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 enhance genetic diversity of traits 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, species can transiently reverse their relative abundances, but sometimes only after long lag periods. If constant temporal environmental change is applied, the community exhibits a shift toward stable dominance by species with intermediate gene flow. Notably, populations of fast-adapting high gene flow species can increase under environmental change because the change suppresses superior competitors with lower gene flow. This eco-evolutionary competitive release stabilizes ecosystem function. The community dynamics observed here parallel the purely ecological successional dynamics following disturbances. 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; Sanford and Kelly 2010) 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; Polechová et al. 2009; Kremer et al. 2012).

A major body of theory explores the conditions under which 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). When populations are locally adapted, immigrant alleles 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 alleles can impose a “migration load” on populations, reducing population size due to lower average fitness of 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 motivated studies of 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; Polechová et al. 2009; 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; Uecker et al. 2014), 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 populations to persist. Still, little is known about how evolutionary response to rapid environmental change impacts abundance patterns, apart from equilibrium abundance of individual populations (Polechová et al. 2009). 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*). 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).

Among the factors that determine population response to environmental change are initial population size and genetic diversity in the trait(s) 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 (Barton 2001). 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; Polechová et al. 2009). I reframe this theory to 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; Polechová et al. 2009; 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), Barton (2001) and Polechová et al. (2009), a stochastic version of which was studied by Polechová and Barton (2015). The model I use is a deterministic model of a population with logistic growth and a quantitative trait z subject to hard selection with 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 last term in equation 1.

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 equation 2, respectively

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

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 ($\frac{\partial \bar{r}}{\partial \bar{z}}$). 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 gives change to due spatial trends in abundance, and the second term gives change due to average individual fitness. Note that here there is no frequency or density-dependent selection, i.e. intraspecific competition (or apparent competition) is not dependent on z in any way, beyond the effects of z on N. This assumption may be well-justified for traits involved in abiotic stress-tolerance (e.g. cold or heat tolerance) where selection does not result in any diversity in z.

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, $\frac{\partial ln(N)}{\partial x} = 0$. I ignore spatial boundary conditions that would result in asymmetric gene flow.

Barton (2001) allowed genetic variance within a population (V_G) to change as a function of gene flow. 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 ecologists commonly study are important 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 (known as migration load, equation 1). The equilibrium census population size (Polechová and Barton 2015) as a proportion of carrying capacity K, $\hat{N}$, is given by

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

where the second term on the right gives migration load. Migration load can thus introduce uneven community structure when species differ in σ or r_m. To identify the maximum σ capable of persistence I set $\hat{N}$ to zero and solve the inequality to obtain

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

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

To study how interspecific variation in σ could structure communities along spatiotemporal environmental gradients, I now consider a community of species that vary only in σ (but not other parameters e.g. K, V_S, V_E). For mathematical convenience I start with communities lacking species interactions. I follow with simulations that introduce competition among species.

In the Barton (2001) model, greater σ increases V_G and migration load and thus decreases equilibrium population size. From equation 4, the proportional reduction in $\hat{N}$ due to migration load is equal to $\frac{b\sigma}{2\sqrt{V_S}r_m}$. I differentiate with respect to σ to obtain

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

which gives the slope of species equlibrium abundance versus gene flow. Thus the species abundance distribution for a community (McGill et al. 2007) could be obtained using the distribution of σ and applying equation 6. The parameters on the right of equation 6 are each constrained to be positive so that when holding these constant across species of varying σ there is a negative relationship between σ and $\hat{N}$. The effect of migration load is stronger and abundance distribution is steeper as the selective gradient b is steeper.

Note that in the equation (4) for $\hat{N}$, species that differ in b (the slope of selective gradients) will have similar differences in $\hat{N}$ as species differing in σ. The product $b\sigma$ gives change in optimal phenotype z over one dispersal standard deviation (Kirkpatrick and Barton 1997). Here I focus on variation in σ among species, given that interspecific variation in dispersal ability of propagules and gametes is a major interest in community ecology.

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 (Polechová et al. 2009; 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 $\frac{\partial \bar{r}}{\partial \bar{z}}$ (third term on right-hand side of equation 2).

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 equillibrium population size, $N = \hat{N}$ and $\bar{z} = \theta_x$ where the subscript x on θ indicates the optimal trait is for location x. I chose biologically plausible parameter values (although below I study other values): $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, $x = 0$ and thus $\theta_x = 0$ (Polechová and Barton 2015). I then imposed an instantaneous change in θ_x such that a new phenotype, $\theta_{x1} = 1$, was favored, and the change in selection was the same at all locations, i.e. the slope b of the spatial gradient did not change, $\theta_1(x) = bx + 1$ (Figure 1). This scenario is mathematically convenient because all populations experience the same relative change and dynamics 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 mean phenotype $\bar{z}$ of the two species were equal before environmental change, but with the second species having greater variance within any local population (i.e. greater V_G, Figure 1). I found rapid adaptation to θ_{x1} in the high gene flow species with the low σ species lagging far behind (Figure 1). I then simulated communities with a log uniform distribution of σ values across 100 species under the same conditions as the two example species to illustrate the differences in adaptation due to σ.

