et al. 2011). Here,

89   we present theoretical predictions for local and regional species richness when dispersal and

90   dispersal stochasticity are explicitly considered at different spatial scales. We investigate the

91   effects of dispersal stochasticity on species richness at two different spatial scales– the entire

92   metacommunity and the local community – to simulate different sources of stochasticity in natural

93   communities at local (e.g. patch isolation within complex landscapes; Ricketts 2001) and regional

94   (e.g., climatic fluctuations as in Driscoll and Lindenmayer 2009) scales.

95

96   **Methods**

97

98   *The model*

99   We begin with Mouquet and Loreau's (2002, 2003) source-sink metacommunity model. At

100   the local scale, P_{ik} is the proportion of microsites occupied by species i in community k. The

101   metacommunity is constituted of N communities that differ in their local conditions, where S

102   species compete for a limited proportion of vacant microsites $(1 - \sum_{i=1}^{S} P_{ik})$. Each species i is

103   characterized by a set of reproduction parameters, c_{ik}, each of which measures the potential local

104   reproductive rate of species i in community k, and a set of mortality rates, m_{ik}. The distribution of

105   parameters is such that each species exhibits different reproductive rates in the different

106   communities, allowing them to potentially coexist regionally.

107   When there is no dispersal ($a = 0$) between localities, the species with the highest local basic

108   reproductive rate (c_{ik}) excludes all other species in each locality, since mortality rates (m_{ik}) are the

109   same for all species. In contrast, if localities are linked by dispersal ($a > 0$), local coexistence is

110   possible because each species has a locality in which it is favored, and thus emigration from these

111   'source' areas allows them to (co-) exist in 'sink' areas where they are competitively inferior. The

112   main equations of the model are:

113

114    $$\frac{dP_{ik}}{dt} = (I_{ik} + (1-a)c_{ik}P_{ik})(1 - \sum_{i=1}^{S} P_{ik}) - m_{ik}P_{ik} \qquad (1)$$

115   with immigration $I_{ik} = \frac{a}{N-1}\sum_{l \neq k}^{N} c_{il}P_{il}$ \qquad (2)

116

117   We used a recent implementation of this model (Mouquet *et al.* 2011) that relaxes the strict

118   assumption of regional similarity with a simple parameter that regulates the degree of regional

119   similarity (ω; see Supplementary material Appendix A1 for details), which was set so that the

120   source-sink dynamic was strong ($\omega = 0.8$), resulting in a hump-shaped pattern of local diversity

121   with dispersal. Under these conditions, we tested the effect of temporal variability in dispersal on

122   patterns of species richness in metacommunities. See Supplementary material Appendix A1 for

123   details on the model parameters.

124

125   *Temporal variation in dispersal*

126   In developing this model, we assume that all emigrants from a local community are

127   combined and equally redistributed at a constant rate to other communities, with no individuals

128   returning to the community from which they emigrated. We introduced temporal variability in

129   dispersal by changing the proportion of dispersers through time to generate predictions about the

130   effect of dispersal stochasticity on local and regional species richness. Variable dispersal dynamics

131   were generated using a sequence of random numbers from a uniform distribution. We calculated

132   realized dispersal (i.e. actual dispersal value used in the model equations) for each dispersal event

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133   as: $a = \bar{a} \pm s$; where a is realized dispersal; $\bar{a}$ is mean dispersal ($\bar{a} = 0$: no dispersal; $\bar{a} = 1$: all

134   individuals dispersed); s is a random number from a uniform distribution between 0 and 0.5. We

135   evaluated other distributions of random numbers (e.g. Gaussian) and found that, under these model

136   parameters, there were no qualitative differences on the effects of dispersal stochasticity. The

137   signal of s was randomly assigned for each dispersal event to simulate either increases

138   (homogenization events) or decreases in dispersal (i.e. isolation events). When $s = 0$, there is no

139   stochasticity and all realized dispersal values are equal to mean dispersal ($a = \bar{a}$); as s increases, the

140   deviations from mean dispersal increase leading to an increase in dispersal stochasticity. Because

141   dispersal is bounded between 0 and 1, we constrained the variability to the range of possible

142   dispersal values in order to avoid border effects that would come from high values of s. For

143   example, at mean $a = 0.2$, values of dispersal were only simulated with a maximum s of 0.2 so that

144   no negative dispersal values could be generated.

145

146   *Spatial scale of variability*

147   Any source of dispersal stochasticity in natural communities is likely to be mediated by the

148   combination of process occurring at local and regional scales (Ricklefs 1987, Zobel 1997). From

149   this, we extended our modelling framework to investigate the effects of dispersal stochasticity at

150   two different scales– metacommunity and community. Dispersal stochasticity at the

151   metacommunity level means that all species in all communities have the same realized dispersal

152   value in every unit of time (Mouquet and Loreau 2002, Mouquet and Loreau 2003). This simulates,

153   for example, variability in isolation and connectedness of local communities at regional scales as a

154   response to large-scale fluctuations (e.g., climatic fluctuations as in Driscoll and Lindenmayer

155   2009). The predictions generated at this scale of stochasticity (i.e. regional), are comparable with

156   previous results found with the previous models that did not considered dispersal stochasticity

157   (Mouquet and Loreau 2002, Mouquet and Loreau 2003). Alternatively, stochasticity was

158   implemented at community level, where each community has a different value of realized dispersal

159   in each unit of time; all species within each community have the same dispersal value. This

160   scenario corresponds to a lower scale fluctuation regime, as for instance, through patch isolation

161   within complex landscapes (e.g. Ricketts 2001).

