Eco-evolutionary community turnover following environmental change

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Abstract

Co-occurring species often differ in intraspecific genetic diversity, which in turn can affect adaptation in response to environmental change. Specifically, the simultaneous evolutionary responses of co-occurring species to temporal environmental change may influence community dynamics. Local adaptation along environmental gradients combined with gene flow can promote genetic diversity of traits under selection within populations. Here I build off existing quantitative genetic theory to study community dynamics of locally adapted species in response to temporal environmental change. I show that species with greater gene flow have lower equilibrium population size due to maladaptive immigrant genotypes (migration load). However, following abrupt environmental change that leaves all species initially maladapted, high gene flow species adapt faster due to greater standing genetic diversity. As a result, communities may undergo a transient reversal in relative abundance, sometimes only after substantial lag periods. If constant temporal environmental change is applied, the community exhibits a shift toward stable dominance by species with intermediate gene flow. High gene flow species can sometimes increase abundance under environmental change if environmental change supresses superior competitor but lower gene flow species. The community dynamics observed here parallel the purely ecological successional dynamics following disturbances and are analogous to the transient benefit of hypermutator alleles under changing environments. My results demonstrate how interspecific variation in life history can have far-reaching impacts on eco-evolutionary community response to environmental change.

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1   Introduction

Genetic diversity in quantitative traits serves as the raw material for selection (Lush 1937). Understanding how rapid changes in selection impact populations is a question with tremendous importance in biodiversity conservation, agriculture, and medicine (Gomulkiewicz and Holt 1995; Bell and Gonzalez 2009; Read et al. 2011; Alexander et al. 2014; Lasky et al. 2015; Bay et al. 2017). A substantial portion of genetic diversity in phenotypes within species is maintained due to population adaptation to local environments (Turesson 1922; Clausen et al. 1940; Leimu and Fischer 2008; Hereford 2009). Local adaptation is defined as a genotype-by-environment interaction favoring home genotypes (Kawecki and Ebert 2004). When populations are locally adapted, greater gene flow can increase within-population diversity due to immigration from populations adapted to other environments (Barton 2001; Lenormand 2002; Garant et al. 2007). Given that local adaptation is common (Leimu and Fischer 2008; Hereford 2009) and multiple co-occurring species can be simultaneously adapted to local environments, these processes could impact genetic diversity of co-occurring species and community responses to environmental change. Here I build on previous theory to study the complex role gene flow plays in communities due to its effect on genetic diversity, which induces migration load on populations but also speeds up adaptation (Pease et al. 1989; Kremer et al. 2012).

Spatial selective gradients are an important force that maintains genetic variation within species (Leimu and Fischer 2008; Hereford 2009; Sanford and Kelly 2010). Gene flow across selective gradients can be a major source of within-population diversity, with the level of gene flow influencing the level of diversity (Barton 2001). A substantial body of theory explores the conditions under which such selective gradients lead to stable polymorphism and local adaptation (Haldane 1930; Slatkin 1973; Felsenstein 1977; Kirkpatrick and Barton 1997; Behrman and Kirkpatrick 2011; Yeaman and Whitlock 2011; Le Corre and Kremer 2012). In systems where populations are locally adapted, many immigrants to a given location may be poorly suited to the local environment, as these immigrants originate from populations adapted to different environments (Haldane 1956; Mayr 1963; Kirkpatrick and Barton 1997; Lenormand 2002; Polechová and Barton 2015). These maladapted immigrants can impose a "migration load" on populations, reducing population size due to lower average fitness among individuals in a population (Barton 2001; Lenormand 2002; Farkas et al. 2013; Polechová and Barton 2015). Assuming organisms have a limited ability to disperse into appropriate environments (e.g. passive dispersers), migration load increases with increasing rate and spatial scale of gene flow (among other factors discussed below, Slatkin 1973; Kirkpatrick and Barton 1997; Polechová and Barton 2015).

The observation that humans are rapidly changing global environments has spurred interest in understanding temporal changes in selection (Bay et al. 2017; Siepielski et al. 2017). Environmental change can cause population decline, extinction, or persistence

via plasticity or evolution (Aitken et al. 2008). Theoretical and experimental studies have largely focused on two scenarios of environmental change: 1) a rapid, abrupt shift from a historical selection regime to a new one (Gomulkiewicz and Holt 1995; Orr and Unckless 2008) or 2) sustained change in selection through time (Pease et al. 1989; Lynch and Lande 1993; Gonzalez et al. 2013). Most theoretical studies have focused on the binary outcome of whether species survive or go extinct following environmental change. For example, a number of authors have investigated factors influencing the probability of evolutionary rescue (Gomulkiewicz and Holt 1995; Orr and Unckless 2008; Bell and Gonzalez 2009), which is defined as adaptation that prevents extinction following environmental change (Gonzalez et al. 2013). Pease et al. (1989) and Lynch and Lande (1993) studied the maximal rates of environmental change that allow species to persist (avoid extinction). An emerging area of inquiry has investigated community evolutionary rescue, roughly defined as evolutionary rescue of multiple co-occurring species (Fussmann and Gonzalez 2013; Kovach-Orr and Fussmann 2013; Low-Décarie et al. 2015). Still, little is known about how evolutionary response to rapid environmental change impacts abundance patterns. Despite this gap, community and ecosystem processes are strongly influenced by abundance dynamics of component species, such that understanding abundance responses to environmental change is a key goal of community and ecosystem ecology (Loreau 2010; Clark et al. 2014*b*).

Among the factors that determine population response to environmental change are initial population size and genetic diversity in the trait under selection. When populations are initially small before environmental change, a species faces a greater risk of stochastic extinction following environmental change (Gomulkiewicz and Holt 1995). Additionally, if genetic variants do not exist within a population that are beneficial after environmental change then a population will wait for new mutations or immigrant alleles (e.g. Orr and Unckless 2008), a scenario most relevant when adaptation is oligogenic. Alternatively, standing variation within populations may allow more rapid adaptation, if adaptive variants are already present at the time of environmental change (Bonhoeffer and Nowak 1997). Such standing variation can be caused by gene flow along spatial selective gradients (Kirkpatrick and Barton 1997). In particular, quantitative genetic models of local adaptation are relevant to adaptation to anthropogenic change because phenotypes involved in climate adaptation are often complex with polygenic architecture (Bay et al. 2017).

The effects of rapid environmental change on biodiversity are partly influenced by how multiple co-occurring species simultaneously respond to environment (Bradshaw 1984; Jackson and Overpeck 2000; Gilman et al. 2010; Urban et al. 2012). Typically studies of community and ecosystem responses to environmental change focus on ecological mechanisms, e.g. interspecific variation in demographic and physiological response to environment (Deutsch et al. 2008; Clark et al. 2014*a*; Lasky et al. 2014). For example, interspecific variation in dispersal ability is expected to have major effects on community response to environmental change, as some species are better able to track

spatial shifts in environmental niches (Ackerly 2003; Gilman et al. 2010; Urban et al. 2013). However, most approaches ignore another level of complexity: intraspecific variation and evolutionary response within members of a community. Authors have studied how multiple species simultaneously evolve following environmental change using simulation (De Mazancourt et al. 2008; Moran and Ormond 2015; Vanoverbeke et al. 2015). However, many multi-species models typically focus on species that begin having niche differentiation along climate gradients (e.g. De Mazancourt et al. 2008; Price and Kirkpatrick 2009; Norberg et al. 2012; Moran and Ormond 2015), but what happens for species occupying similar climatic niches remains to be explored (but see Fussmann and Gonzalez 2013; Osmond and Mazancourt 2013). To date there have been few analytical results for how evolutionary responses of multiple species impact community responses to environmental change.

Here I build on an existing quantitative genetic theory of local adaptation (Barton 2001) and adaptation to a shifting optimum (Pease et al. 1989; Lynch and Lande 1993). I reframe this theory to ask how locally-adapted populations respond following environmental change. I demonstrate the complex role interspecific variation in gene flow plays in communities due to its effect on genetic diversity, which induces migration load on populations but also causes faster adaptation (Pease et al. 1989; Kremer et al. 2012). I then ask how interspecific variation in gene flow and other traits impact community dynamics following environmental change due to ecological and evolutionary processes.

2   Model and Results

I start with a model of locally-adapted populations following Pease et al. (1989) and Barton (2001), a stochastic version of which was studied by Polechová and Barton (2015). The model I use is a deterministic model of a quantitative trait z subject to a spatially-varying selective gradient. The mean per capita reproductive rate is given by

$$\bar{r} = r_m(1 - \frac{N}{K}) - \frac{(\bar{z} - \theta)^2}{2V_S} - \frac{V_P}{2V_S} \tag{1}$$

where r_m is population growth rate of optimal phenotype individuals at low density, N is census population size, K is carrying capacity, and V_P is variance of phenotype z. The first term on the right-hand side of equation 1 determines a reduction in fitness due to negative density dependence. The second term gives reduction in fitness due to the mismatch between the population mean phenotype $\bar{z}$ and the local optimum θ, and V_S gives the inverse strength of stabilizing selection. Even if the population is adapted to the local optimum (i.e. $\bar{z} = \theta$) there still may be many maladapted individuals (i.e. $V_P > 0$), whose contribution to population mean fitness is determined by the third term on the right-hand side of equation 1.

4

The optimal trait value θ changes in space (x) at rate b such that $\theta(x) = bx$ (Kirkpatrick and Barton 1997). The mean trait $\bar{z}$ at a given location x changes through time due to curvature of the cline in space, asymmetric gene flow (modeled as a Gaussian with standard deviation σ) across the cline due to spatial trends in abundance, and selection, given by the first three terms on the right hand side of the following equation, respectively

$$\frac{\partial \bar{z}}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial ln(N)}{\partial x} \frac{\partial \bar{z}}{\partial x} + V_G \frac{\partial r}{\partial z}. \tag{2}$$

The final term in equation 2 is the classic quantitative genetic result where change in the mean trait $\bar{z}$ is a function of genetic variance (V_G) multiplied by the selection function $(\frac{\partial r}{\partial z})$. Population dynamics at x are given by

$$\frac{\partial N}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 N}{\partial x^2} + \bar{r}N \tag{3}$$

where the first term on the right-hand side of equation 3 gives change to due spatial trends in abundance and unequal immigration versus emigration, and the second term gives change due to average fitness of individuals.

Assuming constant K through space, a stable equilibrium exists where all populations are locally adapted along the linear environmental gradient b, i.e. $\bar{z} = \theta$ at all x (Barton 2001). An additional consequence of local adaptation and a linear cline in $\bar{z}$ is that $\frac{\partial^2 \bar{z}}{\partial x^2} = 0$ and constant population size in space, $\frac{\partial ln(N)}{\partial x} = 0$. Here I ignore spatial boundary conditions that would inevitably result in asymmetric gene flow.