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 than low σ species in communities in a stable environment (eqn. 4), the faster adaptation of high σ species may allow them to increase their relative abundance following an environmental change. These two example 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 species is more abundant for an interval following the environmental change (Figure 2). The reversal is transient because the stable environment after change favors low σ.

In a diverse community with species having a range of gene flow one can ask how composition might shift due to different evolutionary responses. From the aforementioned simulation of species with a range of σ values (Figure 1E), I calculated which species was most abundant at each time point. Under equilibrium, the species with lowest σ has highest N (eqn. 4 and Figure 2). Following an instantaneous shift in θ,

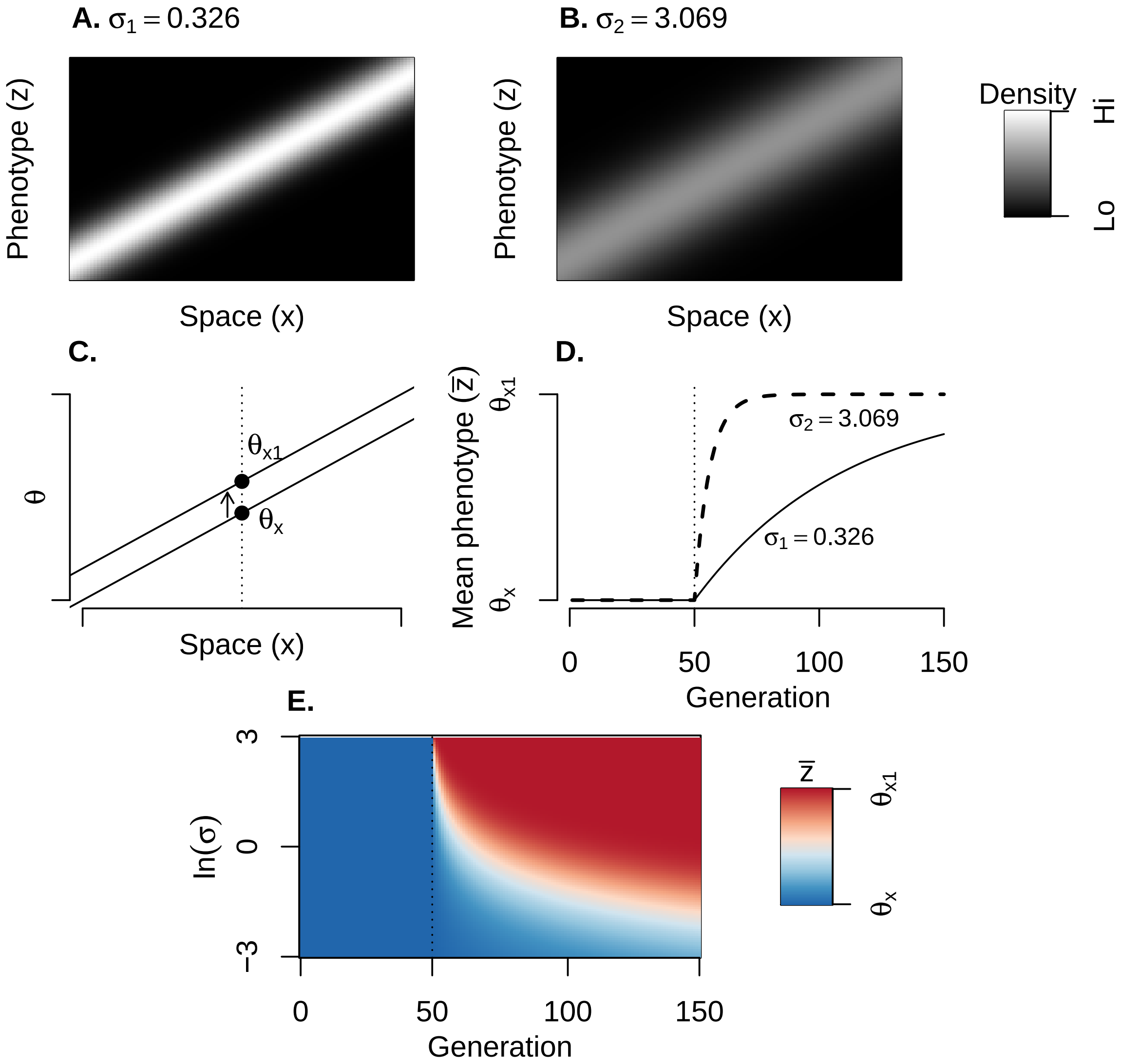

Figure 1: In a locally adapted system, interspecific variation in σ, determining the rate and scale of gene flow, determines differences in genetic diversity and rate of adaptation. Species with low (A) and high (B) σ (gene flow) are subject to the same selective gradient b (favoring an increase in phenotype 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 $\theta_{x1} - \theta_x = 1$.