162

163   *Numerical simulations*

164   Each metacommunity consisted of 20 local communities, each initiated with 20 species. At

165   the start of each simulation, we attributed the same proportion of microsites to each species in all

166   local communities ($P_{ik} = 0.01$, for all i and k). In order to investigate the joint effects of dispersal

167   stochasticity and mean dispersal on species richness, we generated predictions for every

168   combination of dispersal parameters (0 to 1 with increments of 0.1) and dispersal stochasticity (0 to

169   0.5 with increments of 0.1). For each dispersal scenario, we generated 100 independent simulations

170   using an Euler approximation ($\Delta t = 0.01$) of equation (1) until equilibrium was reached in all local

171   communities within a metacommunity. Dispersal stochasticity was only implemented after

172   equilibrium was reached (100000 iterations), after which community dynamics were simulated for

173   an additional 100000 iterations under variable dispersal. Preliminary work had shown that the final

174   communities were qualitatively similar whether stochasticity was implemented at the initiation of

175   the simulation or at equilibrium, although it was impossible to distinguish between the two sources

176   of extinctions (i.e. deterministic or stochastic) when dispersal stochasticty was implemented at the

177   beginning of simulations. We thus opted to implement dispersal stochasticity after communities

178   reached equilibrium to disentangle extinction events that result from deterministic competitive

179   interactions within each local community under constant dispersal from those resulting from

180   increased dispersal stochasticity.

181   We kept mortality rates constant across species ($m_{ik} = 0.3$), and based competitive

182   hierarchies on potential local reproductive rate c_{ik} (species i in community k). After the very early

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183   stage of community development ($t = 2000$), we assumed that a species went extinct from a local

184   community when its proportion of occupied sites was lower than an extinction threshold ($=0.01$).

185   We computed values for local richness (α), regional richness (γ), and species turnover (β) at the end

186   of each run. These measures were calculated assuming additive partitioning of components of

187   species diversity (*sensu* Lande 1996): $\gamma = \beta + \overline{\alpha}$. Where $\overline{\alpha}$ is the mean α diversity in the

188   metacommunity (i.e. across all communities). Additionally, to account for the influence of

189   dispersal and dispersal stochasticity on the relative abundance of species, we used the Rao quadratic

190   entropy decomposition of diversity in α, γ, and β (de Bello et al. 2010). This additional analysis is

191   presented in Appendix A2. For every combination of dispersal and dispersal stochasticity, we

192   analyzed the average values over the 100 simulations. Figure 1 gives an example of the dynamics

193   of the same community with and without dispersal stochasticity. During the time series, we

194   recorded dispersal sequences and the identity of species that went extinct in each community.

195   Additionally, we also calculated the dispersal deviation ($= (a - \overline{a})/\overline{a}$) at each extinction event,

196   which measures the degree to which extinction occurred following a low or high dispersal event.

197   **Results**

198   *Species richness and dispersal stochasticity*

199   Without dispersal stochasticity, we found the expected hump-shaped relationship between

200   dispersal and local species richness (e.g. Mouquet and Loreau 2002, 2003). With the inclusion of

201   increased dispersal stochasticity, the position of the peak (hump) of species richness shifted from

202   intermediate to higher values of dispersal, and the height of the peak was reduced, allowing for the

203   coexistence of fewer species locally (Fig. 2). This effect was stronger when dispersal was

204   implemented at the community level (i.e. each community had a different dispersal sequence); for

205   instance at intermediate levels of dispersal ($a = 0.5$), local species richness was reduced up to 25%

206   (16 to 12 species) under metacommunity-level stochasticity, while under community-level dispersal

207   stochasticity, the reduction was up to 50% (16 to 8 species).

208   Increasing dispersal stochasticity shifted the predicted decline of spatial turnover of species

209   (beta diversity) to intermediate levels of dispersal and was consistent at metacommunity- and

210   community-level dispersal stochasticity (Fig. 2a, b). This effect is clearer from low to intermediate

211   levels of dispersal where the spatial turnover of species was enhanced more than tenfold with

212   dispersal stochasticity (e.g. 1 to 14 species at $a = 0.3$; Fig. 2a). Finally, we found that increased

213   dispersal stochasticity at the metacommunity-level did not have a discernable effect on regional

214   richness (Fig. 2a). At the community level, however, there was a reduction in regional species

215   richness at intermediate levels of dispersal (14 to 8 at $a = 0.6$; Fig. 2b). Results from the Rao

216   diversity index of species turnover, local, and regional richness (Fig. 2a, b), which incorporate

217   patterns of relative abundances by down-weighting the importance of rare species, were generally

218   similar to those produced when only considering patterns of species richness (Supplementary

219   material Appendix A2). However, the magnitude of the effect of dispersal stochasticity on species

220   diversity was reduced as a direct result of the down-weight of rare species, inherent of using Rao's

221   diversity index.

222

223   *Pattern of species extinctions*

224   Most species that went extinct as a result of increased stochastic dispersal were those with

225   lower local reproductive rates (i.e. the worse local competitors) (Fig. 3a). These results were similar

226   for both dispersal scenarios (see Supplementary material Appendix A3). More than 90% of the

227   extinctions occurred after reductions in dispersal at low to intermediate levels that match the peak in

228   local species richness ($a < 0.5$; Fig. 3b) and were caused by isolation events rather than by

229   increasing dispersal events (i.e. reductions in dispersal; see Fig 3c). In fact, the great majority of

230   dispersal events leading to extinctions (> 93%) were negative (i.e. isolation events) with respect to

231   mean dispersal at the time of extinction (Fig 3c). At high mean dispersal, extinctions were caused

232   by both isolation and homogenization events (Fig 3c).

