1   **Biodiversity Inhibits Species' Evolutionary Responses to Changing**

2   **Environments**

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31 **ABSTRACT**

32 Despite growing interplay between ecological and evolutionary studies, the question of how

33 biodiversity influences evolutionary dynamics within species remains understudied. Here,

34 using a classical model of phenotypic evolution in species occupying a patchy environment,

35 but introducing global change affecting patch conditions, we show that biodiversity can

36 inhibit species' evolution during global change. The presence of several species increases the

37 chance that one or more species are pre-adapted to new conditions, which restricts the

38 ecological opportunity for evolutionary responses in all the species. Consequently,

39 environmental change tends to select for changes in species abundances rather than for

40 changing phenotypes within each species. The buffering effects of species diversity that we

41 describe might be one important but neglected explanation for widely observed niche

42 conservatism in natural systems. Furthermore, the results show that attempts to understand

43 biotic responses to environmental change need to consider both ecological and evolutionary

44 processes in a realistically diverse setting.

INTRODUCTION.

Understanding how ecosystems respond to environmental change is fundamental to explaining diversity patterns and to predicting future responses to anthropogenic global changes. Broadly, ecosystems can either respond by ecological changes in species abundance and composition, or by evolutionary changes in the constituent species. Despite growing recognition that ecological and evolutionary dynamics interact strongly (Yoshida *et al.* 2003; Bonsall *et al.* 2004; Pulido & Berthold 2004; Davis *et al.* 2005; Hairston *et al.* 2005), the question of how biodiversity affects the evolutionary responses of species to environmental change has been neglected. Evolutionary theory typically treats species in isolation, considering the population genetics of single populations or pairs of interacting species such as hosts and parasites. In principle, the presence of co-occurring species might stimulate evolution within species, for example by initiating co-evolutionary interactions (Stenseth & Maynard Smith 1984; Christensen et al. 2002; Thompson & Cunningham 2002; Otto & Nuismer 2004). Alternatively, interactions among co-occurring species might inhibit evolution and promote stasis (Stenseth & Maynard Smith 1984; Ackerly 2003; Brockhurst *et al.* 2007). However, those few studies that have considered the effect of species richness on species evolution have focused on constant physical environments, rather than looking at the interaction between ecological and evolutionary responses to environmental change.

Here, we use a modified version of the Levene model, a classical model widely used at the interface between ecology and evolution (Levene 1953; de Meeus & Goudet 2000; Kisdi 2001), to show that biodiversity inhibits evolution within species during global change. The model considers coexisting and evolving species in a metacommunity (Leibold *et al.* 2004) consisting of patches linked by dispersal but differing in environmental conditions. In a stable environment the community comprises a guild of species each specialised on one of the patches (Levene 1953; Kisdi 2001). An individual's fitness is determined by the match between a single phenotypic trait, which can evolve, and the optimum phenotype in the patch where it lives (see Materials and Methods). Given this starting point, we ask how does biodiversity affect the system's response to a period of global change represented by an average increase in optimum phenotype across patches (Fig. 1). Possible biological examples are (1) an overall global warming affecting optimum trait values for plant species in a series of microclimates; each may become cooler or warmer, but the global trend is to become warmer, or (2) the effect of globally increased nitrogen deposition or acidification that affects particular locations differently.

78   In our model, species richness is maintained by occupation of distinct patches in the

79   environment by each species. Therefore, the effects of environmental heterogeneity and

80   species richness are potentially confounded. To distinguish the effects of environmental

81   heterogeneity and biodiversity, we consider amounts of evolution for each species under three

82   treatments shown in Fig. 1. First, under treatment A, we simulated each species in turn alone

83   in an environment containing just one patch, i.e. a spatially uniform environment. Sixteen

84   hundred runs with different initial and final optima of the patch were performed, such that

85   runs differed in the rate and magnitude of environmental change affecting the patch (Fig. 1,

86   Treatment A). For treatments B and C, we grouped the 1600 runs of initial and final optima to

87   obtain 800 systems with two patches, 400 systems with four patches, and 100 systems with

88   sixteen patches. Under treatment B, we simulated each species in turn, alone in an

89   environment containing all the patches (Fig. 1, Treatment B). Under treatment C, we

90   simulated all species together in an environment containing all the patches (Fig. 1, Treatment

91   C). Runs of these systems for a given number of patches differ both in rates of environmental

92   change in each patch and in the similarity in optima between patches. Matched runs of

93   treatment B and C allow comparison of the same species evolving in the same heterogeneous

94   environment but with or without the presence of other species. Matched runs of treatment A

95   and B allow comparison of the same species experiencing the same conditions of

96   environmental change in a given patch but depending on whether other ecologically distinct

97   patches are present or not. We explore results for a range of dispersal rates and a range of

98   species environmental tolerances.

99

100   **MATERIAL AND METHODS**

101   **Population dynamics**

102   The model assumes an environment of 1, 2, 4 or 16 patches, each characterised by a different

103   optimum phenotype, X_i. The model was programmed in R (R Development Core Team 2003).