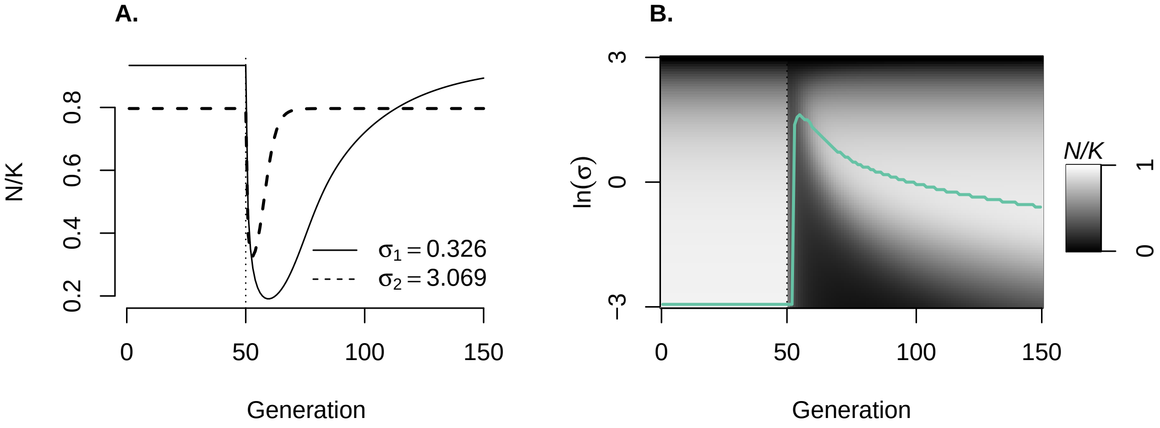

Figure 2: Changes in population size following an abrupt environmental change for species differing only in σ. (A) Time series of population size of two species (the same species as in Fig. 1A-B,1D), one with high σ and high V_G (dashed line) and one with low σ and low V_G (solid line). Populations are 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 $\theta_{x1} - \theta_x = 1$.

higher σ species dominate but gradually give way to lower σ species because all species $\hat{N}$ are unchanged. However, the lag before poor dispersers adapt can be quite long given the very low rate of adaptation for the lowest σ (Figure 2). This interspecific variation in adaptation following environmental change will likely have impacts on the distribution of traits in a community, which is often of interest to community and ecosystem ecologists (Muscarella and Uriarte 2016; Šímová et al. 2018). For example, ecosystem function may be influenced by the mass-averaged functional traits in a community (Grime 1998). I study dynamics in community-weighted mean z in the Appendix.

I next studied how factors that mediate the tradeoffs associated with σ (migration load versus speed of adaptation) impact community dynamics. Because the transient advantage of higher σ species comes from the faster approach of $\bar{z}$ to new θ (Equation 2), the magnitude of environmental change might influence the degree of community turnover. Under a weak shift in θ, the benefit to adapting faster for high 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 dominate following the environmental shift) is also large. Notably, subtle shifts in environment lead to 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

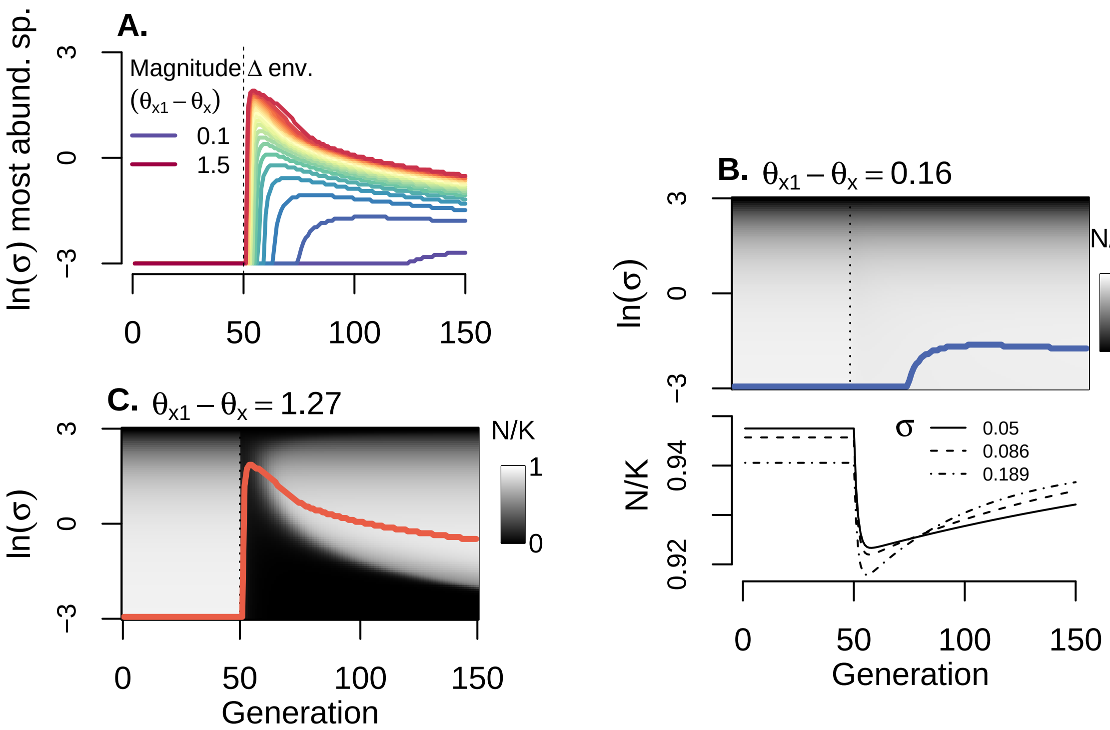

Figure 3: How the magnitude of environmental shift affects the magnitude of community turnover. (A) In general, the greater the environmental change, the higher the σ of the most abundant species soon after the environmental change (B). When the environmental change is too extreme, all species go extinct, 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_x for the first 50 generations, when an instantaneous environmental change to $\theta_x 1$ occurs. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$.

differences between species in maladaptation take time to erode the initial advantage (Figure 3). Despite the lag in reversal of species relative abundances, the differences among species in $\bar{r}$ are quickly evident in the form of differences in $\frac{\partial N}{\partial t}$ (i.e. there is rapid emergence of differences among species in slope of N trajectories, Figure 3B).