Barton (2001) allowed genetic variance within a population in the trait z under selection (V_G) to change as a function of gene flow. Thus the level of gene flow influences migration load and rate of adaptation. As gene flow increases, so does immigration of maladaptive genotypes into any given population such that $V_G = b\sigma\sqrt{V_S}$ and $V_P = V_G + V_E$ where V_E is stochastic environmental variation in z (Barton 2001).

2.1   Impacts on community structure

Two traits that population biologists and community ecologists commonly study are of clear importance in this model: the rate and scale of dispersal/gene flow (determined by σ) and reproductive rate at low density (r_m). Maladapted immigrants depress mean fitness resulting in migration load (equation 1). Migration load can thus introduce uneven community structure when species differ in σ or r_m. The equilibrium census population size (Polechová and Barton 2015) as a proportion of carrying capacity K, $\hat{N}$, is given by

$$\hat{N} = 1 - \frac{b\sigma\sqrt{V_S} + V_E}{2V_S r_m} \tag{4}$$

5

175 . To identify the maximum σ capable of persistence I set $\hat{N}$ to zero and solve the
176 inequality to obtain

$$\sigma < \frac{2V_S r_m - V_E}{b\sqrt{V_S}} \tag{5}$$

177 Here I am interested in complex effects of species traits that might yield unexpected
178 results under environmental change. While greater r_m decreases migration load
179 (equation 4) it does not impact the rate of adaptation $\frac{\partial \bar{z}}{\partial t}$ (equation 2). However, gene
180 flow, σ, plays a more complex role.

181 To study how interspecific variation in σ could structure communities along spatiotem-
182 poral environmental gradients, I now consider a community of species that vary only
183 in σ (but not other parameters e.g. K, V_S, V_E). For mathematical convenience I do
184 not consider species interactions in the majority of the results below (e.g. analytical
185 results). In many communities studied by ecologists, many species have weak interac-
186 tions with other species, e.g. bird species might have very weak interactions with most
187 other species. However, I also present simulation results below showing that many
188 of the key conclusions of my analyses are qualitatively unchanged when including
189 interspecific competition.

190 In the Barton (2001) model, greater σ increases V_G and migration load. Varying
191 migration load among species results in variation in equilibrium census population
192 size. From equation 4, the proportional reduction in $\hat{N}$ due to migration load is equal
193 to $\frac{b\sigma}{2\sqrt{V_S}r_m}$. I differentiate with respect to σ to obtain

$$\frac{d\hat{N}}{d\sigma} = -\frac{b}{2\sqrt{V_S}r_m} \tag{6}$$

194 which gives the slope of species equilibrium abundance versus gene flow. Thus the
195 shape of the species abundance distribution across species of varying σ is obtained
196 from equation 6. The parameters on the right of equation 6 are each constrained
197 to be positive so that when holding these constant across species of varying σ there
198 is clearly a negative relationship between σ and $\hat{N}$. The effect of migration load is
199 stronger and abundance distribution is steeper as the selective gradient b is steeper,
200 as stabilizing selection around the phenotypic optiumum is stronger (smaller V_S), or
201 as the fitness at low population density (r_m) decreases.

202 Note that in the equation (4) for $\hat{N}$, σ and b appear together in a product and nowhere
203 else, thus species that differ in b, the slope of selective gradients, will have similar
204 differences in $\hat{N}$ as species differing in σ. The product $b\sigma$ gives effective gene flow
205 across selective gradients, or the change in optimal phenotype z over one dispersal
206 standard deviation (Kirkpatrick and Barton 1997). Here I focus on variation in σ
207 among species, given that interspecific variation in dispersal ability of propagules and
208 gametes is a major interest in community ecology. However, it would be possible to
209 reparameterize analyses below in terms of a composite, B, relevant for the process of
210 gene flow across selective gradients $B = b\sigma$ (cf. Kirkpatrick and Barton 1997).

6

2.2 Abrupt environmental change and transient community turnover

The interesting effects of gene flow in a community context arise from the dual role of σ following environmental change. Greater σ can have a fitness benefit when population mean traits differ from the optimum, $\bar{z} \neq \theta$, such as in populations that have experienced recent environmental change (Kremer et al. 2012) or populations colonizing new environments. Greater σ proportionally increases V_G, which proportionally increases the speed of adaptation $\frac{\partial \bar{z}}{\partial t}$ for a given selection regime $\frac{\partial r}{\partial z}$ (third term on right-hand side of equation 2, first two terms remain zero).

I studied the effect of σ on the speed of adaptation using numerical simulations. I simulated non-overlapping generations whose dynamics were governed by discretized versions the above equations. Simulations were intialized with a locally-adapted population at equilibrium population size, $N = \hat{N}$ and $\bar{z} = \theta$. I chose biologically plausible parameter values (although below I study other values): $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta = 0$ (Polechová and Barton 2015). I then imposed an instantaneous change in θ such that a new phenotype, $\theta_1 = 1$, was favored, and the change in selection was the same at all locations, i.e. in my scenarios of environmental change the slope b of the spatial selective gradient did not change (Figure 1). This scenario is mathematically convenient because all populations experience the same relative change and subsequent evolution and thus no spatial trend in abundance emerges ($\frac{\partial ln(N)}{\partial x} = 0$) nor does the cline in $\bar{z}$ change ($\frac{\partial^2 \bar{z}}{\partial x^2} = 0$). As a result, V_G is unchanged.

I first compare evolution of z for two species differing only in σ ($\sigma_1 = 0.326$ and $\sigma_2 = 3.069$). Both species were subject to the same selective gradient $b = 0.05$ and the clines in the phenotype z of the two species were equal in mean before environmental change, but with greater dispersion around the mean within any local population (i.e. greater V_G, Figure 1). I found the rapid adaptation to the new θ in the high gene flow species with the lagging low σ species far behind (Figure 1).

It is clear that faster adaptation following a shift in environment (Figure 1) will lead to more rapid recovery of population mean fitness because the difference between $\bar{z}$ and θ decreases more rapidly (eqn. 1). Although species with high σ are less abundant in communities in a stable environment (eqn. 4), the faster adaptation of these species may allow them to increase their relative abundance following an environmental change. But if the environment stabilizes following the change, the effects of the change may be transient. I here analyze results from simulations of these transient community dynamics.

To demonstrate the possibility of transient community turnover I tracked the change in N over time following the instantaneous environmental shift for the two species shown in Figure 1A-B. These species differ only in σ ($\sigma = 0.326$ and $\sigma = 3.069$, respectively) and exhibit a transient reversal in relative abundance as the high σ
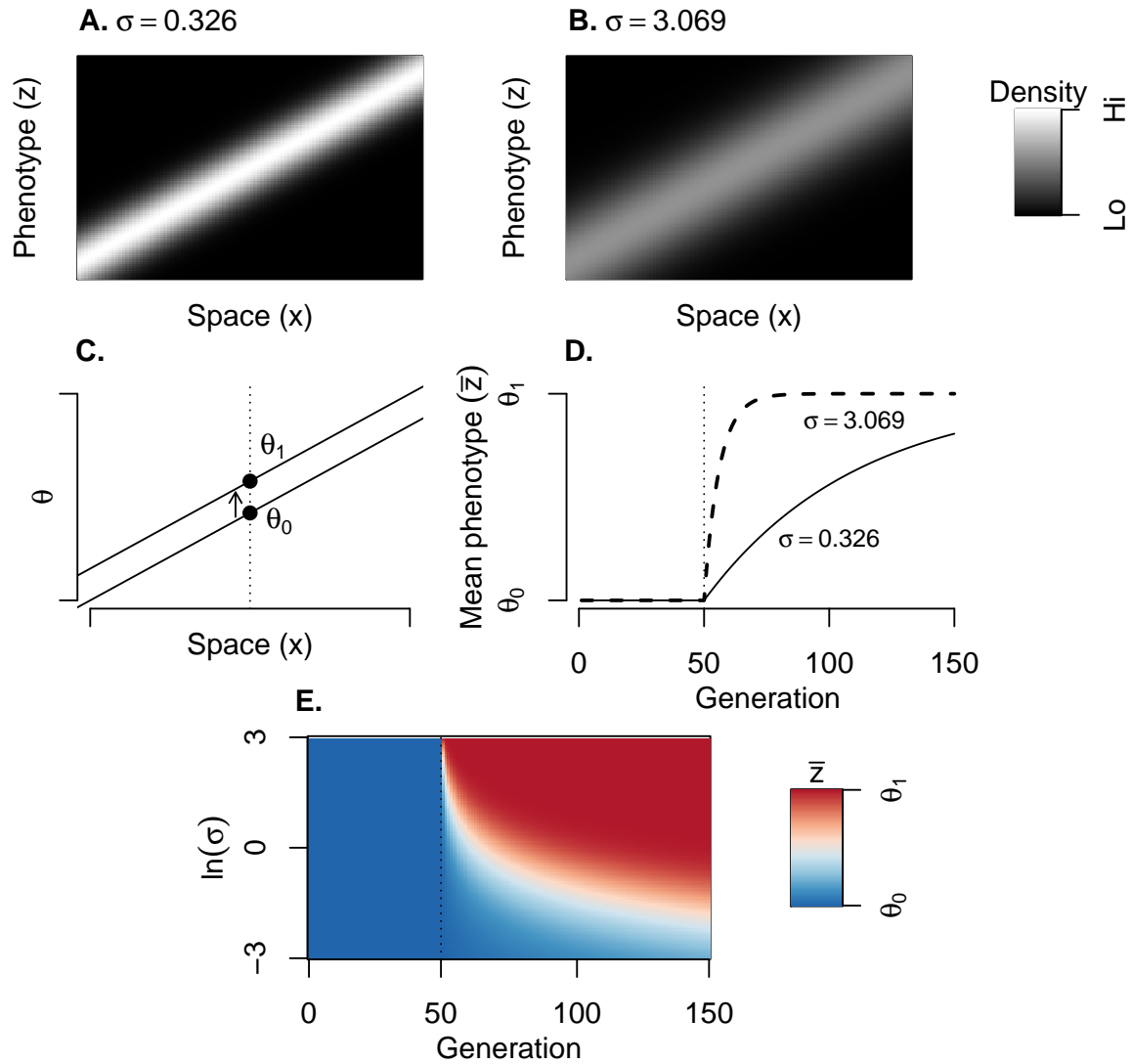
Figure 1: In a locally adapted system, variation in σ, the scale of gene flow, among species determines differences in genetic diversity and rate of adaptation. Species with low (A) and high (B) σ (gene flow) are subject to the same selective gradient b (favoring an increase in phenotype value through space from left to right) and all populations are locally adapted. However, the high σ species (B) has higher diversity of the trait under selection within populations (V_G) at a given location in space (evident via thicker gray region for any given location along the x-axis) due to maladaptive immigration. I simulated an instantaneous change in optimal phenotype (C) at generation 50. Higher σ species adapt to the new optimum faster, (D) comparing low and high σ species, (E) comparing trait evolution for species with a range of σ values. (E) Blue is the optimal trait prior to the change, and all species begin locally adapted despite differences in V_G. Red is the optimal trait following the change, and high σ quickly adapt while low σ species lag. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta_1 - \theta_0 = 1$.
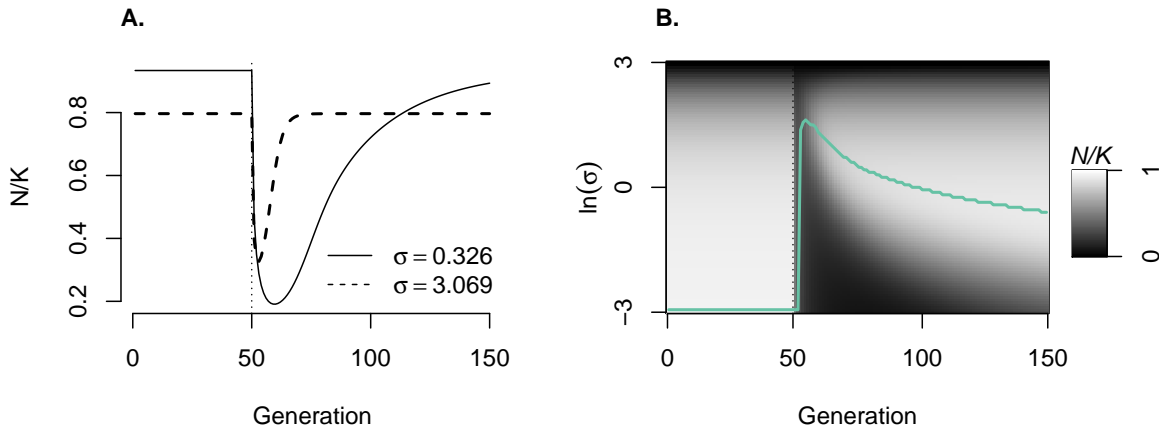
Figure 2: Changes in population size following an abrupt environmental change for species differing only in σ. (A) Time series of population size of two species (the same species as in Fig. 1A-B,1D), one with high σ and high V_G (dashed line) and one with low σ and low V_G (solid line). Populations are at equilibrium for the first 50 generations, after which an instantaneous environmental change occurs. Following this change, the species with high σ adapts faster and reaches equilibrium N before the species with low σ. (B) comparing N trajectories for species with a range of σ values. High σ quickly adapt while low σ species lag. The most abundant species at any generation is indicated by the green line. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta_1 - \theta_0 = 1$.