233

234   **Discussion**

235

236   *Consequences of dispersal stochasticity on species richness*

237   Overall, our results show that dispersal stochasticity mediates local and regional richness in

238   source-sink metacommunities. We found a strong negative effect of increased dispersal

239   stochasticity on local species richness and a shift in the position of the peak in the dispersal-local

240   species richness relationship to higher levels of dispersal than found in previously published models

241   without dispersal stochasticity (e.g., Mouquet and Loreau 2003). This result might help to explain

242   some of the observed disparity between empirical results and theoretical predictions (Logue et al.

243   2011). For example, most empirical studies that have manipulated dispersal typically find increases

244   in local species richness, while very few have found the predicted declines in local species richness

245   at high levels of dispersal (reviewed in Myers and Harms 2009). This might be expected from our

246   predictions that suggest that the maximum species richness is attained at rates of immigration much

247   higher than are typically implemented in experimental studies (Cadotte 2006).

248   We have found that regional species diversity was mainly affected by dispersal stochasticity

249   at the community level, but not at the metacommunity level. This lack of a major effect on regional

250   species richness can be attributed to the fact that most species extinctions occurred at the local

251   community scale and did not directly translate to increased regional extinctions. On the other hand,

252   values of species spatial turnover at intermediate levels of dispersal were higher with dispersal

253   stochasticity at both the local and regional scale, reflecting the strong effect on local, but regional,

254   diversity. While dispersal stochasticity does not strongly affect regional species richness, it does

255   add heterogeneity in the distribution of species richness among communities. These responses to

256   unpredictable dispersal events altered metacommunities differently depending on their initial mean

257   levels of dispersal. Reductions in dispersal generally benefit species that are better local

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258   competitors and therefore exclude worse competitors from localities. Alternatively, increases in

259   dispersal affect communities in both directions; from low to intermediate levels, increases in

260   dispersal events benefits species that are worse local competitors. At very high mean dispersal,

261   however, further increases in dispersal favour better regional competitors and homogenize of the

262   metacommunity (Mouquet and Loreau 2003; empirical examples in Forbes and Chase 2002, Kneitel

263   and Miller 2003, Matthiessen and Hillebrand 2006, Ostman et al. 2006). As a consequence, the

264   landscape is homogenized by species that have great competitive abilities at the scale of the

265   metacommunity, thus making it less likely to undergo extinction as a result of further stochastic

266   events.

267   As expected, dispersal stochasticity had a qualitatively similar, but weaker effect on species

268   diversity than on species richness (Appendix 2). This is because Rao's diversity, like other

269   diversity estimates, down-weights the importance of rare species which play a strong role in the

270   observed richness results. Thus, while our results are quite relevant for conservation concerns for

271   rare species vulnerable to extinctions, they are moderated somewhat by the more common species

272   that dominate diversity measurements. Dispersal stochasticity might be less important for diversity

273   than for richness, which may play a stronger role in ecosystem functions dominated by common

274   species. However, rare species may play a particular role in the stability of ecosystems if they

275   possess functional traits that provide insurance to the functioning the ecosystem in response to

276   environmental variation (Loreau et al. 2003, Lyons et al. 2005). Future work should explore the

277   functional consequences of dispersal stochasticity in spatially structured ecosystems (Massol et al

278   2011).

279   As a result of our theoretical study, we suggest that any predictions about the effects of

280   dispersal stochasticity in natural communities should be relative to mean dispersal of those

281   communities (i.e. whether communities are highly or poorly connected) and also include

282   information on the nature of extreme dispersal events (i.e. isolation or homogenization events). For

283   example, changes in dispersal that result predominately in dispersal reductions (e.g. following a

284   drought) may have greater effects on species that can coexist locally in communities that are

285   isolated from neighboring communities (e.g. isolated fragments) by further increasing species

286   extinction risk. Further investigations on the effects of dispersal stochasticity could extend this

287   framework by including different relative proportions of high-low dispersal events to mimic

288   specific stochastic dispersal scenarios or the colour of environmental variability (i.e., whether or not

289   it is temporally autocorrelated; e.g. Vasseur and Yodzis 2004). Moreover, these predictions could

290   be tested in a variety of experimental venues (e.g. Logue et al. 2011) by implementing variable

291   dispersal in spatially structured metacommunities (e.g. Carrara et al. 2012).

292

293   *Scale of dispersal stochasticity*

294   We found a stronger effect of dispersal stochasticity on local and regional diversity when

295   dispersal varied at the community scale than at the metacommunity scale. As discussed above,

296   dispersal stochasticity at the local scale inflates the effect of stochasticity by spatially

297   "desynchronizing" the dispersal sequences. It results in a greater number of variable dispersal

298   events when stochasticity is implemented at local scale and thus enhances the probability of

299   extreme dispersal events. With metacommunity-scale stochasticity, there were only 200 realized

300   dispersal values per simulation, whilst with community-scale stochasticity, we simulated 4000

301   realized dispersal values for each community. Such unevenness across scales reflects the

302   hierarchical nature of metacommunities. For example, regional processes that are likely to affect

303   overall metacommunity dispersal (e.g. changes in wind patterns, ocean currents, etc) are more likely

304   to occur at different scales than stochasticity at the community level (e.g. disturbance, fire, etc). We

305   know of no competitive metacommunity experiments that have manipulated the scale of dispersal