Migration load is ameliorated by high r_m (equation 4), thus r_m may impact eco-evolutionary community dynamics. Greater r_m reduces the effects of maladaptive immigration on $\hat{N}$ and allows for persistence (i.e. $\hat{N} > 0$) of species with higher σ (inequality 5). My simulations showed opposing effects of r_m on community dynamics. When r_m is low, high σ species cannot persist and thus the magnitude of community turnover is lower. However, because r_m is low, the recovery of species from low density is slow, and the community is dominated by relatively higher σ species for a long period of time (Figure 4). By contrast, high r_m allows for high σ species and the rapid environmental change causes strong, but shorter lived, community turnover.

Interspecific trait variation is often correlated across multiple trait axes, corresponding to ecological strategies and life histories. Thus it is unlikely that empirical variation in σ would be independent of other traits. To explore potential impacts of trait covariation, I studied the situation where σ and r_m positively covary such that higher gene flow species also exhibit higher per capita population growth when rare. For example, plants with high reproductive rates tend to have greater dispersal distances (Beckman et al. 2018). To test how this trait covariation would influence eco-evolutionary community turnover, I simulated a positive relationship similar to the observed empirical relationship (Beckman et al. 2018), $r_m = a + cln(\sigma)$, where a is an intercept and c determines the rate at which r_m increases for species of higher σ. This correlation has opposing effects on migration load and $\hat{N}$: r_m decreases load but σ increases load (equation 4). Thus intermediate σ species have greatest abundance at equillibrium (Figure 4). Notably, this correlation between r_m and σ leads to weaker eco-evolutionary community turnover because intermediate σ species were already dominant before environmental change so their dominance after environmental change means the community is relatively consistent.

Migration load is also ameliorated under shallower environmental gradients (lower b), though low b also reduces V_G and hence adaptation. In nature, the slope of environmental gradients varies in space and are thought to be important drivers of biodiversity patterns (Yeaman and Jarvis 2006). An important observation is that in a system with low b, there will be predominantly gene flow between like environments. The slope of the curve relating species abundance to gene flow ($\frac{d\hat{N}}{d\sigma}$) is proportional to b thus lower b will result in a abundance curve, i.e. a more even community. That is, migration load is reduced and species differing in σ have similar abundances.

I investigated the impacts of varying the slope of spatial gradients on turnover in communities following rapid environmental change. When I varied b, the most obvious impact is on the magnitude of community turnover following environmental change. Immediately after the environmental change, high σ species dominate when b is low. Note that when b is low, differences in abundance of species differing in σ are subtle due to low migration load, though there is relatively high turnover in which species are most abundant following the environmental change. When b is high, the environmental change results in turnover favoring species of intermediate σ. Surprisingly, the change in relative species abundances following the environmental change happens at a similar rate regardless of b (lines in Figure 5 have similar trajectories following environmental change), although higher b results in faster return to equilibrium because the initial community turnover was less. The consistency of the rate of community turnover is likely due to species proportional differences in V_G and rate of adaptation being constant despite differences in b (equation 2).

Barton (2001) and Polechová and Barton (2015) investigated how faster change in environments at range margins, i.e. increasing magnitude of b, impacts local adaptation.