251 species is more abundant for an interval following the environmental change (Figure 2).
252 These simulations used the same aforementioned parameter values: $b = 0.05$, $V_S = 1$,
253 $V_E = 0.05$, $r_m = 0.5$, $\theta_0 = 0$, and $\theta_1 = 0$.

254 Looking more broadly across species with a range of gene flow one can ask how
255 composition of a diverse community might shift due to different evolutionary responses
256 to environmental change driven by interspecific variation in σ. From the aforementioned
257 simulation of species with a range of σ values (Figure 1E), I calculated at any time
258 point which species was most abundant. It can be seen that under equilibrium, the
259 species with lowest σ has highest N (eqn. 4 and Figure 2). Following an instantaneous
260 shift in θ, higher σ species dominate but gradually give way to lower σ species because
261 all species $\hat{N}$ are unchanged. However, the lag before poor dispersers adapt can be
262 quite long given the very low rate of adaptation for the lowest gene flow species (Figure
263 2).

264 Given that higher σ species have higher V_P and hence migration load (Equation 1),
265 the transient advantage of higher σ species comes from the faster approach of $\bar{z}$ to
266 θ (Equation 2). Thus the magnitude of environmental change might influence the
267 strength of community turnover, i.e. the change in relative abundances of species
268 differing in σ. Under a weak shift in θ, the benefit to adapting faster for high
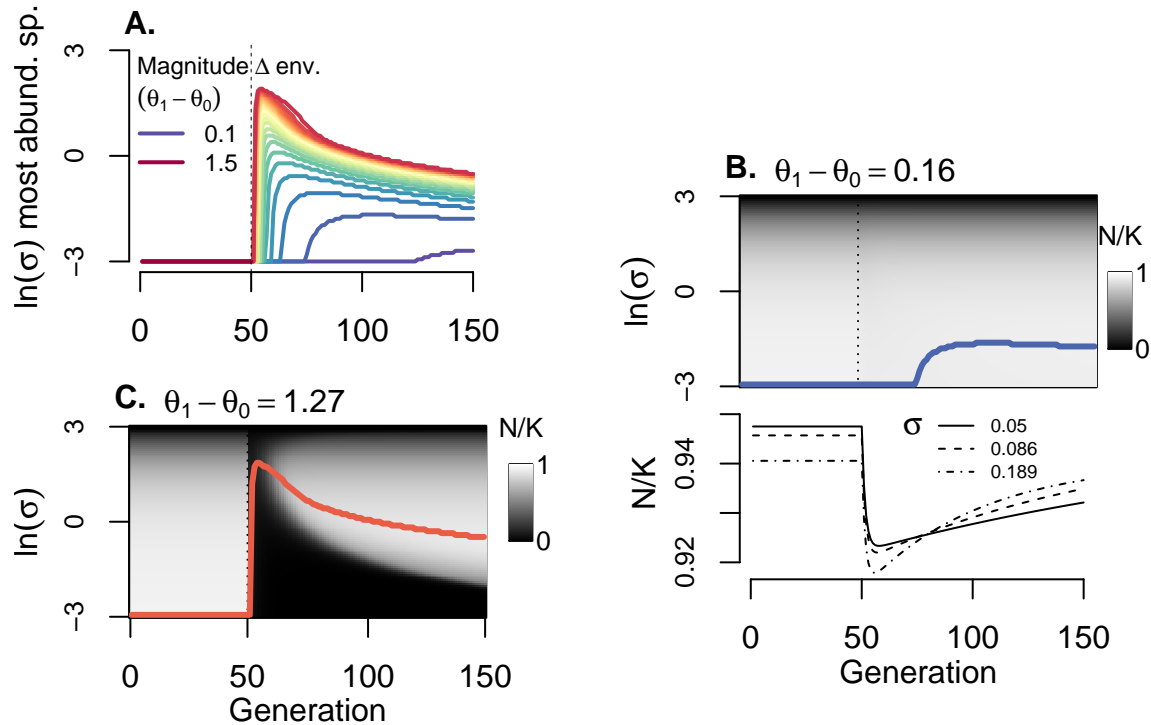
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Figure 3: How the magnitude of environmental shift affects the magnitude of community turnover. (A) In general, the greater the environmental change, the higher the σ of the most abundant species soon after the environmental change (B). When the environmental change is too extreme, all species go extinct, as for a change in θ of 1.5 in this example. (C) When environmental change is smaller, a lag between environmental change and change in species relative abundances can occurr. Populations are at equilibrium and adapted to θ_0 for the first 50 generations, when an instantaneous environmental change to θ_1 occurs. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$.

σ species is lower. Figure 3 illustrates these effects. When the magnitude of the environmental shift is large, community turnover (as determined by which species transiently dominate the community following the environmental shift) is also large. Notably, subtle shifts in environment lead to more subtle, though delayed changes in the most dominant species (blue lines in Figure 3). This lag emerges because when a species starts with greater N at equillibrium the differences between species in $\bar{r}$ after environmental change can take time to erode the initial advantage (Figure 3). Though there is a lag before changes in species relative abundances, the differences among species in $\bar{r}$ are evident shortly after environmental change in the form of differences in $\frac{\partial N}{\partial t}$ (i.e. differences among species in slope of N trajectories are quickly visible in Figure 3B).

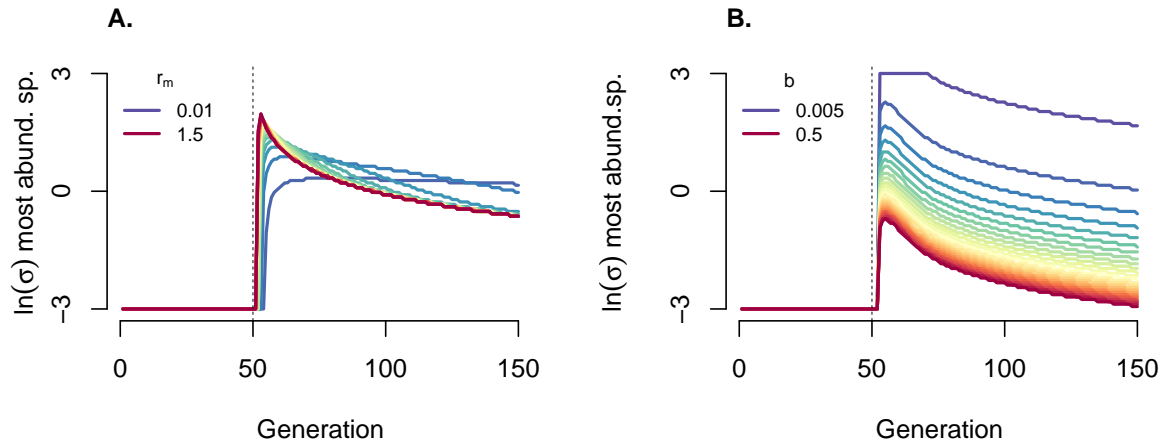I investigated how community turnover depends on species' per capita population

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Figure 4: (A) r_m affects the magnitude of community turnover following an abrupt environmental change. Greater r_m results in an initially greater commuity turnover. High r_m reduces migration load and allows high σ species to leverage their faster adaptation following environmental change. Lower r_m increases migration load, limits the ability of high σ to take advantage of their faster adaptation, but also slows the rebound of eventually dominant species with low σ. (B) The slope of the spatial selective gradient (b) affects the magnitude of community turnover following an abrupt environmental change. Greater b results in dominance by intermediate σ species folowing abrupt environmental change (imposed after 50 generations). Lower b allows higher σ species to briefly dominate, although in these scenarios migration load is low and relative abundance at equillibrium ($\hat{N}$) under stable environments (generations 1-50) is only weakly related to σ. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta_1 - \theta_0 = 1$.

growth rates at low density (r_m). Greater r_m reduces the effects of maladaptive immigration on $\hat{N}$ (equation 4). Greater r_m also allows for persistence (i.e. $\hat{N} > 0$) of species with higher σ (inequality 5). Low r_m reduces the maximum possible σ because low r_m enhances migration load, thus there is less of a change in the species σ with maximal abundance following environmental change (Figure 4A). However, the recovery of species from low density is strongly dependent on r_m and thus the return to equilibrium is slow, and the community is dominated by relatively higher σ species for a longer period of time. When r_m is high, more species with high σ can persist and the rapid environmental change causes strong community turnover. Additionally, higher r_m allows high σ species to increase in abundance as their traits approach the new optimum (Figure 4A). However, the lower σ species are also able to increase in population at a faster rate and the community reverts to equilibrium at a faster pace.