306   stochasticity explicitly. In predator-dominated systems where resistance to predation is analogous

307   to competition (Chesson and Kuang 2008), Cadotte and Fukami (2005) showed that dispersal had a

308   positive or neutral effect at local scales but consistently negative effects on the metacommunity

309   scale. These results were explained by an interaction between scale-dependent effects of dispersal

310   and the removal of spatial refuges from predators. Even though this experiment focused on a

311   different community assembly mechanism (predation vs. competition), it generally supports our

312   conclusion that the scale of dispersal stochasticity is central to building a more predictive

313   understanding of the ecological consequences of extreme dispersal events on community richness,

314   composition and dynamics. This is particularly important given the increasing numbers of reports

315   suggesting that spatial and temporal patterns of environmental variability are becoming more

316   unpredictable with global change (e.g. more frequent/intense droughts, floods, storms, etc.; Karl

317   and Easterling 1999, Schar et al. 2004).

318

319   *Species extinctions patterns*

320   We found that dispersal stochasticity had an asymmetrical affect on community species

321   composition by increasing the extinction probability of worse local competitors within each local

322   community. Metacommunities with low to intermediate levels of mean dispersal were also more

323   likely to lose species as a result of increased stochasticity relative to highly connected

324   metacommunities. The inclusion of stochasticity in dispersal revealed that probabilities of

325   extinction in dispersal-limited communities were much higher than anticipated under constant

326   dispersal dynamics. Such underestimation of species extinction probabilities can have implications

327   in terms of forecasting changes in species diversity in isolated communities during the

328   fragmentation processes (e.g. isolated fragments; Gonzalez *et al.* 1998, Fahrig 2003, Damschen *et*

329   *al.* 2008). In contrast, from intermediate to high levels of dispersal, metacommunities are

330   homogenised and dominated by strong competitors (Mouquet and Loreau 2002) that are more

331   abundant and less vulnerable to variability on dispersal. This is consistent with empirical evidence

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332   of the potential impacts of increases in dispersal on metacommunities such as those in freshwater

333   ponds (Forbes and Chase 2002) and pitcher plant micro-ecosystems (Kneitel and Miller 2003).

334

335   *Extending dispersal stochasticity to other metacommunity paradigms*

336   We generated predictions for a particular type of metacommunity– source-sinks. However,

337   dispersal stochasticity will likely be important for communities assembled under different

338   coexistence mechanisms, including neutral or competition-colonization metacommunities (Leibold

339   *et al.* 2004). Unravelling the consequences of dispersal stochasticity in competitive

340   metacommunities with these alternative mechanisms of coexistence will require additional

341   theoretical work, but we here make some general conjectures.

342   Under neutral dynamics, local diversity is determined by migration rates from the

343   metacommunity and local community size (Hubbell 2001, Etienne 2005). Increasing dispersal

344   generally leads to homogenization among communities by increasing local diversity and decreasing

345   beta diversity (Economo and Keitt 2008). These effects are mediated by rates of speciation (or

346   immigration from outside the metacommunity) and are likely to also be affected by dispersal

347   stochasticity. Extreme dispersal events (i.e. isolation or homogenization) are thus likely to lead to

348   extinctions that will or not will be compensated by new species arrivals depending on the rates of

349   speciation (or immigration). For example, high speciation rates are likely to enhance community

350   differentiation (e.g. Richardson et al. 2001, Latimer et al. 2005), which would be further enhanced

351   with reductions in dispersal events (i.e. isolation). In contrast, if speciation rates are low, a series of

352   extreme dispersal events are unlikely to alter the regional diversity (Economo and Keitt 2008).

353   Competition-colonization tradeoffs occur when there are costs associated with either

354   competitive or dispersal abilities (Hastings 1980, Tilman 1994, Calcagno *et al.* 2006); coexistence

355   occurs because inferior competitors are able to persist in the landscape due to their higher

356   colonization ability (Tilman 1994). Depending on the strength of the tradeoff, there are

357   colonization rates below which coexistence is not possible, and upper thresholds above which only

358   the superior colonizer survives (Calcagno et al. 2006). In this scenario, we expect that increased

359   stochasticity in colonization rates (as a result of dispersal stochasticity) would reduce the "window"

360   of coexistence by driving either the strong or the weak competitors extinct (depending on the

361   direction of stochasticity). Since colonization rates in this model framework are species-specific, it

362   is foreseeable that the impacts of stochasticity would depend on whether stochasticity is modelled

363   separately for either colonizer and the competitor (i.e. species-specific stochasticity), or whether

364   both species are subjected to a similar stochasticty regime (metacommunity-level).

365

366   *Conclusions*

367   In natural systems, dispersal rates are often likely be variable owing to a variety of

368   stochastic factors, be they environmental, demographic and/or otherwise. However, most

369   theoretical and empirical studies treat dispersal rates as a constant. Furthermore, global climate

370   change is expected to increase the frequency and magnitude of environmental extremes (e.g. Karl

371   and Easterling 1999), which can also increase stochasticity in dispersal among species within

372   metacommunities (Nathan *et al.* 2000, Levin *et al.* 2003). Our results illustrate that temporally

373   variable dispersal patterns can have an important influence on species' coexistence and richness at

374   local and regional spatial scales. In our source-sink metacommunity model, the principal

375   mechanism underlying such an effect is the increased risk of extinction of inferior competitors

376   during episodes of reduced dispersal (isolation). Increased dispersal stochasticity is thus more

377   likely to affect dispersal-limited metacommunities than highly connected metacommunities (e.g.,

378   Cottenie et al. 2003). To achieve a broader understanding of the consequences of dispersal

379   stochasticity on metacommunities dynamics, it will be useful to extend this framework to other

380   relevant metacommunity paradigms. Incorporating dispersal stochasticity in metacommunity

381   theory is an important step to enhance our understanding of the role of dispersal in community

382   dynamics and should be considered in future empirical and experimental studies on

383   metacommunities in an increasingly variable and heterogeneous world (Myers and Harms 2009,

384   Logue et al. 2011).

385

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500

501   Supplementary material (available online as Appendix oXXXX at

502   www.oikosoffice.lu.se/appendixXXXX). Appendix A1–A2.