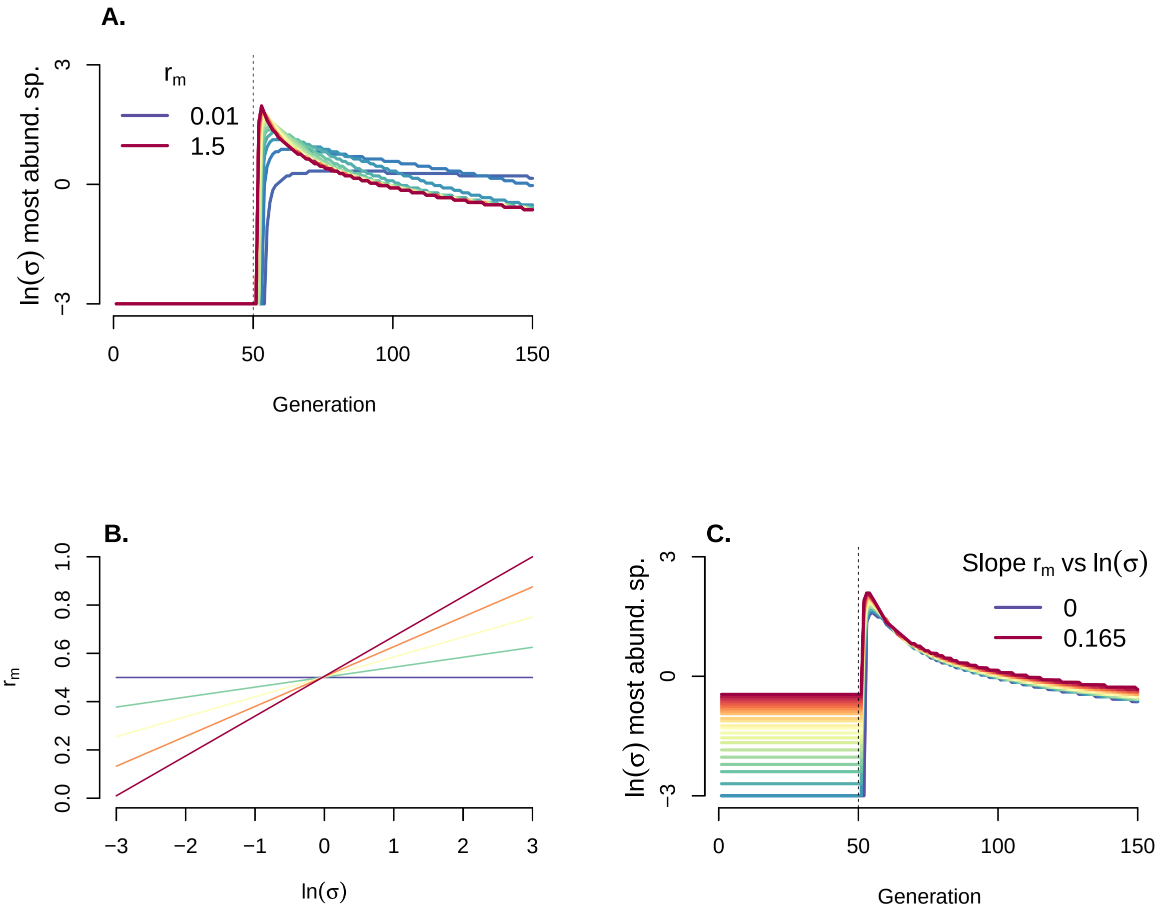

Figure 4: (A) r_m affects the magnitude of community turnover following an abrupt environmental change. Greater r_m results in an initially greater commuity turnover because r_m reduces migration load and allows high σ species to leverage their faster adaptation following environmental change. Lower 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 low σ species. (B) Correlation between reproductive rate at low density (r_m) and gene flow (σ) affects the magnitude of community turnover following an abrupt environmental change (C). 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 $\theta_{x1} - \theta_x = 1$.

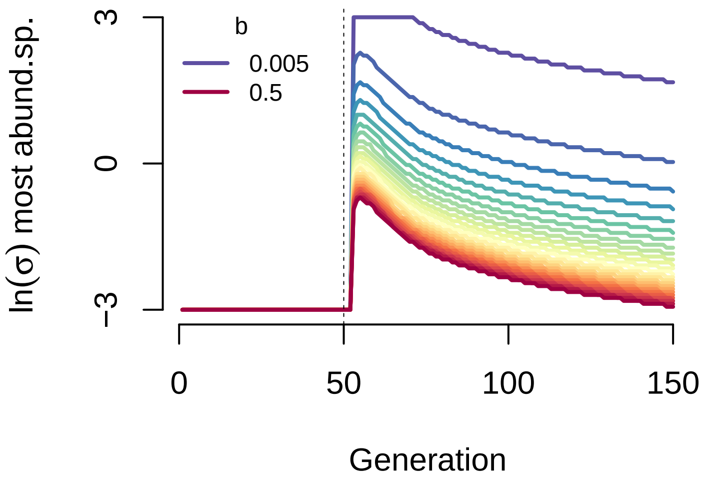

Figure 5: The slope of the spatial selective gradient (b) affects the magnitude of community turnover following an abrupt environmental change. Greater b results in dominance by intermediate σ species folowing abrupt environmental change (imposed after 50 generations). Lower b allows higher σ species 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 $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\theta_{x1} - \theta_x = 1$.

My results on how b influences community turnover due to differential evolutionary response to environmental change may apply to such changes in b in space. The present model can be applied assuming that the rate of change in b is subtle, such that $\partial \bar{z}/\partial x$ remains approximately linear. If b is sharper at range margins (for an assemblage of species, this would correspond to ecotones at the margin of ecoregions, for example along very steep altitudinal gradients), migration load would be stronger at margins and would have a stronger influence on community composition at equilibrium (i.e. steeper $\frac{d\hat{N}}{d\sigma}$). However, following environmental change, the change in species rank abundance will be greater in the range core (low b) while there would be lesser change in species rank at range margins (high b).