104   Dynamics of each species were followed by keeping track of the abundances, phenotypes and

105   locations of their descendents. Population dynamics followed this sequence:

106   *i) Dispersal.* a fraction of propagules produced in a patch (see step *iv*) disperse

107   globally to all patches while the rest remain in their parental patch. Different patches thus

108   contribute different numbers of individuals to the next generation. We ran the model for

109   dispersal rates equal to 10^{-4}, 10^{-3}, 0.1, 0.2, 0.5, 0.8 and 1.

110   *ii) Recruitment.* Patches recruit individuals from the pool of propagules up to a

111   carrying capacity of $K=10,000$. Individuals thus compete for recruitment sites as in a lottery

112   and phenotypes have a probability of being recruited proportional to their frequency in the

113   pool.

114   *iii) Growth.* At the end of the season, recruited individuals have a biomass that

115   depends on the similarity between their phenotypic trait, *x* and the optimum phenotype X_i of

116   the patch they find themselves in:

117    $biomass = 95 \times \exp\left(-\dfrac{(x - X_i)^2}{2 \times \omega^2}\right)$, where ω determines the growth range of individuals, with ω^2

118   inversely proportional to the strength of stabilizing selection. ω is thus the parameter that

119   controls the environmental tolerance of phenotypes; we ran the model for $\omega = 10^{-4}$, $5\ 10^{-4}$, 10^{-3},

120    $2\ 10^{-3}$ and 10^{-2}.

121   *iv) Reproduction.* Sexual reproduction occurs within a patch among individuals of the same

122   species. The number of propagules produced locally by species is their local biomass times

123   their fecundity, where the fecundity is assumed to be the same for all the species. The

124   offspring phenotypes are drawn from a normal distribution with mean and variance equal to

125   the mean and variance of the phenotype distribution of the parental local population

126   (weighted by biomass; Lande 1976). Simulations assuming clonal reproduction, in which

127   offspring inherit a phenotype drawn from a Gaussian distribution around their parent's

128   phenotype, yielded the same conclusions as those we present here (Fig. S1).

129   The model is intermediate between a soft and hard selection model (Christiansen

130   1975, Wallace 1975), with local density regulation in patches (soft selection) but a variable

131   contribution of each patch to the next generation (hard selection). Under stable conditions,

132   distinct phenotypic species each specialized on the environment of a single patch can coexist

133   assuming that patches are distinct relative to the environmental tolerance of individuals and

134   that dispersal is not too high (otherwise generalist phenotypes evolve; de Meeus & Goudet

135   2000; Kisdi 2001).

136

137   **Environmental change**

138   We modeled climate change as a linear change in optimum trait values in each patch from

139   initial values drawn at random between limits (0.945 to 0.975) to final values drawn at

140   random between higher limits (0.955 and 0.985). We ran the model under constant conditions

141   for 400 generations to obtain steady state before climate change began, starting with each

142   species assigned an initial phenotype matching the optimum for one of the patches. Climate

143   change occurred over 50 generations from their initial values to final values. After climate

144 change, we ran the model for a further 50 generations to let the communities recover from the

145 climate change. We then calculated the final amount of phenotypic evolution for each species

146 as the "standard deviation" of final trait values from the ancestral phenotype:

147 $$\sqrt{\frac{\sum_{individuals}\left(FinalPhenotype_{individual} - AncestralPhenotype\right)^2}{n_{individuals}}}\,.$$

148 We chose this measure because a simpler measure such as the change in mean phenotype

149 would be inaccurate in cases in which a species diversifies to occupy patches with both higher

150 and lower optimal phenotypes than its ancestral patch, i.e. it could yield an amount of

151 evolution of zero when in fact considerable evolutionary change had occurred. Extinct species

152 were excluded from calculations of amounts of evolution. By choosing different random and

153 final patch values our simulations incorporate variation in both the similarity of optima

154 between patches and the relative rate of environmental change versus evolution, the key

155 parameters affecting species' responses.

156

157 **RESULTS**

158 Increasing the number of species in the system reduces the amount of evolution in those

159 species that survive environmental change (Fig. 2a). Increased heterogeneity on its own, in

160 terms of the presence of additional empty patches (Treatment B, indicated by hatched bars

161 and dashed lines in Figs. 2 & 3), can increase or decrease the amount of evolution compared

162 to a single species in a uniform environment (Treatment A), depending on exact conditions

163 (discussed further below). However, when other species are present (Treatment C, indicated

164 by solid bars and lines in Figs 2 & 3), the amount of evolution in species that survive climate

165 change is reduced on average, compared to the same species on its own in either a uniform

166 (Treatment A) or a heterogeneous (Treatment B) environment. For example, with sixteen

167 species present, the average amount of evolution per species is 73% less than when the same

168 species is on its own in a uniform environment (Treatment C versus Treatment A) and 81%

169 less than the same species with all sixteen patches present but empty (Treatment C versus

170 Treatment B, for medium values of dispersal and environmental tolerance as in Fig. 2).

171   The reason why diversity decreases the amount of evolution is that, as diversity

172 increases, species are increasingly restricted to only those patches with final optima close to

173 the species' initial optimum phenotype, despite being able to evolve to occupy more

174 dissimilar patches when other species are absent (Fig. 2b). In other words, competitive

175 interactions among co-occurring species promote stabilizing selection and niche conservatism

176 (Holt & Gaines 1992; Ackerly 2003, 2004): species migrate to occupy new patches with

177 conditions closely matching their initial phenotype, rather than adapting to change in their

178 original patch. We now discuss the mechanisms in more detail and the effects of varying key

179 parameters of dispersal and environmental tolerance.