503

Figure captions

Figure 1. Examples of simulations of community dynamics under (a) constant and (b) variable dispersal dynamics. Metacommunities with variable dispersal ($a = 0.3$; $s = 0.25$) are quite responsive to changes in dispersal, leading to more extinctions than metacommunities with no dispersal stochasticity ($a = 0.3$; $s = 0$). In the bottom graphs, each solid line indicates the abundance of a different species in the community; dashed lines indicate the extinction threshold ($= 0.01$).


Figure 2. Local richness (alpha), spatial turnover (beta) and regional (gamma) species richness as function of dispersal (x axis) for two spatial scales of dispersal stochasticity – (a) metacommunity and (b) community levels; lines with increasing thickness indicate values of dispersal stochasticity (i.e. 0, 0.1, 0.2, 0.3, 0.4 and 0.5). We present means over 100 simulations (standard deviations are omitted for clarity but are always inferior to 2%). Predictions are only presented for scenarios where deviations from mean dispersal do not exceed realized dispersal of 0 or 1. For example, for a $= 0.2$, values of dispersal stochasticity are only shown for a maximum dispersal stochasticity of 0.2 so that the range of dispersal values were between 0 and 0.4. This procedure avoided any potential border effect (see *Methods* section for details).

Figure 3. Species extinctions under variable dispersal dynamics: (a) Densities of extinct and remaining species in relationship to their local competitive abilities (as indicated by their local reproductive rate). These analyses were done using all recorded extinction events following the implementation of dispersal stochasticity (i.e. pooled across all levels of stochasticty). Densities were calculated using a kernel density estimation procedure (*Density* function; base package; R Development Core Team, 2011) (b) Histogram of frequencies of species extinctions at each dispersal level; dashed grey line indicates the median = 0.3. (c) Boxplots showing deviations from

mean dispersal at time of extinction; deviations were calculated as $(a - \bar{a})/\bar{a}$ with a as realized

dispersal and $\bar{a}$ as mean dispersal at time of extinction; this measure ranges between -1 and 1.
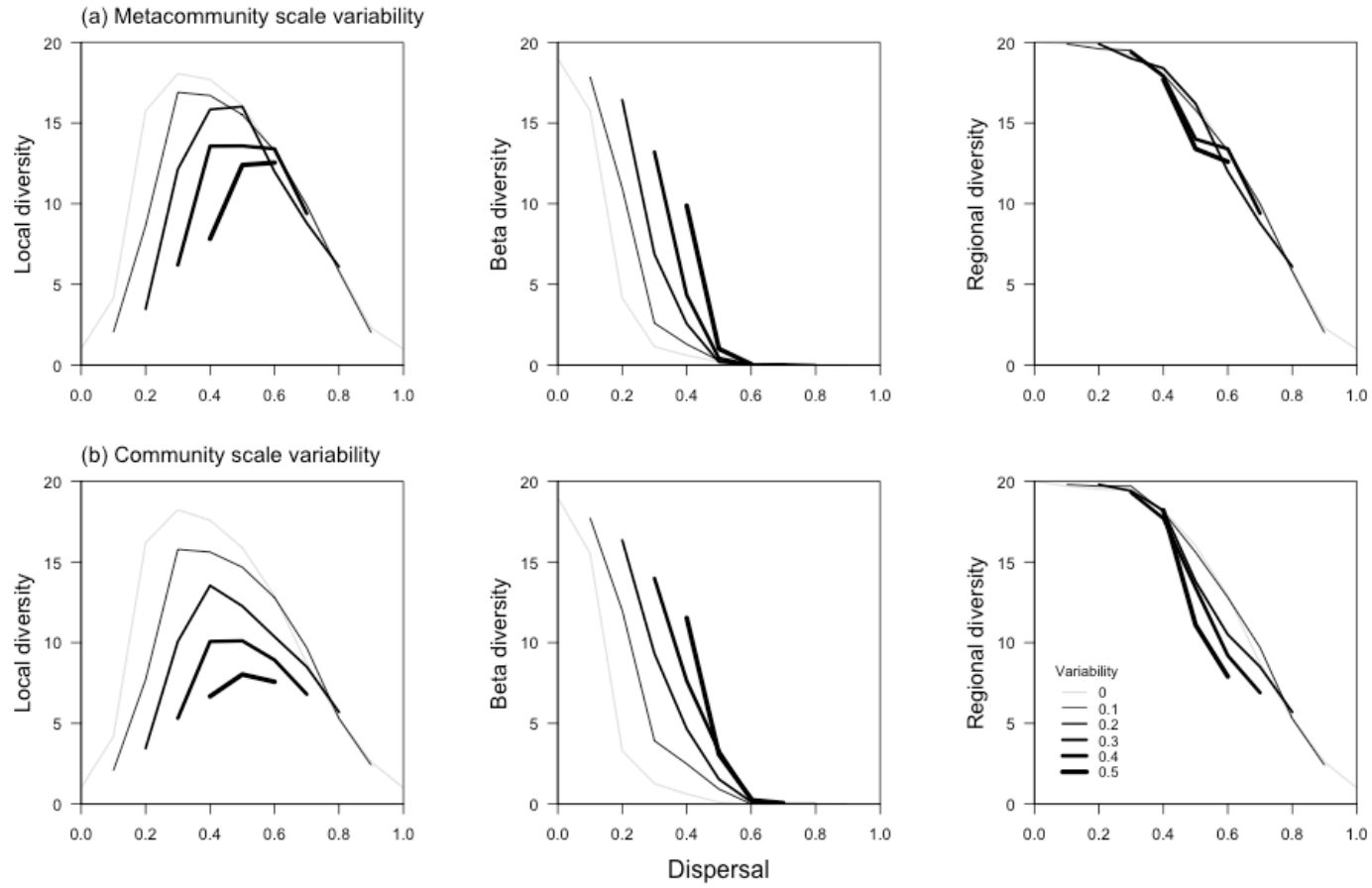
Solid grey line indicates the general predictions of local richness for different mean dispersal under