In nature, the slope of environmental gradients varies in space. These patterns can influence gene flow across selective gradients by determining the spatial proximity of distinct environments, and hence can effect migration load (Yeaman and Jarvis 2006).

11

296 An important observation is that in a system with low b, there will be predominantly
297 gene flow between like environments. The slope of the species abundance curve $\left(\frac{d\hat{N}}{d\sigma}\right)$
298 is proportional to b thus lower b will result in a more shallow curve. That is, migration
299 load is reduced and species differing in σ have similar abundances.

300 I investigated the impacts of varying the slope of spatial gradients on turnover in
301 communities following rapid environmental change. When I simulated systems of
302 varying b, the most obvious impact is on the magnitude of community turnover
303 following environmental change. Before the environmental change, low σ species
304 dominate regardless of b. Immediately after the environmental change, high σ species
305 dominate when b is low. Note that when b is low, differences in abundance of species
306 differing in σ are subtle due to low migration load, though there is relatively high
307 turnover in which species are most abundant following the environmental change.
308 When b is high, the environmental change results in turnover favoring species of
309 intermediate σ. Surprisingly, the change in relative species abundances following the
310 environmental change happens at a similar rate regardless of b (lines in Figure 4B have
311 similar trajectories following environmental change), although higher b results in faster
312 return to equilibrium because the initial community turnover was less. Regardless
313 of b, species proportional differences in V_G are unaffected, as they are proportional
314 to σ and thus species differences in $\partial z/\partial t$ are of the same proportional relationship
315 (equation 2).

316 Barton (2001) and Polechová and Barton (2015) investigated how faster change in
317 environments at range margins, i.e. increasing magnitude of b, impacts local adaptation.
318 My results on how b influences community turnover due to differential evolutionary
319 response to environmental change may apply to such changes in b in space. The
320 present model applies assuming that the rate of change in b is subtle, such that $\partial\bar{z}/\partial x$
321 remains approximately linear. If b is sharper at range margins (for an assemblage of
322 species, this would correspond to ecotones at the margin of ecoregions, for example
323 along very steep altitudinal gradients), migration load would be stronger at margins
324 and there migration load would have a stronger influence on community composition
325 at equilibrium (i.e. steeper $\frac{d\hat{N}}{d\sigma}$). However, following environmental change, the change
326 in species rank abundance will be greater in the range core (low b) while there would
327 be lesser change in species rank at range margins (high b).

328 Interspecific trait variation is often correlated across multiple trait axes, corresponding
329 to ecological strategies and life histories. Thus it is unlikely that interspecific variation
330 in σ would be independent of other traits. To explore potential impacts of trait
331 covariation, I studied the situation where σ and r_m positively covary such that higher
332 gene flow species also exhibit higher per capita population growth when rare. For
333 example, plants with small seeds often have higher fecundity (Aarssen and Jordan
334 2001) and greater dispersal distances (Turnbull et al. 1999). To test how such a
335 correlation would influence community turnover following environmental change, I
336 simulated a scenario where $r_m = a + c ln(\sigma)$ where a is an intercept and c determines
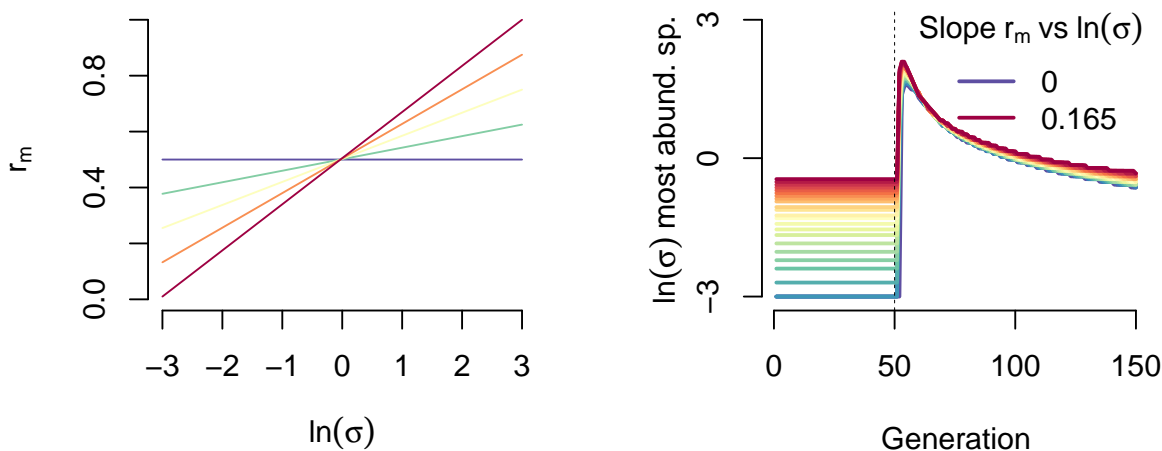
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Figure 5: Correlation between reproductive rate at low density (r_m) and gene flow (σ) affects the magnitude of community turnover following an abrupt environmental change. Greater correlation results in dominance by intermediate (as opposed to low) σ species at equillibrium under constant environments. After 50 generations the instantaneous environmental change occurs and higher σ species briefly dominate. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $\theta_1 - \theta_0 = 1$.

the rate at which r_m increases for species of higher σ. This correlation results in opposing effects on $\hat{N}$: as r_m increases, $\hat{N}$ increases (equation 4) but as σ increases, $\hat{N}$ decreases. Thus there is a different relationship between σ and species abundance at equillibrium: intermediate σ species have greatest abundance (Figure 5). Notably, this correlation between r_m and σ has relatively less impact on community turnover during the transient after an environmental change, though a stronger correlation between r_m and σ results in much faster return to community equilbrium because intermediate σ species were already dominant before environmental change.

2.3 Community turnover under sustained environmental change

Temporal environmental change can take any functional form. Above I simulated an instantaneous shift in environment that then stabilized (Gomulkiewicz and Holt 1995; Orr and Unckless 2008). Alternatively, environments may undergo more gradual sustained directional shifts (Pease et al. 1989; Lynch and Lande 1993). Evolution of a quantitative trait under stabilizing selection in response to sustained environmental change has been analyzed previously by Pease et al. (1989) and Lynch and Lande (1993). Selection, population growth, and adaptation in the Lynch and Lande (1993) model were formulated the same as in the model here, with genetic variance enhancing the rate of adaptation to a shifting optimum (though in their model gene flow was

13

356 not included). In the Lynch and Lande (1993) model, the optimum θ changes at a
357 rate k per unit time t. After a enough time has passed to allow for a balance between
358 adaptation versus the shifting optimum, the mean trait ($\bar{z}$) lags behind the optimum
359 ($\theta_0 + kt$) a stable distance which Lynch and Lande (1993) calculated as equal to $-k\frac{V_S}{V_G}$.
360 In the present model, greater σ increases V_G and thus lower lag in $\bar{z}$ behind the shifting
361 optimum. Substituting the Barton (2001) equation for V_G in a locally adapted system
362 into the previous expression results in a lag in $\bar{z}$ equal to

$$(\theta_0 + kt) - \bar{z} = -\frac{k\sqrt{V_S}}{b\sigma} \tag{7}$$

363 i.e. lag in $\bar{z}$ for a given species was proportional to σ^{-1}. Thus stronger stabilizing
364 selection reduces the lag, though to a lesser degree than identified by Lynch and Lande
365 (1993; $\sqrt{V_S}$ versus V_S, Kremer et al. 2012). This is because when stabilizing selection
366 is stronger (low V_S) the fitness advantage of adapted genotypes is higher but stronger
367 stabilizing selection also reduces V_G from immigration, slowing adaptation. I show
368 here that on balance the effect of stabilizing selection is to reduce the lag (equation 7).
369 Additionally, the lag increases as the selective gradient b becomes shallower because
370 this also reduces V_G.

371 Lynch and Lande (1993) also derived the critical rate of environmental change above
372 which populations go extinct (assuming large N_e) as $k_c = V_G\sqrt{2\frac{r_m - \frac{V_P}{2V_S}}{V_S}}$. Substituting
373 the Barton (2001) equation for V_G in a locally adapted system into the previous
374 equation results in

$$k_c = b\sigma\sqrt{2r_m - \frac{b\sigma}{\sqrt{V_S}} - \frac{V_E}{V_S}} \tag{8}$$

375 This equation shows how k_c is non-monotonically related to σ, i.e. k_c is greatest for
376 intermediate values of σ. Low σ species have low V_G, and hence slower $\frac{\partial \bar{z}}{\partial t}$ but high σ
377 species suffer from high migration load (high V_P). The difference in this sustained
378 environmental change scenario (compared to the abrupt change scenario above) is
379 that slower $\frac{\partial \bar{z}}{\partial t}$ continues to be a drag on $\bar{r}$, whereas after the abrupt change that then
380 stops, slower $\frac{\partial \bar{z}}{\partial t}$ becomes unimportant as $\bar{z}$ approaches θ.