180

181 **Effect of environmental heterogeneity on evolution with just one species present**

182 In a single patch system, species either adapt to the change or go extinct, depending on the

183 rate of environmental change relative to the species' environmental tolerance and potential

184 evolutionary rate (Burger & Lynch 1995). If we increase the number of patches, but still with

185 only one species present, the species can either occupy all, some or none of the patches at the

186 end (contrast species 10 and 16, Treatment B, Fig. 1). Increasing the number of patches

187 increases the chance of species surviving, except at very high dispersal rates, in which case

188 species are maladapted to all patches (Fig. 3 d-f, dashed lines).

189   Environmental heterogeneity can either increase or reduce the amount of evolution for

190 the following reasons. Additional patches can have optima during or after the period of

191 change that are similar to those in the species' initial patch. This is especially likely with a

192 large number of patches. In some cases, this prevents a species adapting to change in its own

193 patch, even if it could do so with no other patches present (Fig. 1, compare Treatments A and

194 B for species 10). This scenario reflects niche conservatism: the species tracks its optimal

195 environment by migrating to new patches rather than by adapting to changes in its initial

196 patch. The amount of evolution is reduced. In other cases, additional patches with similar

197 optima provide 'stepping stones' for the species to survive and adapt to the changes in its own

198 patch, when it would not have been able to with no other patch present (Fig. 1, compare

199 Treatments A and B for species 16). This can lead to an increase in the amount of evolution

200 with increasing heterogenity. Which outcome occurs in a given simulation depends on the

201 similarity of patch optima and their trajectories during environmental change.

202   The frequency of those two cases, and hence the average effect of patch heterogeneity

203 on evolution, varies with the number of patches, the rate of environmental change, the

204 dispersal rate, and the environmental tolerance of species (Fig. 3 a-c, dashed lines). At

205 intermediate values of dispersal and environmental tolerance, the amount of evolution

206 decreases with two or four patches compared to a single patch, because species migrate into

207 patches with final optima similar to initial conditions in their original patch (Fig. 1 –

208 Treatment B, species 10; Fig. 2b, mid and dark grey dashed lines). However, with sixteen

209 patches present, the amount of evolution is greatly increased, because patches tend to have

210 more similar optima and provide 'stepping-stones' for species to adapt to conditions farther
211 removed from their original phenotype (Fig. 1 – Treatment B, species 16; Fig. 2b, light grey
212 dashed lines). With very high dispersal rates and very low environmental tolerances, the
213 amount of evolution decreases monotonically with patch number: very high dispersal rates
214 prevent local adaptation because of remixing of the population, whereas low environmental
215 tolerance leads to high mortality in patches with optima divergent from the species'
216 phenotype. With high environmental tolerances and low dispersal rates, the amount of
217 evolution increases monotonically with the number of patches: high environmental tolerance
218 enables the species to colonize new patches and survive under changing conditions, and low
219 dispersal allows local adaptation to take place (Fig. 3a-c, dashed lines). To summarize, there
220 are no simple predictions concerning the effects of patch heterogeneity on amounts of
221 evolution when only a single species is present.
222
223 **Effect of biodiversity on evolution for a given environmental heterogeneity**
224 The situation changes in diverse communities, i.e. when all the patches contain a separate
225 species at the start of the run. The presence of other species increases the chance of extinction
226 compared to a single species in a multi-patch system (Fig. 3 d-f, contrast solid and dashed
227 lines). This occurs because of strong lottery competition and the increased chance that other
228 species are pre-adapted to the final environmental conditions. There are rare cases in which
229 the amount of phenotypic evolution is increased for a given species, but the average amount
230 of phenotypic evolution per species is decreased because diversification into multiple patches
231 is inhibited (contrast Fig.1, Treatment B and C for the two example species; Fig. 3a-c,
232 contrast solid and dashed lines). The decrease is significant under nearly all scenarios when
233 environmental tolerance is intermediate or high, but weak and not significant for most
234 scenarios with low environmental tolerance (Fig. 3). This is because extinction in response to
235 environment change is so high when environmental tolerance is low that species barely meet
236 other species in treatment C. For example, in an environment with two species at the lowest
237 environmental tolerance, a species alive at the end of a run has only between 1 and 8% chance
238 of being in competition with the other species. To conclude, the presence of other species
239 decreases phenotypic evolution per species because diversification into multiple patches is
240 inhibited.
241
242 **Combined effect of biodiversity and environmental heterogeneity on species evolution**

243   Increasing both the number of different patches and the number of species decreases the

244   amount of phenotypic evolution under all conditions (Fig. 3 a-c, solid lines). Across all trials,

245   species surviving in the 2, 4 and 16 species cases evolved on average between 6 to 36, 15 to

246   55 and 16 to 70% less than they did on their own with just their own initial patch present.