no dispersal stochasticity (see Fig. 2). Black circles indicate "outliers" that fall outside the boxplot
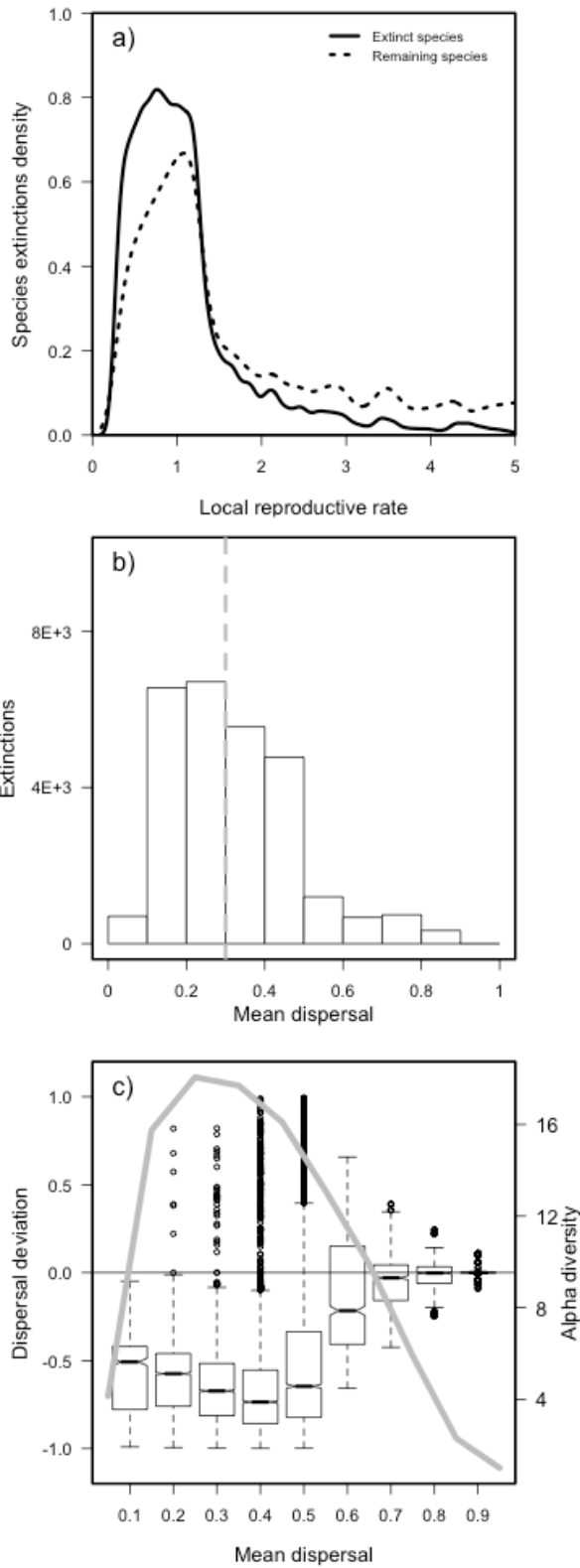
maximum or minimum range (i.e. < 5% of the data points).

Figure 1
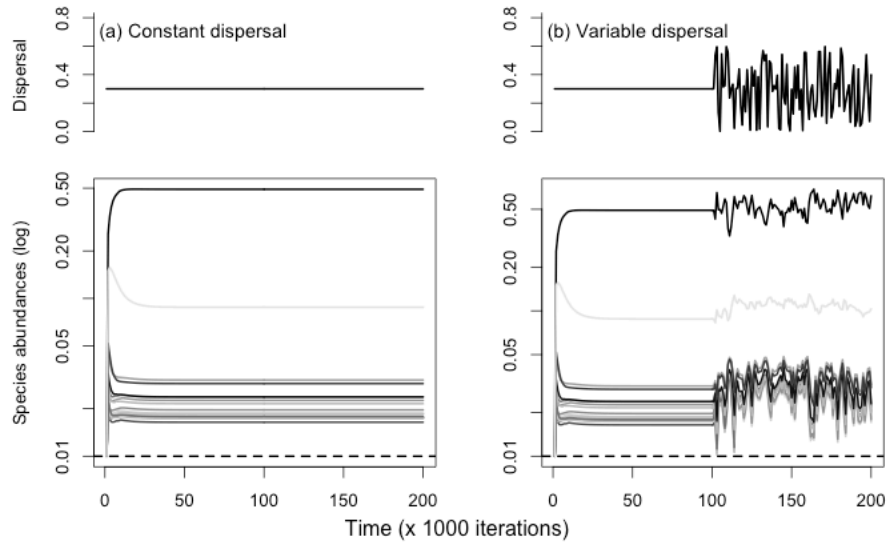
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Figure 2

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540

541 **Figure 3**

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543

544   **Supplementary material**

545   **Appendix A1 - Generating the model parameters**

546

547   We generated a matrix of parameters for a source-sink metacommunity as proposed by

548   (Mouquet *et al.* 2011). We used two types of matrices of local reproductive rate c_{ik} parameters.