381 To determine how the shifting optimum impacts community structure as t becomes
382 large, I substituted the lag in $\bar{z}$ to the previous equation for $\hat{N}$ (equation 4). Thus at
383 equilibrium trait lag under an environment shifting so that the optimal trait changes
384 at rate k,

$$\hat{N} = 1 - \frac{b\sigma\sqrt{V_S} + V_E}{2V_S r_m} - \frac{k^2}{2b^2\sigma^2 r_m} \tag{9}$$

385 where the first substracted term gives migration load, which worsens with σ, while the
386 second substracted term gives the adaptation lag, which is ameliorated by σ. These
387 opposing effects result in species with intermediate values of σ being most abundant

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388 (Figure 7). Differentiating with respect to σ gives
389

$$\frac{d\hat{N}}{d\sigma} = \frac{k^2}{b^2\sigma^3 r_m} - \frac{b}{2\sqrt{V_S}r_m} \tag{10}$$

390 . The maximum $\hat{N}$ is attained by species with σ that cause the right hand side of
391 equation 10 to equal zero, i.e. the σ with maximum $\hat{N}$ is equal to $(2k^2\sqrt{V_S})^{1/3}/b$. This
392 expression shows that the dominant species identity depends on only a few parameters.
393 Note this expression equals zero when k is zero, thus consistent with results on locally
394 adapted systems in constant environments where zero σ is favored due to lack of
395 migration load (equation 6). Thus greater rates of environmental change through time
396 (k) favor higher σ species, but at a decreasing rate $(k^{\frac{2}{3}}$, equation 10). Additionally,
397 stronger stabilizing selection favors relatively lower σ species, due to the reduced
398 migration load.

399 In this scenario of sustained environmental change, steepening selective gradients
400 (higher b) results in a lower σ having maximum $\hat{N}$. Thus the results here parallel
401 those for transient community turnover following an abrupt change in environment:
402 at range margins or ecotones where b may be steeper, the magnitude of change in the
403 most abundant species will be less, compared to where b is shallower.

2.4   Effects of species interactions

405 I simulated both scenarios of environmental change with non-zero species interactions,
406 specifically interspecific competition. Simulations are presented in greater detail in
407 the appendix. Adding weak Lotka-Volterra interactions ($\alpha_{ij} = 0.01$) in a diverse
408 community results in little effect on the trend in which species are most abundant
409 following environmental change (Figures 9, 10, 12). However, adding stronger com-
410 petition in lower diversity communities can result in extended supression of low σ
411 species following environmental change. Following abrupt change, this supression
412 can last hundreds of generations. Under both scenarios of change, higher σ species
413 that dominate communities can actually see increased absolute abundance following
414 environmental change, despite going from being locally-adapted to being maladapted
415 (e.g. Figure 12C). This surprising change results from the release from competitive
416 supression by low σ species.

2.5   Impacts on community-mean traits

418 Interspecific variation in adaptation following environmental change will likely have
419 impacts on the distribution of traits in a community, which is often of interest to
420 community and ecosystem ecologists (Muscarella and Uriarte 2016; Šímová et al. 2018).
421 For example, ecosystem function may be influenced by the mass-averaged functional
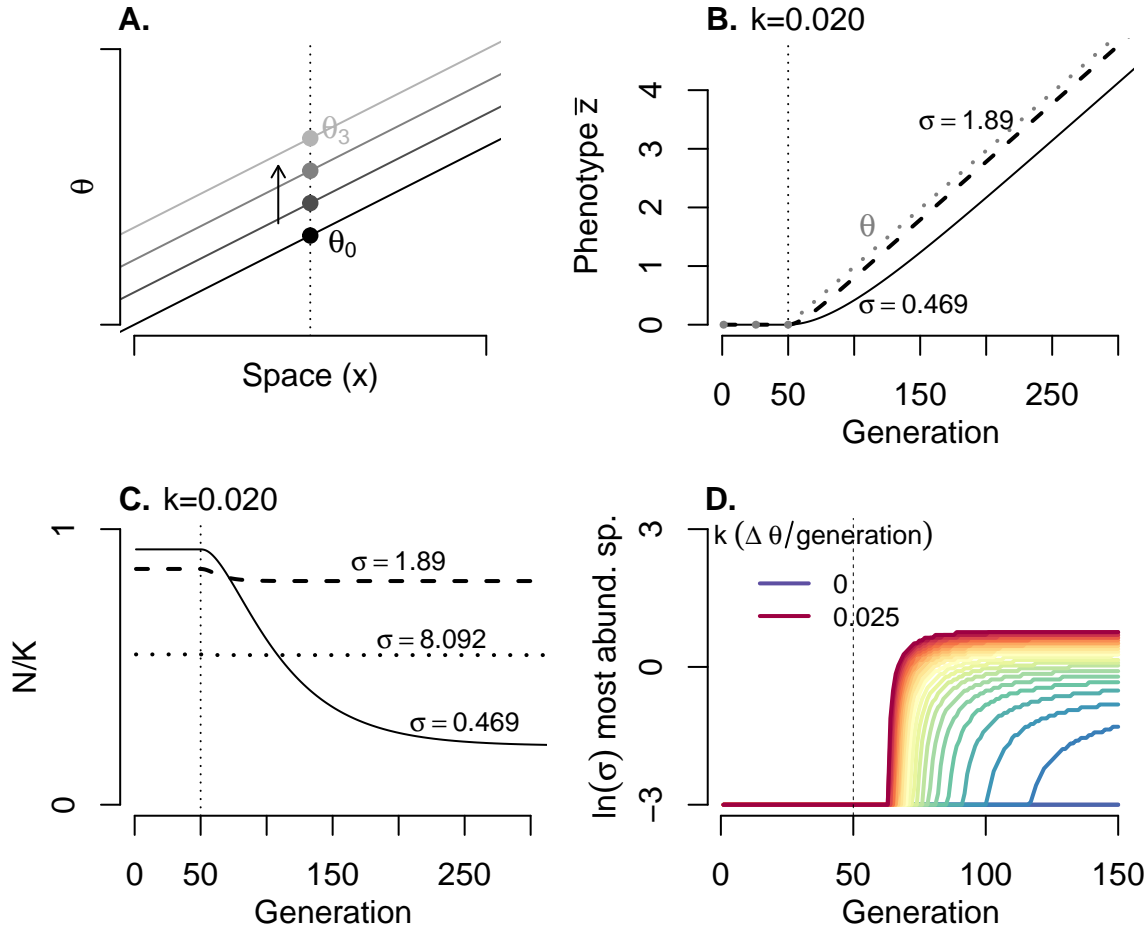
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Figure 6: Effects of a sustained environmental change (i.e. a change in θ through time). (A) Illustration of the scenario of shifting θ across all locations, from a historical θ_0 to which species were locally adapted, to new θ. (B-D) Environment is constant (constant θ) until the vertical dashed line at which point θ changes at a constant amount k each generation. (B-C) Illustration with $k = 0.020$ for example species. (B) Evolution of $\bar{z}$ for two example species differing in σ relative to the shifting optimum (θ). (C) Population size trajectories for the same two species in addition to one higher σ species. (D) Effects of differing rate of environmental change (k) on community turnover (i.e. the most abundant species under environmental change). Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$
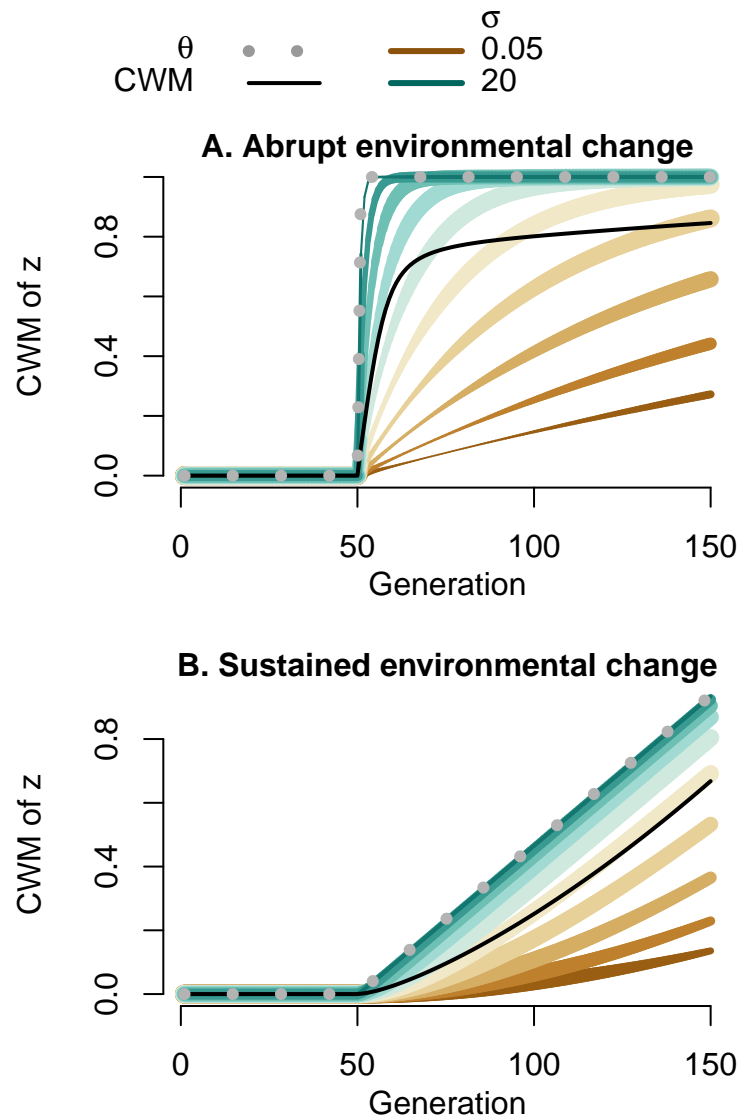
Figure 7: Effects of environmental change on community-weighted mean (CWM) traits under selection due to eco-evolutionary responses. Example species with a range of σ values are shown (colors), with line thickness indicating relative abundance. As in earlier presented simulations, communities were composed of species with a log uniform distribution of σ values. The CWM (black line) at each timepoint is an abundance-weighted average of z. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$. For (A), $\theta_1 - \theta_0 = 1$. For (B), $k = 0.009$.

422 traits in a community (Grime 1998). Under the scenario of abrupt environmental
423 change, the slow adaptation and return to equillibrium abundance of species that
424 dominate communities may have interesting effects on changes in community-weighted
425 mean (CWM) traits. Indeed, following abrupt environmental change, initially there is
426 a very rapid phase of change in CWM driven by fast-adapting high σ species (Figure
427 8). However, there is an abrupt slow-down in change in CWM as most high σ species
428 have adapted but low σ species remain maladapted. Nevertheless, the low migration
429 load of these low σ species contributes to their fitness and abundance and hence
430 influence over CWM traits (Figure 9). By contrast, when there is sustained change in
431 θ over time, species exhibit marked variation in their ability to adapt to the moving
432 optimum. Although the highest σ species are able to maintain $\bar{z}$ close to the optimum,
433 they are less abundant than intermediate σ species due to migration load (equation 10,
434 Figure 8). Thus the CWM exhibits a substantial and stable lag behind the optimum.