247   This occurs because more species shift to different patches rather than adapting to change in

248   their own patch (Fig. 2b). The effect is strongest at intermediate values of both dispersal and

249   environmental tolerance: if dispersal is too low, species adapt to local conditions; if

250   environmental tolerance is too high, species can diversify to occupy most patches; high

251   dispersal and low environmental tolerance lead to high extinction (Fig. 3 a-c, solid lines).

252   Increasing both the number of different patches and the number of species affects the

253   extinction rate in ways that depend on parameter values. At low and high dispersal rates, and

254   at the lowest environmental tolerance, the chance of extinction increases with diversity (Fig. 3

255   d-f, solid lines). At intermediate dispersal rates and intermediate or high environmental

256   tolerances, extinction rate rises then falls with diversity (Fig. 3 d-f, solid lines). To conclude,

257   species diversity tends to promote stabilizing selection on ecological traits, inhibiting

258   evolutionary responses within species and leading to niche conservatism. As a result, a greater

259   proportion of the system's response to the change in environment occurs through changes in

260   species abundances (fig. 4), rather than evolutionary changes in species phenotypes.

261

262   **DISCUSSION**

263   We conclude that species diversity can have profound effects on evolution. Because most

264   ecological trait variation is among species rather than within them, at least in non-neutral,

265   competitive communities, environmental changes tend to select for changes in relative species

266   abundances rather than for changing phenotypes within each species. In addition, species in a

267   diverse communities tend to have, on average, lower effective population sizes than those on

268   their own as a result of competitive interactions, which might slow down rates of adaptive

269   evolution (Johansson In Press) and increase the role of drift relative to selection. Other

270   models have considered evolution in species rich systems. Stenseth and Maynard Smith

271   (1984) used a general model of evolution in species assemblages occupying a constant

272   physical environment. They concluded that ecosystems may occupy one of two evolutionary

273   modes: a Red Queen scenario in which evolutionary change is perpetual versus a mode of

274   evolutionary stasis among species. They discussed the likely effects of physical

275   environmental change, in terms of evolution in the 'stasis mode' being entirely dependent on

276   external changes, but did not address the question of how species richness and ecological

277 responses affect evolutionary responses to such changes. Other authors have used similar
278 models to ours to explore the initial diversification of an ancestral population into multiple
279 habitats or niches, but again none addressed the question of how diversity affects evolution
280 within species (Dieckmann & Doebeli 1999; Kinzig *et al.* 1999; Tilman & Lehman 2001).
281 Johansson (in press) has independently reached similar conclusions to ours in a model of
282 resource competition among two and three species. Our model shows that the effects increase
283 progressively with addition of more species, and reveals some circumstances in effects are
284 weaker, namely extremely high or extremely low dispersal rates or levels of environmental
285 tolerance. Empirical evidence is even rarer: we know of only one recent study, which shows
286 that adaptive radiation of *P. fluorescens* in a laboratory mesocosm is inhibited by the presence
287 of competing species (Brockhurst *et al.* 2007).

288   Our model assumes a simple mechanism for species coexistence and simple
289 evolutionary mechanisms but the findings were robust across a range of parameters and we
290 believe they would apply in a range of circumstances. The model considers a guild of
291 competing species partitioning a patchy environment. Other formulations would be possible
292 in which species partition use of a continuous range of resources (Lehman & Tilman 1997;
293 Ackermann & Doebeli 2004). In addition, we assume that the aspect of the environment being
294 partitioned by species is also the aspect experiencing environmental change. More complex
295 multi-dimensional environments combining niche axes and general aspects of physical
296 environment could be considered (Ackerly *et al.* 2006). Allowing for additional interactions
297 such as antagonism and mutualism might increase the frequency of scenarios in which
298 diversity stimulates evolution (Fussmann *et al.* 2007; Johnson & Stinchcombe 2007), but we
299 believe the tendency for high diversity of competing species to inhibit evolutionary responses
300 to abiotic change would be robust to all of these alternatives.

301   Real ecosystems typically display much greater diversity than we can simulate in our
302 models. So when and where does most evolution occur? Possible answers include: in
303 marginal or unsaturated environments (Millien 2006); in response to small or very slow
304 environmental changes; or when environmental change creates entirely new conditions
305 outside the range of initial optimal trait values, or new combinations of optima for several
306 traits, in which case large-scale turnover and diversification to fill new niches may occur
307 (Tilman & Lehman 2001; Jackson & Erwin 2006; Carroll *et al.* 2007).