2.3 Community turnover under sustained environmental change

Temporal environmental change can take any functional form. In the previous section 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. This scenario has been analyzed previously by Pease et al. (1989), Lynch and Lande (1993), and Polechová et al. (2009). Here, I build on this framework by explicitly considering the role of gene flow on population dynamics in this scenario. In the Lynch and Lande (1993) model, the optimum θ changes at a rate k per unit time t, so that $\theta(x,t) = bx + kt$ (Polechová et al. 2009). After a enough time has passed to allow for a balance between adaptation versus the shifting optimum, the mean trait ($\bar{z}$) at location x lags behind the optimum a stable distance, which Lynch and Lande (1993) calculated as equal to $-k\frac{V_S}{V_G}$. In the present model, greater σ increases V_G and causes lower lag in $\bar{z}$ behind the shifting optimum. Substituting the Barton (2001) equation for V_G in a locally adapted system into the previous expression results in a lag in $\bar{z}$ equal to

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

i.e. lag in $\bar{z}$ for a given species was proportional to σ^{-1} (Polechová et al. 2009 identified this expression in a population genetic model of this scenario). Thus stronger stabilizing selection reduces the lag, though to a lesser degree than identified by Lynch and Lande (1993; $\sqrt{V_S}$ versus V_S, Kremer et al. 2012). This is because when stabilizing selection is stronger (low V_S) the fitness advantage of adapted genotypes is higher but stronger stabilizing selection also reduces V_G from immigration, slowing adaptation.

Lynch and Lande (1993) also derived the critical rate of environmental change above which populations go extinct (assuming large N_e) as $k_c = V_G\sqrt{2\frac{r_m - \frac{V_P}{2V_S}}{V_S}}$ (see also Polechová et al. 2009). I substitute the Barton (2001) equation for V_G in a locally adapted system into the previous equation to obtain

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

This equation shows how k_c is non-monotonically related to σ, i.e. k_c is greatest for intermediate values of σ (Polechová et al. 2009). Low σ species have low V_G, and hence slower $\frac{\partial \bar{z}}{\partial t}$ but high σ species suffer from high migration load (high V_P). The difference in this sustained environmental change scenario (compared to the abrupt change scenario above) is that slower $\frac{\partial \bar{z}}{\partial t}$ continues to be a drag on $\bar{r}$ (known as lag load), whereas after the abrupt change that then stops, slower $\frac{\partial \bar{z}}{\partial t}$ becomes unimportant as $\bar{z}$ approaches θ.

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

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

where the first substracted term includes migration load, which worsens with σ, while the second substracted term gives the lag load, which is ameliorated by σ. These opposing effects result in species with intermediate values of σ and hence V_G being most abundant (Figure 6, Polechová et al. 2009). Differentiating with respect to σ gives

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

The maximum $\hat{N}$ is attained by species with σ that cause the right hand side of equation 10 to equal zero, i.e. the σ with maximum $\hat{N}$ is equal to $(2k^2\sqrt{V_S})^{1/3}/b$. Note this expression equals zero when k is zero, thus consistent with results on locally adapted systems in constant environments where $\sigma = 0$ is favored due to lack of migration load (equation 6). Thus greater rates of environmental change through time (k) favor higher σ species, but at a decreasing rate ($k^{\frac{2}{3}}$, equation 10).

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

2.4 Effects of species interactions

Species interactions could change the relative importance of some of the processes studied above. For example, interspecific competition could depress the mean fitness of species, pushing them closer to extinction, and also exacerbate relative population differences. I simulated both scenarios of environmental change with non-zero species interactions. Here I present simulation results for species within a community competing with each other, using the Lotka-Volterra form. Instead of equation 1, I used a discrete time version of the following

$$\bar{r} = r_m\left(1 - \frac{N_i - \sum_{i\neq j}^{J} N_j\alpha_{ij}}{K}\right) - \frac{(\bar{z}-\theta)^2}{2V_S} - \frac{V_P}{2V_S} \tag{11}$$

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 $\alpha_{ij} = \alpha_{ji}$.

I here repeat analyses from above, but with $\alpha_{ij} > 0$. Note that per equation 2, I assume adaptation is not influenced by such competitive interactions (i.e. competition does not influence $\frac{\partial\bar{r}}{\partial\bar{z}}$; α_{ij} is unrelated to z_i and z_j) (Fussmann and Gonzalez 2013; cf. Osmond and Mazancourt 2013). In simulations, I initiated species at a low abundance ($N = 10^{-5}$), but then allowed 500 generations for population growth with interspecific competition before imposing change in θ.