2.6 Relationship of eco-evolutionary community turnover to ecological succession

437 The transient dominance of species with higher gene flow following an abrupt environ-
438 mental change is qualitatively similar to classic hypotheses explaining successional
439 turnover in communities. Specifically, early successional species may have better
440 dispersed propagules but lower fitness compared to later successional species. In the
441 present model, gene flow and propagule dispersal are one in the same (σ), i.e. there is
442 no mechanism of gene flow apart from propagule movement (no gamete movement).
443 To more formally investigate the similarity with succession, I studied how species
444 differing in σ in the Barton (2001) model respond to ecological disturbance, with
445 no change in θ. In the absence of any environmental change, consider an ecological
446 disturbance that reduces locally-adapted populations of different species by the same
447 large proportion. For simplicity, I assumed a localized disturbance that introduced
448 non-zero $\frac{\partial^2 N}{\partial x^2}$ (equation 3) but did so orthogonally to b such that asmmetric migration
449 had no effect on trait evolution (i.e. $\frac{\partial ln(N)}{\partial x}$ set equal to zero in equation 2).

450 Successional community turnover arises as species differ in the rate of population growth
451 (eqn 3) due to interspecific variation in immigration (favoring high σ species) and fitness
452 (favoring low σ species). However, note that the fitness advantage of low σ species is
453 dependent on reproduction individuals already present, which are few after disturbance.
454 My simulations showed that the more intense the disturbance, the slower the return
455 to community equillibrium (Figure 9), analogous to the slower return following greater
456 abrupt changes in θ (Figure 3). Under a sustained ecological disturbance (constant
457 proportion of individuals lost each generation) ecological community turnover exhibits
458 qualitatively similar patterns to the eco-evolutionary response to sustained change
459 in θ (Figure 9). Specifically, sustained disturbance resulted in consistent dominance
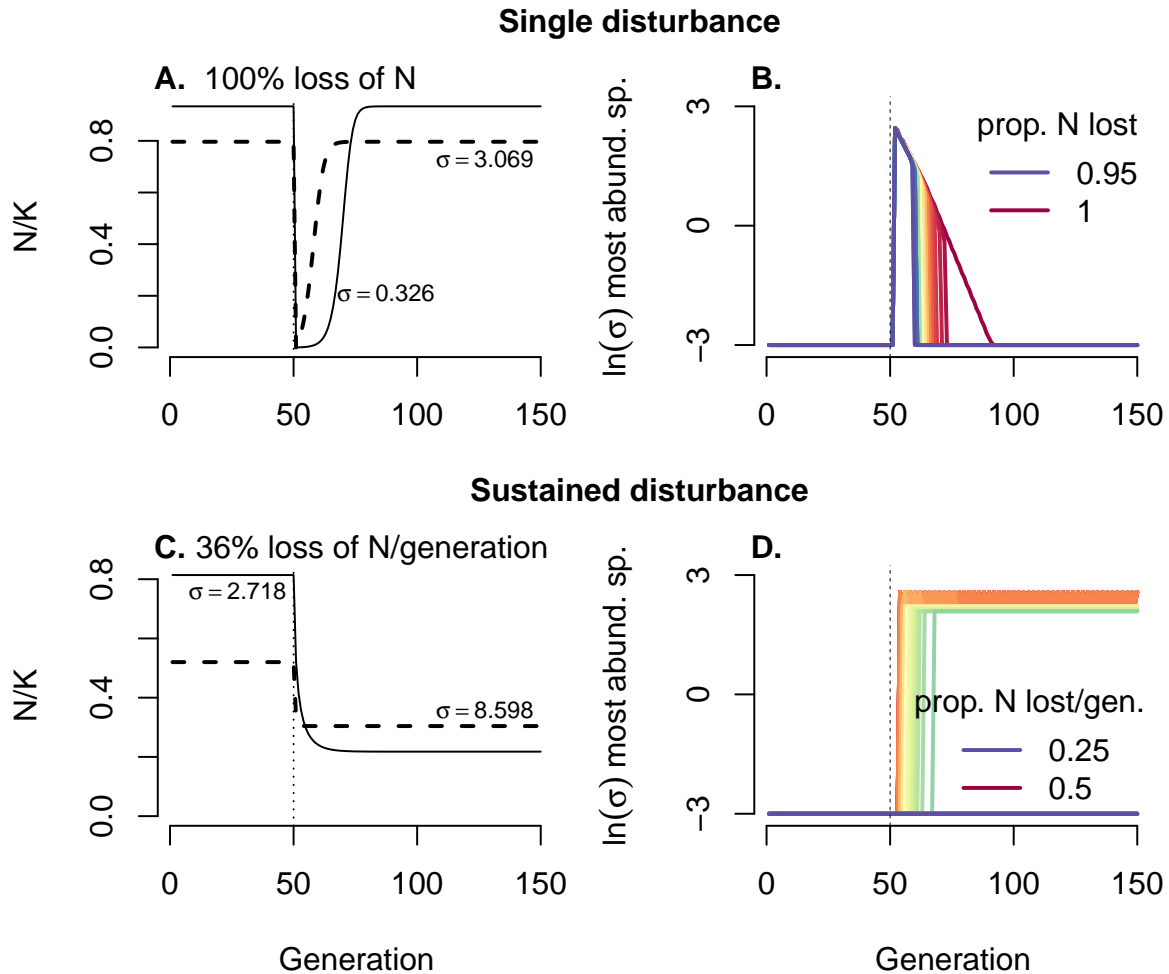460 by species with intermediate σ, similar to these species being most abundant under

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Figure 8: Variation in dispersal (σ) among species determines how communities of locally-adapted populations respond to ecological disturbance. (A-B) A single disturbance removes a large portion of each species' N after generation 50. (C-D) recurring disturbances are imposed in each generation, starting after generation 50. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\frac{\partial^2 N}{\partial x^2} = 5$.

sustained change in optimal phenotypes (Figure 7).

3   Discussion

Evolutionary genetic theory is a rich source of hypotheses for how life history impacts evolution. On this rapidly changing planet, predictions about evolutionary responses to rapid environmental change are of particular importance (Bay et al. 2017; Gienapp et al. 2017). New molecular data are providing a glimpse of the substantial differences among species in population genomic patterns (Romiguier et al. 2014). The present is ripe for studying how interspecific trait differences impact evolutionary response to environmental change and the resulting consequences for community structure and ecosystem function. Here, I took existing quantitative genetic models of adaptation (Lynch and Lande 1993; Barton 2001) and showed how interspecific trait variation gives rise to differences in genetic diversity with non-monotonic effects on community structure and dynamics.

In general, eco-evolutionary community inversions (i.e. reversals in relative abundances) may arise in any system where there is a negative or complex relationship between census population size and adaptibility to environmental change. These changes are driven by the fact that initially numerically abundant species are more maladapted for longer periods of time following environmental change. Genetic variance is has a major influence on the rate of adaptation, but other traits, such as generation time, vary among species in communities and may result in eco-evolutionary community turnover. For example, parasite generation time may be faster than hosts allowing faster adaptation to abiotic environmental change. Both vertebrate hosts (Fraser 2013) and their parasites (Sternberg and Thomas 2014) may be locally-adapted along temperature gradients, though parasites might adapt to climate change faster and increase fitness faster than hosts. Alternatively, when census population size is positively related to genetic variance in a trait under selection (Frankham 1996), evolutionary responses to environmental change may reinforce the ecological responses, reducing community diversity.

I identified a transient benefit to high gene flow following an abrupt environmental change, due to faster adaptation. In their experimental microcosm study, Low-Décarie et al. (2015) demonstrated how gene flow was key to the eco-evolutionary recovery of soil microbial communities responding to a novel herbicide. Studies of genetic variation (Lande and Shannon 1996) from dispersal (Blanquart and Gandon 2011) or mutation (Taddei et al. 1997) have yielded similar results. When environment is constant, low mutation rates are favored, though mutator lineages have transient benefits when they find adaptive mutations (Taddei et al. 1997). Additionally, fluctuating environments can favor higher mutation rates (Travis and Travis 2002) similar to the finding here that sustained environmental change stably favors higher rates of gene flow despite

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resulting maladaptation. Indeed, co-occurring species can exhibit a range of mutation rates (Baer et al. 2007), which may also play a role in species differences in the degree of local adaptation and subsequent responses to environmental change (Orr and Unckless 2008). Here, I did not allow explicit evolution of dispersal distance (σ), though the comparison of population sizes for my "species" of differing σ provide insight into how dispersal would evolve in this system. In a temporally constant environment (prior to generation 50 in simulations), dispersal is maladaptive due to the spatial selective gradient (Balkau and Feldman 1973). However, once temporal change in environment is introduced, greater dispersal can be favored with the functional form of temporal environmental change determining the optimal σ (see Blanquart and Gandon 2011 for more detailed analysis). Here, I did not investigate interspecific variation in phenotypic plasticity, which may supplant local adaptation as a way to respond to environmental gradients. As with migration load, if census population size is related to the degree of local adaptation versus plasticity (i.e. habitat specialization versus generalization) then complex community change following environmental change may result. Under some models, greater dispersal across environmental gradients can favor plastic responses to environment (Sultan and Spencer 2002; reviewed by Hendry 2016).

The form of environmental change may have dramatic effects on how eco-evolutionary responses influence communities. Previous theory has shown how the benefits of genetic variation (Lande and Shannon 1996) and dispersal (Blanquart and Gandon 2011) can depend on the fuctional form of environmental change. I found that communities can exhibit distinct dynamics depending on a scenario of abrupt environmental change (Gomulkiewicz and Holt 1995; Orr and Unckless 2008) versus sustained change (Pease et al. 1989; Lynch and Lande 1993). Specifically, sustained change favors intermediate gene flow species and results in their stable dominance (highest N) in communities, whereas abrupt environmental change results in only transient community change favoring high to intermediate σ species. In nature any form is possible and thus the main purpose of my results is to demonstrate the importance of the form of environmental change. It is unclear whether current anthropogenic climate change will stabilize, as stabilization would require dramatic action (Pachauri et al. 2014).

It is important to note that I modeled community turnover in an arbitrary local population, but these effects are expected to happen across the species ranges. This suggests that there is a large potential spatial extent of eco-evolutionary responses to rapid environmental change, resulting in community inversion across large regions. In nature b is non-linear and rugged, a scenario worthy of study in future simulation of response to temporal environmental change. Furthermore, multiple traits may be under simultaneous spatially-varying selection (Guillaume 2011; MacPherson et al. 2015) and selective regimes on these traits may change simultaneously. Given that environmental change can be complex, with different forms of change in different environmental dimensions, it is possible that in nature changes in selective gradients may take multiple functional forms simultaneously leading to complex changes in

540 relative abundance for species differing in σ.