308   Our results have important implications for understanding evolution in the real world.
309 Biologists long held the view that evolution occurred over longer timescales than ecological
310 processes. Recently this has been challenged by theory and experiments showing that

evolution can occur over short timescales (Agrawal 2003; Yoshida *et al.* 2003; Pulido & Berthold 2004; Davis *et al.* 2005; Hairston *et al.* 2005; Carroll *et al.* 2007). However, measures of evolutionary rates over longer timescales tend to be much slower than rates predicted from simple systems (Kinnison & Hendry 2001; Ackerly 2003, 2004), with many species displaying niche conservatism and tracking change by migration rather than evolution (Pease *et al.* 1989; Ackerly 2003). Numerous mechanisms have been proposed to explain such evolutionary stasis, but none seems fully satisfactory (Hansen & Houle 2004). The buffering effects of species diversity, a ubiquitous feature of natural systems, might be one important but neglected factor explaining why evolution appears to be "too slow". Attempts to understand how focal species or ecosystems respond to environmental change need to consider both ecological and evolutionary processes in realistically diverse assemblages.

AUTHOR CONTRIBUTIONS

All authors contributed equally to this work. E. J. programmed the initial model and performed initial analyses. C. d. M. and T. G. B. contributed equally to devising the model, performing analyses and writing the manuscript.

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417

418 **ONLINE SUPPORTING INFORMATION**

419 The following supplementary material is available for this article:

420 **Figure S1**. Effect of diversity on species' evolutionary change in a model with asexual

421 reproduction.
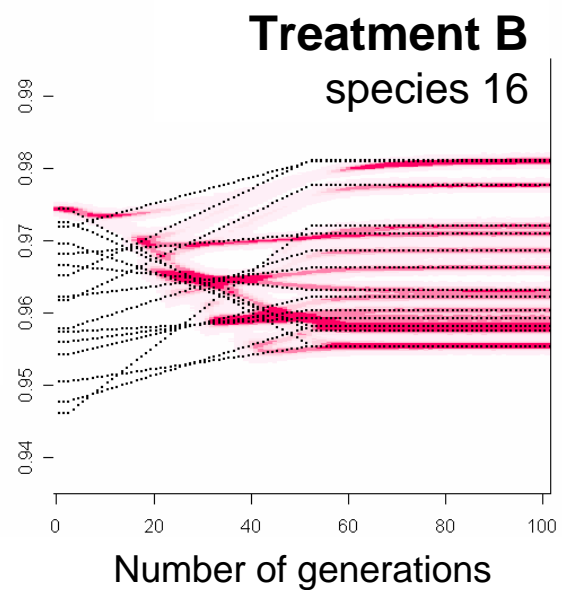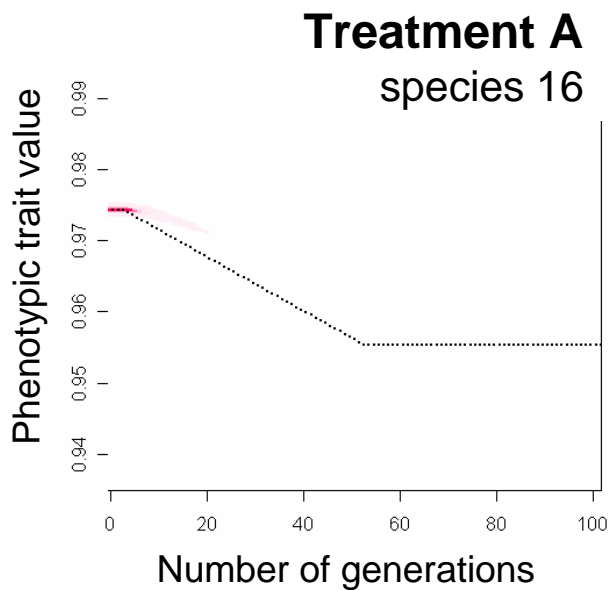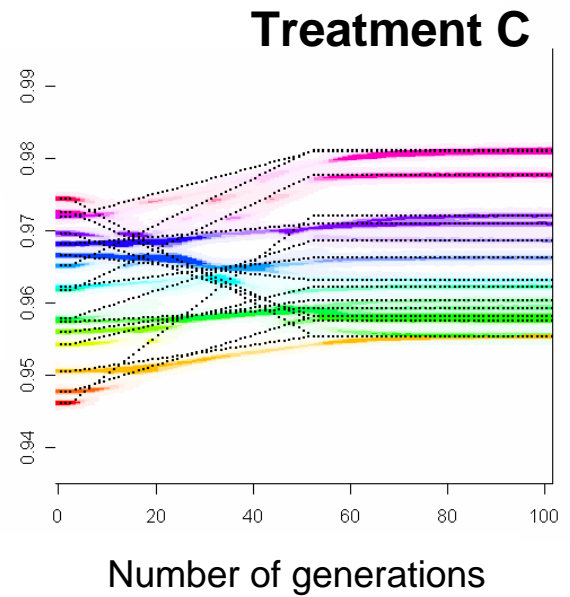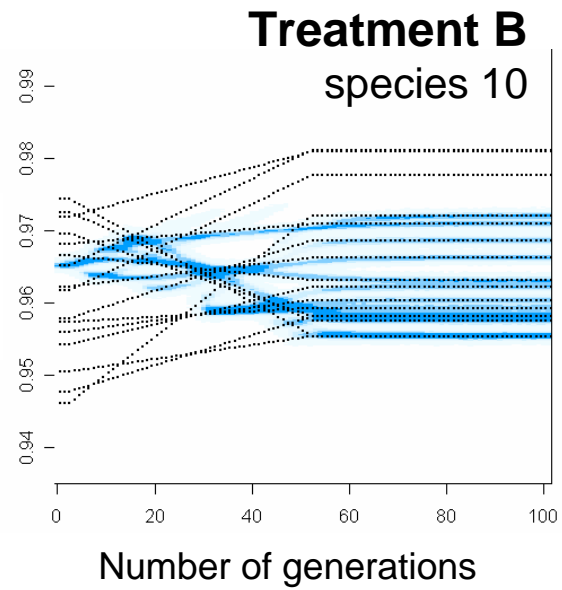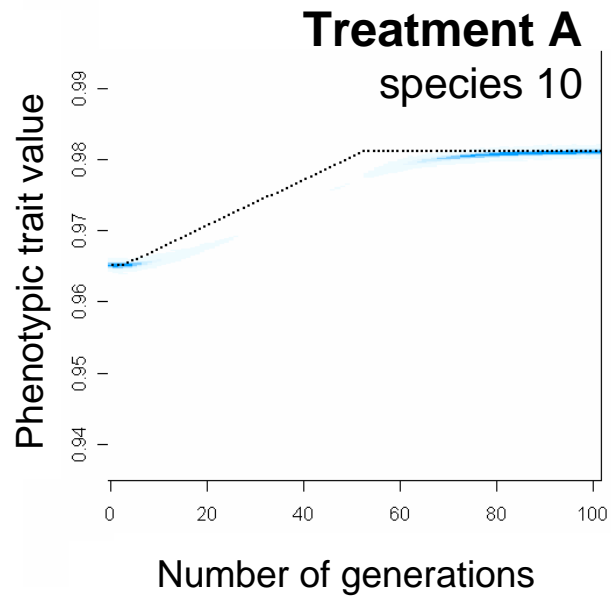
422