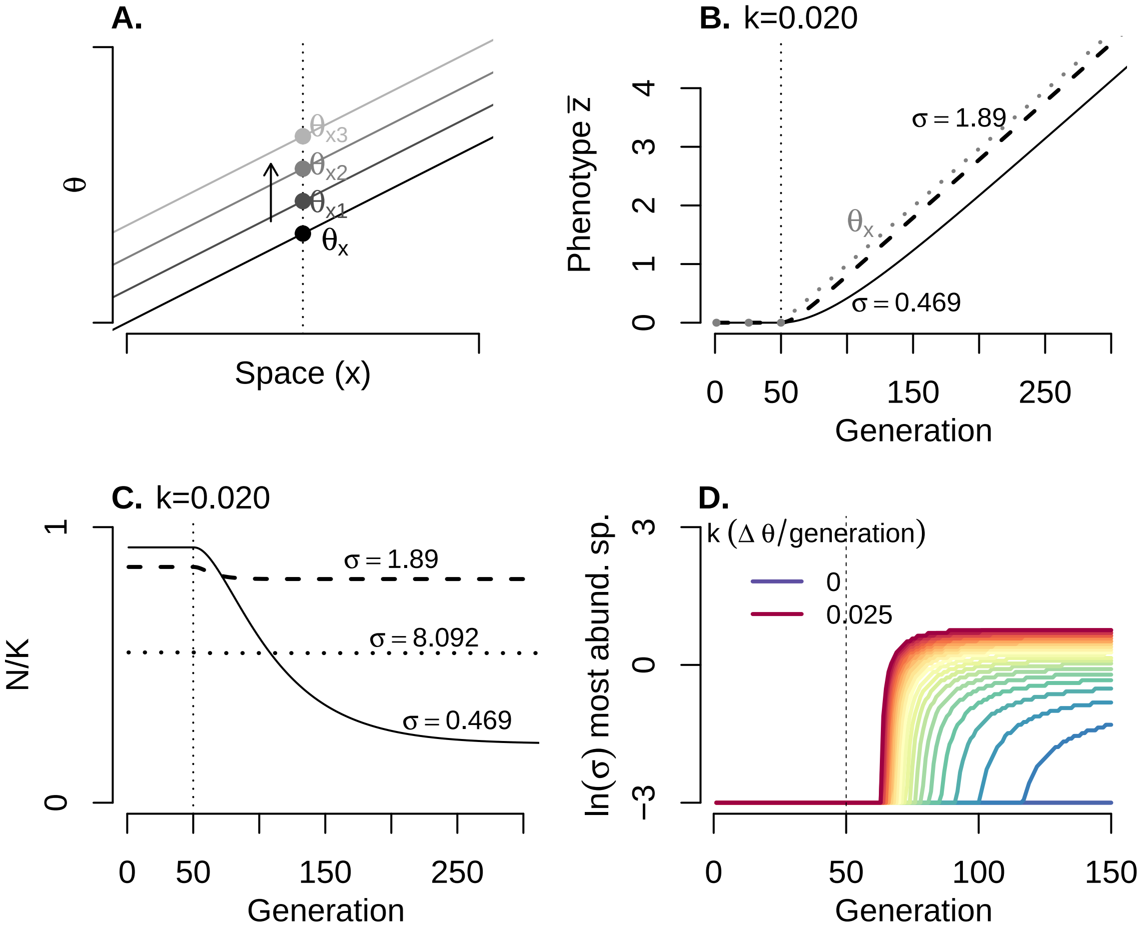

Figure 6: Effects of a sustained environmental change (i.e. a change in θ_x through time). (A) Illustration of the scenario of shifting θ across all locations, from a historical θ_x to which species were locally adapted, to new θ. (B-D) Environment is constant (constant θ) until the vertical dashed line at which point θ_x changes at a constant rate k. (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_x). (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 $r_m = 0.5$

2.4.1 Species interactions and response to abrupt environmental change

The previous simulations involved communities of $J = 100$ species differing in σ but with all $\alpha_{ij} = 0$. I now study 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 12). Adding symmetrical and weak species interactions had only weak effect on turnover in the most abundant community member, compared to the scenario with no interactions (Figure 12). Reductions in population size were nearly equivalent for all species in a diverse community with weak competition. 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 had similar impact on community dynamics, as measured as σ of the most dominant species, regardless of the simulated weak competition.

I also simulated ten strongly competing species ($\alpha_{ij} = 0.75$) and found substantial differences in community dynamics. Here, competition again had little effect on how the σ of the most abundant species changed with time (Figure 12). However, this similarity obscured underlying community changes caused by the combination of eco-evolutionary response to changing θ and 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 (Figure 12). Note that my deterministic simulations lack stochastic extinction, which is likely a major problem for populations at very low density. In my simulations, 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. Thus the dominance of higher σ species is still transient, though with a much slower return to the pre-environmental change equillibrium $\hat{N}$. Higher σ species that dominate communities can actually see increased absolute abundance following environmental change, despite going from being locally-adapted to being maladapted. This surprising change results from the release from competitive supression by low σ species.

2.4.2 Species interactions and 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 (equation 11) under the scenario of shifting θ at rate k throught time. I again began by simulating a diverse community of weakly interacting species ($J = 100$ and $alpha_ij = 0.01$). I found that the σ of the dominant species under environmental change was largely the same regardless of whether $alpha_ij = 0$ or

$alpha_i j = 0.01$ (Figures 6 & 7). When increasing interaction strength ($alpha_i j = 0.75$) in less diverse communities ($J = 10$), I again found similar patterns comparing $alpha_i j = 0.75$ to $alpha_i j = 0$ in terms of which species were most abundant through time (both $J = 10$, Figure 7). However, this similarity obscured differences in relative abundance patterns among communtiy members. Under interspecific competition, the most abundant species had greater relative abundance advantages. Interestingly, in scenarios with interspeicfic competition, higher gene flow species often showed dramatic increases in absolute abundance following the initiation of environmental change (Figure 7). In these simulations, low gene flow species with low migration load were supressed by environmental change and this allowed increased abundance of higher gene flow species better able to adapt to shifting environments.

2.4.3 Ecosystem resilience and interspecific interactions

The increased absolute abundance exhibited by many intermediate to high σ species under environmental change may have important community and ecosystem-level implications. For example, biodiversity can impact ecosystem function when species exhibit compensatory population dynamics through time, stabilizing ecosystem-level processes (Micheli et al. 1999; Loreau 2010). The increased abundance of high σ species under environmental change due to competitive release might stabilize ecosystem function despite declining low σ species. I tested this hypothesis using the assumption that total number of individuals of all species in the community corresponded to ecosystem function.