541 The model studied here was simple and thus it is challenging to determine how
542 important my results are in natural systems. However, gene flow across spatial
543 selective gradients is likely a major source of within-population genetic variation in
544 traits under selection (Yeaman and Jarvis 2006; Paul et al. 2011; Farkas et al. 2013).
545 Findings on ponderosa pine (Yeaman and Jarvis 2006) suggest that spatial variability
546 in b can lead to among-population variability in V_G. Less is known, however, of
547 how adaptability or V_G are related to interspecific variation in census population size
548 (abundance). The negative relationship between these two quantities is the key to
549 community turnover following environmental change in my results, although this result
550 depends on the form of environmental change. It is challenging to determine the
551 importance of my results in nature, at least partly because there is often a substantial
552 lag before better dispersing species dominate communities (Figures 3 & 7), thus
553 researchers may overlook population changes caused by environmental change.

554 It may be a common feature of strongly interacting species that both experience
555 selective gradients driven by the same environmental variable (e.g. temperature).
556 Differences among these species in local adaptation to the same environmental variable
557 might lead to different eco-evolutionary responses to environmental change, causing
558 indirect effects on interacting species (Fussmann and Gonzalez 2013). For example,
559 multiple competing tree species may simultaneously be locally-adapted along environ-
560 mental gradients (Ikeda et al. 2014). Recent work by Brans et al. (2017) has shown
561 similar intraspecific trait clines in multiple co-occurring cladocerans along urbanization
562 gradients drives community patterns. Here I included simluations of competing species,
563 but interactions of different types (e.g. trophic) may yield unexpected eco-evolutionary
564 community responses to changing environments.

565 My work demonstrates how interspecific variation in gene flow alters communities
566 experiencing environmental change. Some authors have suggested assisted gene flow
567 as a technique to mitigate climate change impacts on wild populations, with gene
568 flow facilitating local adaptation of populations suddenly experiencing novel climates
569 (Aitken and Whitlock 2013). My results highlight how such approaches could have
570 important effects on community structure. Aitken and Whitlock (2013) suggested
571 that assisted gene flow efforts should be focused on ecologically dominant species (due
572 to importance for ecosystem functioning) and rare species (to prevent extinction).
573 My results show how such a strategy would likely change community structure, as
574 species not included (historically intermediate abundance species) in assisted gene
575 flow would be expected to decline in abundance due to slower adaptation to climate
576 change. Others have suggested breeding of wild species to promote adaptation to
577 future environments (Oppen et al. 2015). These management efforts would have to
578 be balanced across species of different abundances if they are to limit impacts on
579 community composition.

22

3.1 Conclusion

Community composition is defined by the population sizes of component species, but greater population size might not correspond to greater adaptability to environmental change. This discrepancy can result in complex community turnover as selection regimes shift. The simple model studied here demonstrates some of the potential complexity in community change. Future research would improve our ability to predict responses to environmental change in nature by learning more about the population genetics and ecology underlying adaptation in addition to theoretical investigation of more complex scenarios.

3.2 Acknowledgments

4   Appendix

4.1   Effects of species interactions

Here I present simulation results for when species within a community compete with each other. I simulated simple Lotka-Volterra competition. Instead of equation 1, I used a discrete time version of the following

$$\bar{r} = r_m(1 - \frac{N_i - \sum_{i \neq j}^{J} N_j \alpha_{ij}}{K}) - \frac{(\bar{z} - \theta)^2}{2V_S} - \frac{V_P}{2V_S} \tag{A1}$$

where N_i is the population size of the focal species i and there are J total competitor species each with population sizes of N_j. α_{ij} determines the strength of interspecific competition. Interactions were symmetric among species such that all $\alpha_{ij} = \alpha_{ji}$. My simulations in the main text involved communities of $J = 100$ species differing in σ. I studied a simple scenario with such a community having weak pairwise interactions between all species, $\alpha_{ij} = 0.01$. Because all species experience approximately equal effects of interspecific competition, the relative differences among species in $\hat{N}$ remain approximately the same, albeit with a decrease in the maximum σ capable of persisting (Figure 10).

I here replicate analyses from the main text, but using equation A1 to determine $\bar{r}$. Note that per equation 2, adaptation is not influenced by such competitive interactions (i.e. such competition does not influence $\frac{\partial r}{\partial z}$; α_{ij} is unrelated to z_i) (Fussmann and Gonzalez 2013; cf. Osmond and Mazancourt 2013). In simulations, I initiated species at their equilibrium abundance ($\hat{N}$) in the absence of interspecific competition, but then allowed 150 generations with interspecific competition before imposing change in θ.

4.2   Response to abrupt environmental change

Adding symmetrical and weak species interactions has no qualitative effect on my results. For example, a similar pattern of transient community turnover following environmental change is observed (Figure 10). Reductions in population size were nearly equivalent for all species in a diverse community with weak competition (Figure 10). Thus the main effect of adding weak species interactions in a diverse community was to reduce the maximal σ capable of persisting.

Similarly, variation in the magnitude of abrupt environmental change has similar impact on community dynamics, as measured as σ of the most dominant species, regardless of whether the simulated competition was present (Figure 11).

However, I also simulated three competing species with $\alpha_{ij} = 0.75$. Here, competition had little effect on how the σ of the most abundant species changed with time
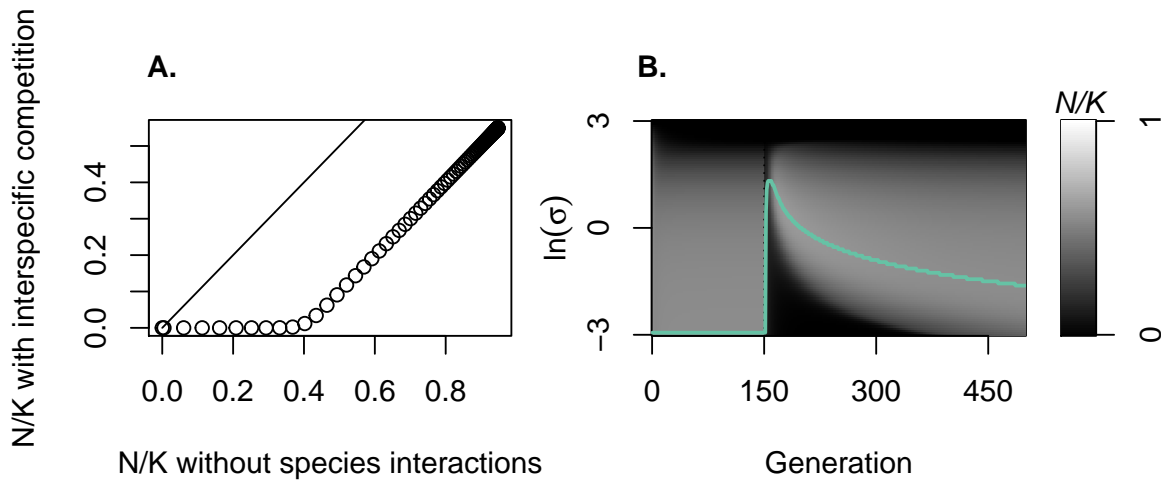
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Figure 9: Community turnover under abrupt environmental change, with interspecific competition. (A) Comparing approximate equilibrium species' N for scenarios differing in presence of interspecific competition. Black circles show species in a diverse (100 species) community with weak interactions ($\alpha_{ij} = 0.01$). Straight line shows one-to-one relationship. (B) Here the trend in abundance for a diverse (100 species) community is shown, where species weakly compete ($\alpha_{ij} = 0.01$) according to Lotka-Volterra models. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta_1 - \theta_0 = 1$.

(Figure 12A-B). However, this similarity obscures underlying community patterns caused by competition. In the presence of strong competition, species that have relatively lower abundance following environmental change remained supressed for longer periods of time and at very low densities (compare Figure 12C and 12D). Note that my deterministic simulations lack stochastic extinction, which is likely a major problem for populations at very low density. In my simulations (Figure 12), the low σ species that dominated under stable environments but reached low density following environmental change are on a steady upward population trend at the end of simulations (Figure 12C). Thus the dominance of higher σ species is still transient, though with a much slower return to the pre-environmental change equillibrium $\hat{N}$.