423 **FIGURE LEGENDS**

424 **Figure 1.** A typical simulation run showing the effects of environmental change on a sixteen

425 species system. **Treatment A:** Two examples showing the one species run with presence of

426 just the patch that it originally was adapted to: species 10 (blue) and species 16 (purple).

427 **Treatment B:** The same two example species with all other patches present but unoccupied.

428 **Treatment C:** All species and patches present. The simulation starts at equilibrium with each

429 species adapted to one of the patches. The optimum phenotype in each patch changes for 50

430 generations towards a new stable value (black dots). Species phenotypes are represented by

431 different colours and intensity represents the density of individuals with each trait value. Both

432 illustrated species can adapt to change in their own patch in isolation, diversify to occupy

433 several patches including their original one in a heterogeneous but unoccupied environment,

434 but they shift from their original patch into other patches in a heterogeneous but occupied
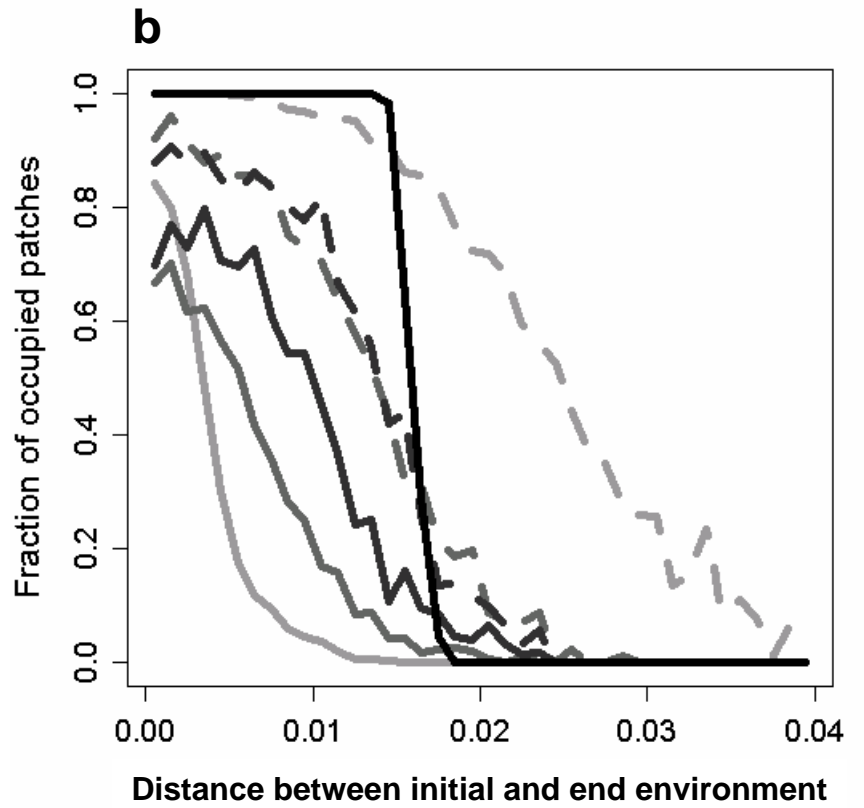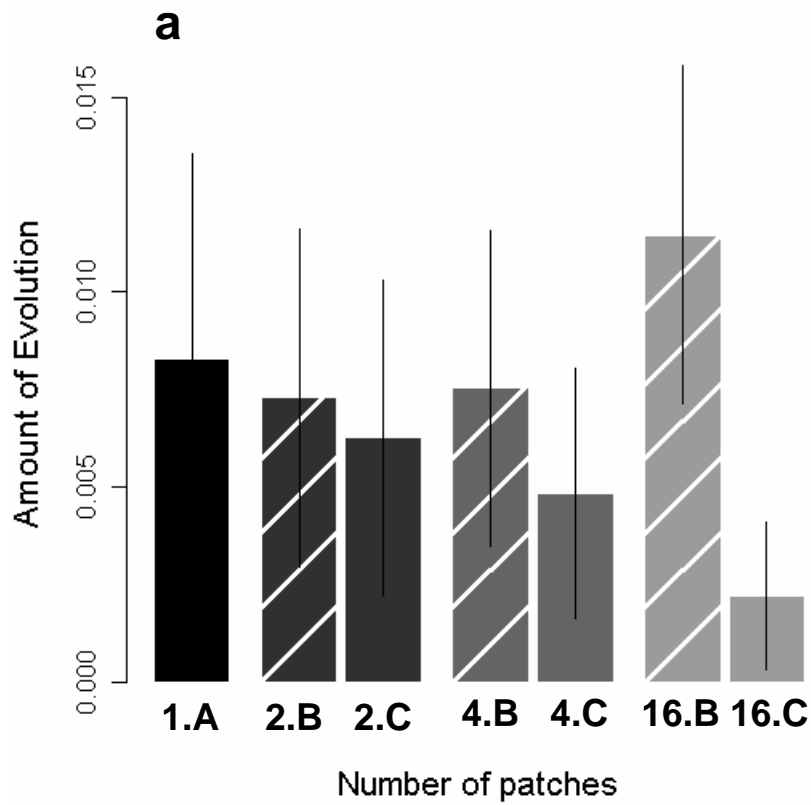
435 environment.

436 **Figure 2**. (a). The amount of evolution per species decreases with diversity. The numbers

437 below each column indicates the number of patches present. The letters indicate the

438 treatment: treatment B with just one species present (also indicated by hatched shading), or

439 treatment C with all species present (also indicated by full shading). The effects of diversity

440 can be compared between treatments B and C in environments with the same numbers of

441 patches (matched by degree of shading) or the same treatment across environments with

442 different numbers of patches. (b) The fraction of final patches that are occupied by a species

443 in relation to the distance between the optimal phenotype of the final patch and of the species'

444 initial patch. The greater the phenotypic distance, the more a species has had to evolve to

445 occupy the patch. When diversity increases, species become more restricted to patches that

446 are similar in optimum phenotype to their initial patch. Shading denotes the numbers of