549   First, we generated a matrix (called *Rand*) with c values randomly chosen between 0 and a maximal

550   reproductive rate c_{max}, which was set to 5. Then, we generated a matrix (called *SRS*) that fitted the

551   constraint of strict regional similarity (Mouquet and Loreau 2002), which means that each species

552   has its $c_{ik} = c_{max}$ in one of the twenty communities and the other parameters are derived such that in

553   each community:

554

555     $$c_{ik} = c_{max}\left(1 - \frac{x_{ik}}{N}\right)^5 + m \qquad\qquad\qquad (S1.1)$$

556

557   with N the number of species, x_{ik} the competitive rank (approximated by species reproductive rates

558   in this model) of species i in community k, m is the mortality rate (such as no species will have a

559   negative potential reproductive rate in any communities). We generated the competitive ranks x_{ik}

560   so that each species is the best competitor in one community, the second best competitor in another

561   community, the third in a third, etc. The exponent, 5, determines a steep local competitive

562   hierarchy i.e. magnitude of differences between best and worst competitor species (Mouquet et al.

563   2011).

564   We then generated each community matrix of realized c_{ik} parameters as combination of the

565   matrices *Rand* and *SRS* following this simple equation:

566

567     $$c_{ik} = \omega c_{ik(SRS)} + (1 - \omega)c_{ik(Rand)} \qquad\qquad\qquad (S1.2)$$

568

569   with ω determining the degree of regional similarity between species within competitive

570   metacommunities, which results in a set of competitive parameters ranging from strict regional

571   similarity ($\omega = 1$) to entirely random matrices ($\omega = 0$). For this analysis we fixed ω to 0.8 since it

572   has been shown to relax the strict assumption of regional similarity (i.e. =1) without qualitatively

573   changing the shape of the dispersal-species richness relationship (see Mouquet et al 2011). If there

574   is a strict regional similarity (or close to), it means that every single species will have a strong

575   "source" i.e. at least one community in which they are the best competitor and therefore disperse

576   strong competitors.

577

578   **References**

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580   hypothesis. *American Naturalist,* **159,** 420-426.

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583

584   **Appendix A2 –** Local (alpha), spatial turnover (beta) and regional (gamma) diversity species

585   richness as function of dispersal (x axis) using the Rao quadratic entropy decomposition of diversity

586   (de Bello et al. 2010). Data is presented for two spatial scales of dispersal stochasticity − (a)

587   metacommunity and (b) community levels; lines with increasing thickness indicate values of

588   dispersal stochasticity (i.e. 0, 0.1, 0.2, 0.3, 0.4 and 0.5). We present means over 100 simulations

589   (standard deviations are omitted for clarity but are always inferior to 2%). Predictions are only

590   presented for scenarios where deviations from mean dispersal do not exceed realized dispersal of 0

591   or 1. For example, for *a = 0.2*, values of dispersal stochasticity are only shown for a maximum

592   dispersal stochasticity of 0.2 so that the range of dispersal values were between 0 and 0.4. This

593   procedure avoided any potential border effect (see *Methods* section for details).
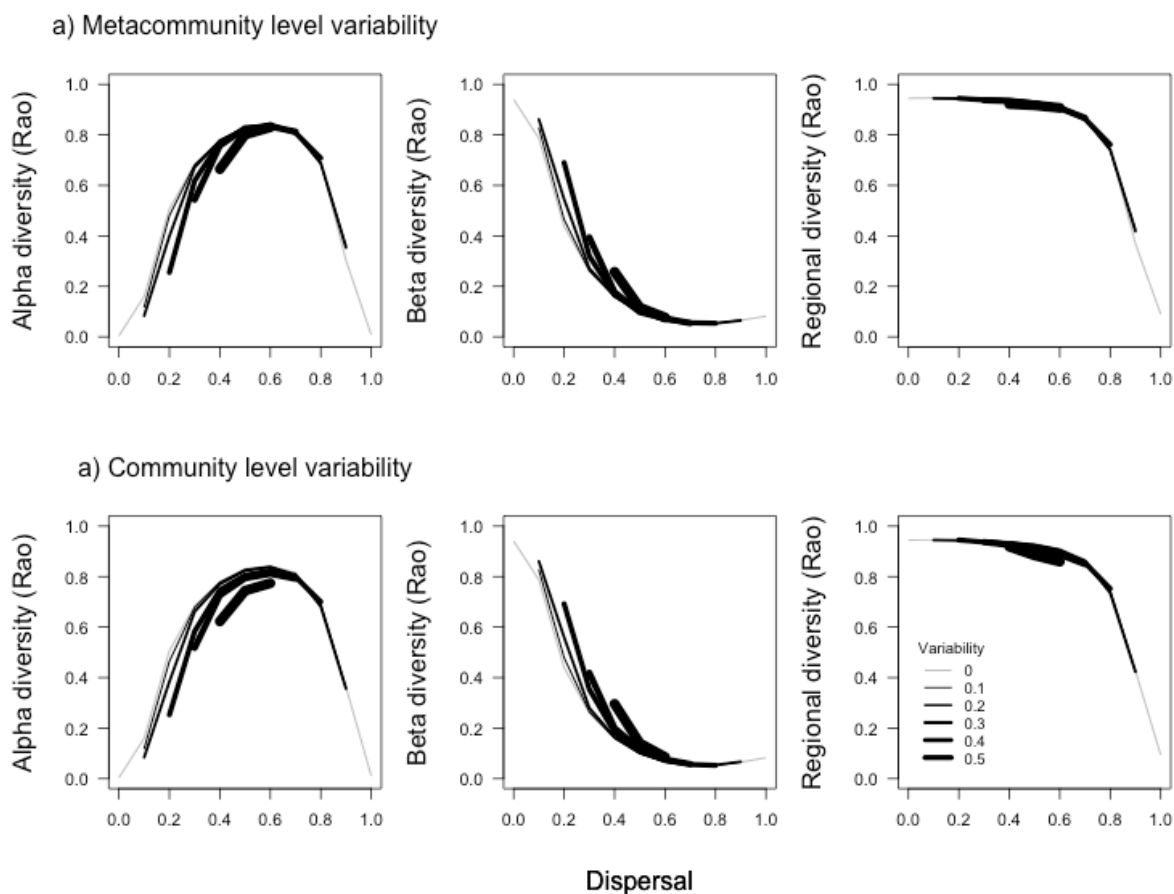