4.3   Sustained environmental change

I also simulated how interspecific competition impacts the eco-evolutionary community response to a sustained environmental change. I used the same model of species interactions as described above (A1) under the scenario of shifting θ at rate k throught time. I began testing a diverse community of weakly interacting species. I found that which species dominated following the intiation of environmental change was largely the same regardless of these weak competitive interactions (compare Figure 12B with
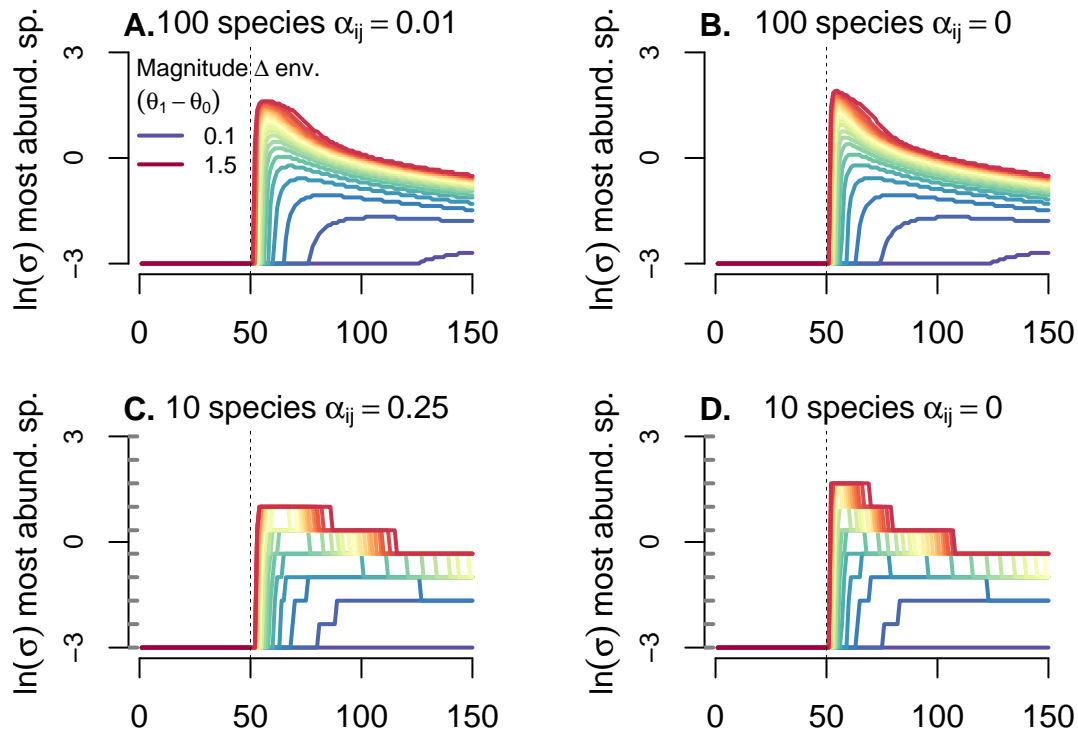
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Figure 10: How the magnitude of environmental shift affects the magnitude of community turnover in the presence in interspecific competition. In general, the greater the environmental change, the higher the σ of the most abundant species soon after the environmental change, regardless of interspecific compeition. (A-B) Weak competition has miniscule impact on community turnover. (C-D) When competition is stronger, similar turnover occurrs though some higher σ species are unable to persist. Gray ticks in (C-D) correspond to the 10 species' simulated values of σ. Populations are at approximate equilibrium and adapted to θ_0 for the first 50 generations, when an instantaneous environmental change to θ_1 occurs. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$.
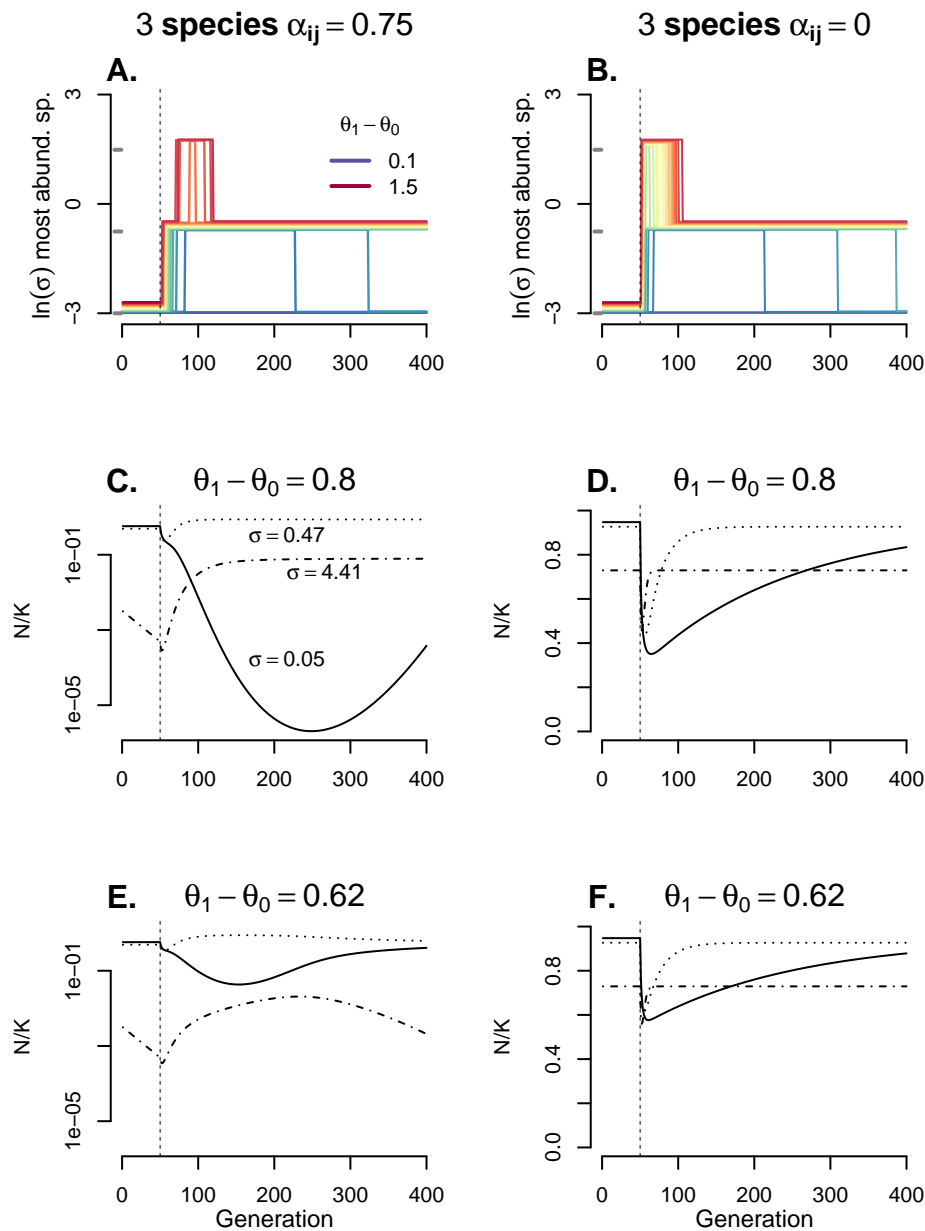
Figure 11: (A-B) How the magnitude of environmental shift affects the magnitude of community turnover in the presence (A, and left panels) or absence (B, and right panels) of interspecific competition in three species communities (species' σ values indicated by gray ticks at left). In general, the greater the environmental change, the higher the σ of the most abundant species soon after the environmental change, and the longer the duration of their dominance, regardless of interspecific competition. Despite the similarity in which species dominate following environmental change (A and B), interspecific competition has major effects on the abundance of lower abundance species (compare C versus D, E versus F). (C-F) show individual species time series (each line), corresponding to species with σ shown as gray ticks in A and B. Note that in order to show the non-zero abundance trajectories of less abundant species, y-axis is log scaled in C and E. Before environmental change at generation 50 to θ_1, σ is negatively related to N. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$.

643 Figure 6D). When increasing interaction strength in less diverse communities, I again
644 found similar patterns in terms of which species were most abundant through time
645 (Figure 12). However, the differences in abundance between species differed. When
646 competition occurred, the most abundant species had greater abundance advantages.
647 Interestingly, higher gene flow species actually had greater absolute abundance fol-
648 lowing the initiation of environmental change with competition (Figure 12C). Thus
649 the environmental change suppressed abundance of low gene flow species with low
650 migration load and this allowed increases in abundance of higher gene flow species
651 that were better able to adapt to shifting environments (compare Figure 12C vs 12E).
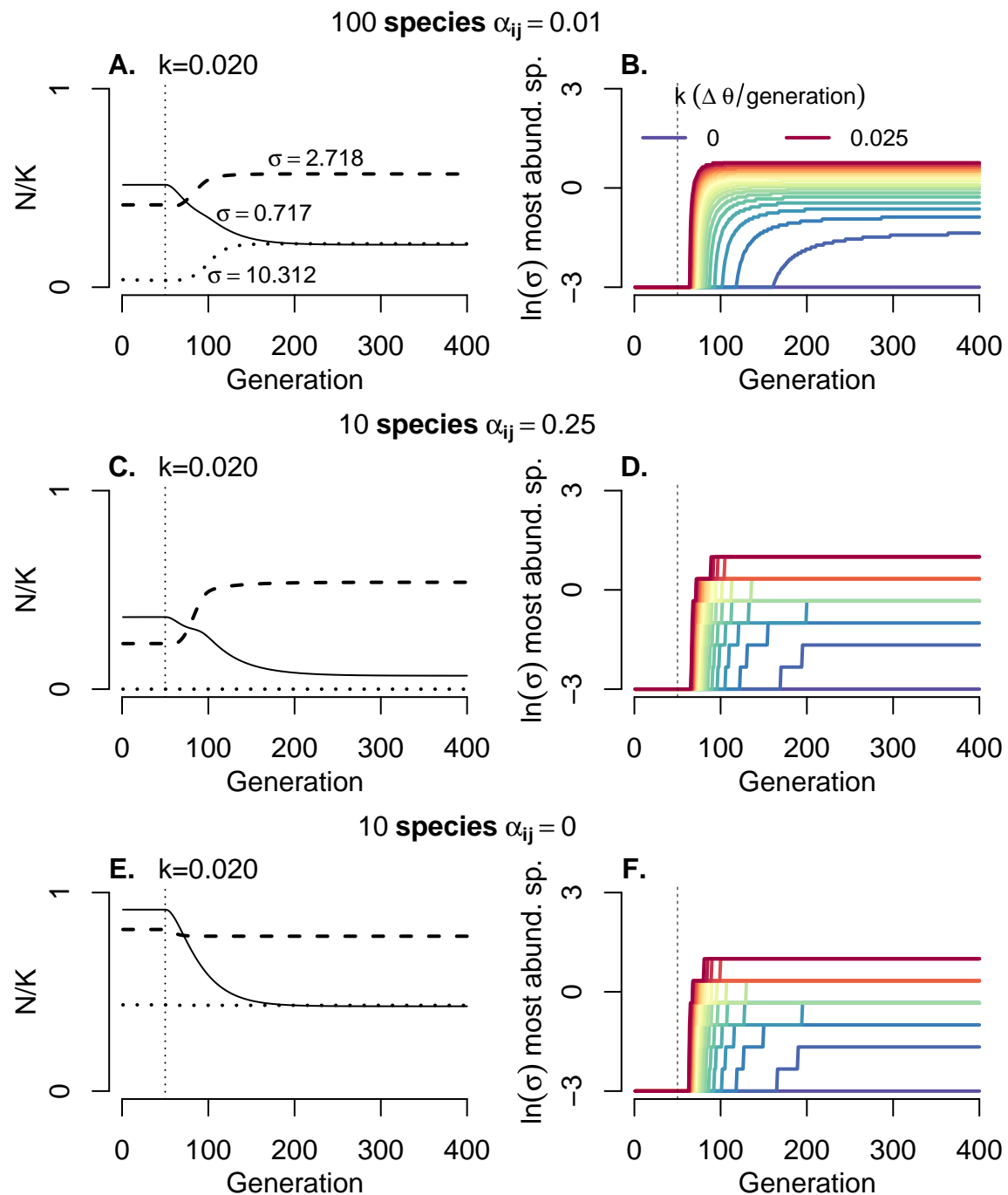
Figure 12: Effects of a sustained environmental change with interspecific competition, with the same three species (A, C, D) highlighted in each scenario, demonstrating how absolute abundance of higher σ species can increase following environmental change. (A-B) Diverse community with weak interactions. (C-D) Community with fewer species and stronger competition. (E-F) A community composed of the same species as (C-D) but with no interspecific competition. Vertical dashed line indicates beginning of environmental change at generation 50. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$

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