447 patches: with 1 (black), 2 (dark intermediate grey), 4 (light intermediate grey), and 16

448 (lightest grey). Dashed lines indicate results from runs with only one species (treatment B),

449 solid lines indicate results from runs with all species present (treatment C).

450 **Figure 3.** The average amount of evolution per species (a-c) and fraction of species going

451 extinct (d-f) across environments containing 1, 2, 4 and 16 patches with only one species

452 (dashed lines, treatments B), or with all species present (solid lines, treatments C), across a

453 range of dispersal and environmental tolerances. Line shading represent dispersal rates of 10^{-4}

454 (black), 0.1 (dark intermediate grey), 0.5 (light intermediate grey), and 1 (lightest grey).

455 Panels (a and d), environmental tolerance 10^{-4}; (b and e) environmental tolerance 10^{-3}; (c and

456 f) environmental tolerance 10^{-2}. Differences between treatments B and C for 2, 4 and 16

457 species are non significant in panel (a) except for the two intermediate values of dispersal

458 with 16 species; they are all significant in panels (b) and (c) except for the highest dispersal

459 rate with 4 and 16 species in the latter panel.

460

461 **Figure 4**. Relative contribution of changing species abundance to the overall response of the

462 community to environmental change, depending on the number of patches and species

463 (Treatment C). The community response was characterised broadly as the change in average

464 phenotype from the start to the end of each simulation. From this the contribution of changes

465 in species abundance were calculated as the sum of change in mean phenotype due to

466 changing species abundances, defined as the change in relative abundance of the species

467 multiplied by the initial patch value. Note that an equivalent measure to the standard deviation

468 used for evolutionary responses within species cannot be calculated for ecological response

469   (because there is no single starting phenotype around which to calculate a standard deviation),

470   but the measure we use suffices to show the increase in importance of ecological changes.