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596

597   **Appendix A3 – Species extinctions patterns obtained for community (local) and**

598   **metacommunity (regional) scales dispersal stochasticity**. Species extinctions patterns at (a)

599   metacommunity and (b) community scales dispersal stochasticity. Line plots (left-hand side)

600   present densities of extinct and remaining species in relationship to their competitive abilities (as

601   indicated by their local reproductive rate); densities were calculated using a kernel density

602   estimation procedure (*Density* function; base package; R Development Core Team, 2011).

603   Boxplots (right-hand side) showing deviations from mean dispersal at time of extinction. These

604   deviations were calculated as $(a - \bar{a})/\bar{a}$ with a as realized dispersal and $\bar{a}$ as mean dispersal at time

605   of extinction event; this measure ranges between -1 and 1.   solid red line indicates the general

606   predictions of local richness for different mean dispersal under no dispersal stochasticity (see Fig.

607   2). Black circles indicate "outliers" that fall outside the boxplot maximum or minimum range (i.e.

608   < 5% of the data points).
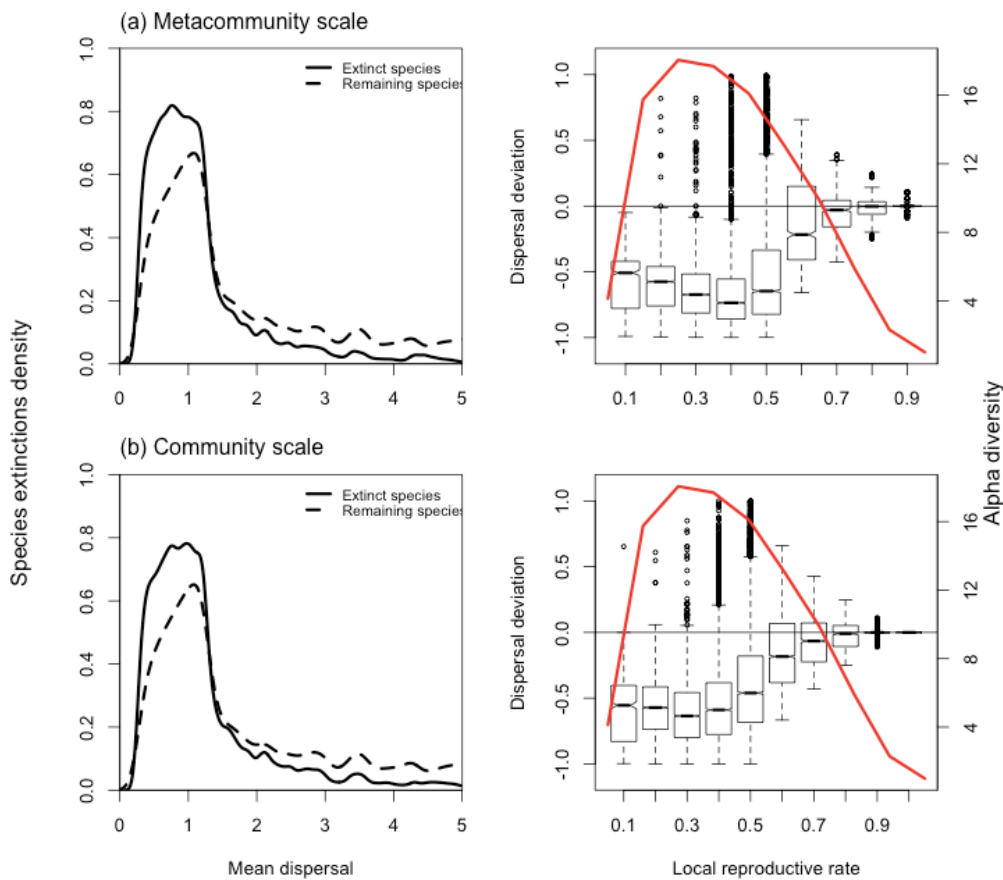
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