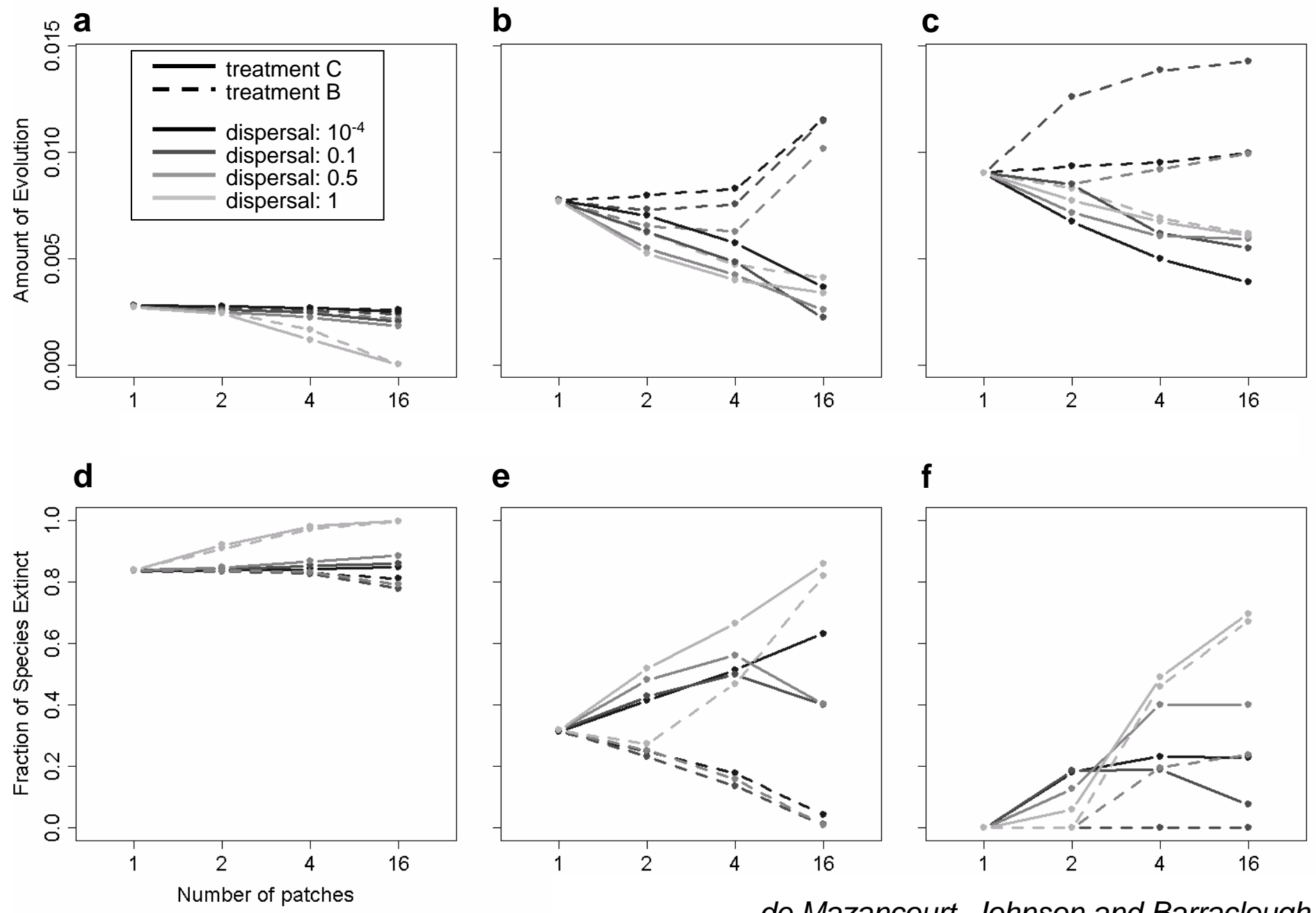471   Dispersal=0.1 and environmental tolerance = 0.001.

472

de Mazancourt, Johnson and Barraclough
Fig. 1

a

Amount of Evolution (y-axis): 0.000, 0.005, 0.010, 0.015

x-axis categories: 1.A, 2.B, 2.C, 4.B, 4.C, 16.B, 16.C

Number of patches

b

Fraction of occupied patches (y-axis): 0.0, 0.2, 0.4, 0.6, 0.8, 1.0

x-axis: 0.00, 0.01, 0.02, 0.03, 0.04

Distance between initial and end environment

de Mazancourt, Johnson and Barraclough
Fig. 2

environmental tolerance: 10^{-4} environmental tolerance: 10^{-3} environmental tolerance: 10^{-2}

a

Amount of Evolution

treatment C
treatment B

dispersal: 10^{-4}
dispersal: 0.1
dispersal: 0.5
dispersal: 1

b

c

d

Fraction of Species Extinct

Number of patches

e

f

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Fig. 3

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Fig. 4