I quantified biomass resilience using approaches specific to each scenario of environmental change. For abrupt change, I calculated the time (number of generations) until the community regained 75% of the biomass seen at equilibrium before the environmental change. For sustained change, I calculated the biomass in the final generation of simulations (500 generations following the initiation of change - when populations had stabilized) as a proportion of the biomass under stable environments.

In both cases, simulations showed that communities with stronger interspecific competition also showed greater resilience under strong environmental change. In diverse communities with weak interspecific competition, biomass either returned faster or was maintained at higher relative levels, compared to similar communities without interspecific competition (Figure 8). Communities with fewer species (10 species) but stronger interspecific competition exhibited even greater resilience relative to comparable communities without interspecific competition, under both scenarios of environmental change. This resilience is clearly due to increases in abundance of high σ species, which were released from competitive supression by previously dominant but slow adapting low σ species, and which themselves adapted to changing environments rapidly (Figures 7 & 8).

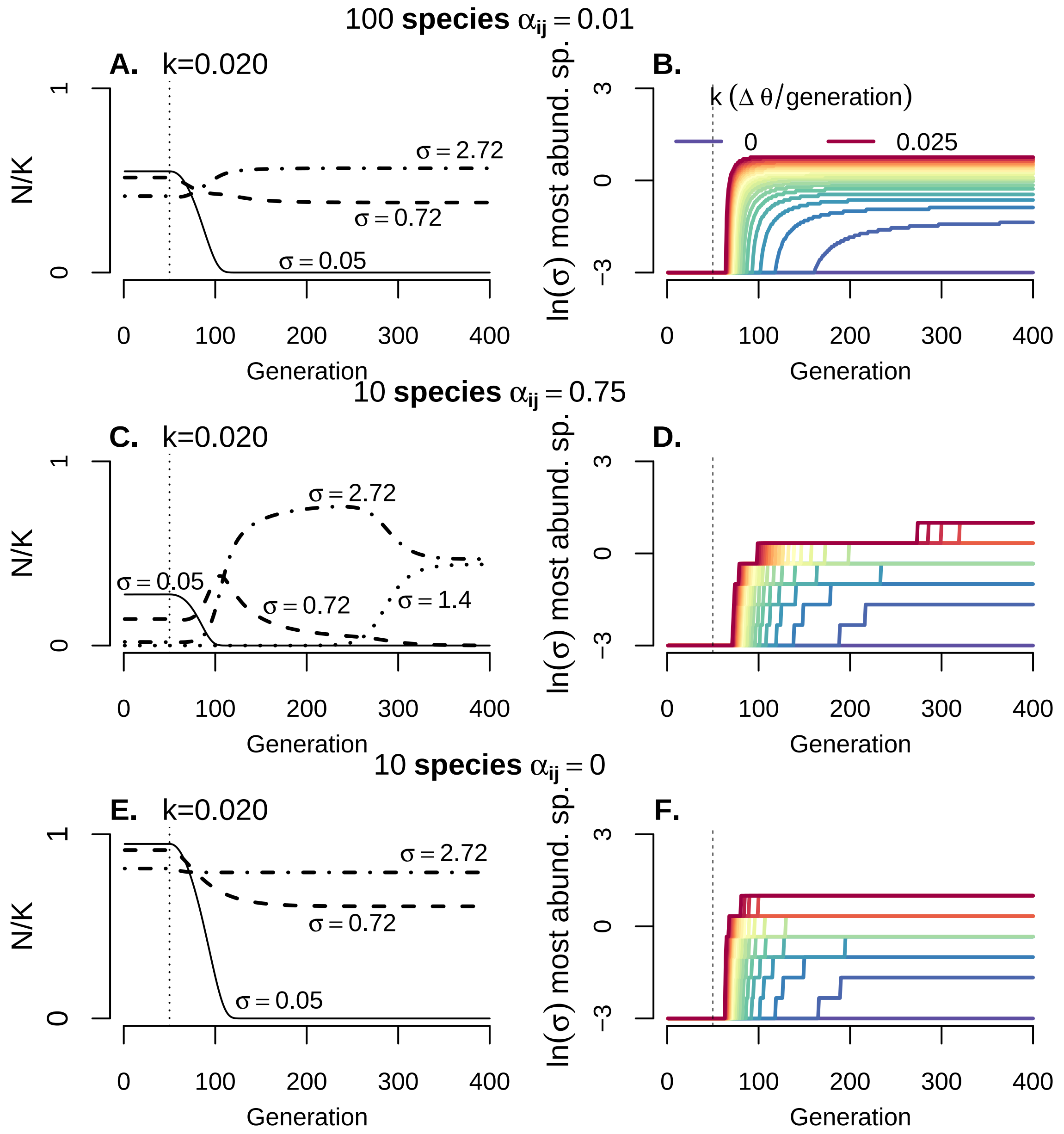

Figure 7: Effects of a sustained environmental change with interspecific competition, with example species highlighted in each scenario. Left panels demonstrate how absolute abundance of higher σ species can increase following environmental change, despite. (A-B) Diverse community with weak interspecific competition (C-D) Community with fewer species and strong interspecific 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 (450 generations were run under a stable environment before those shown). Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$

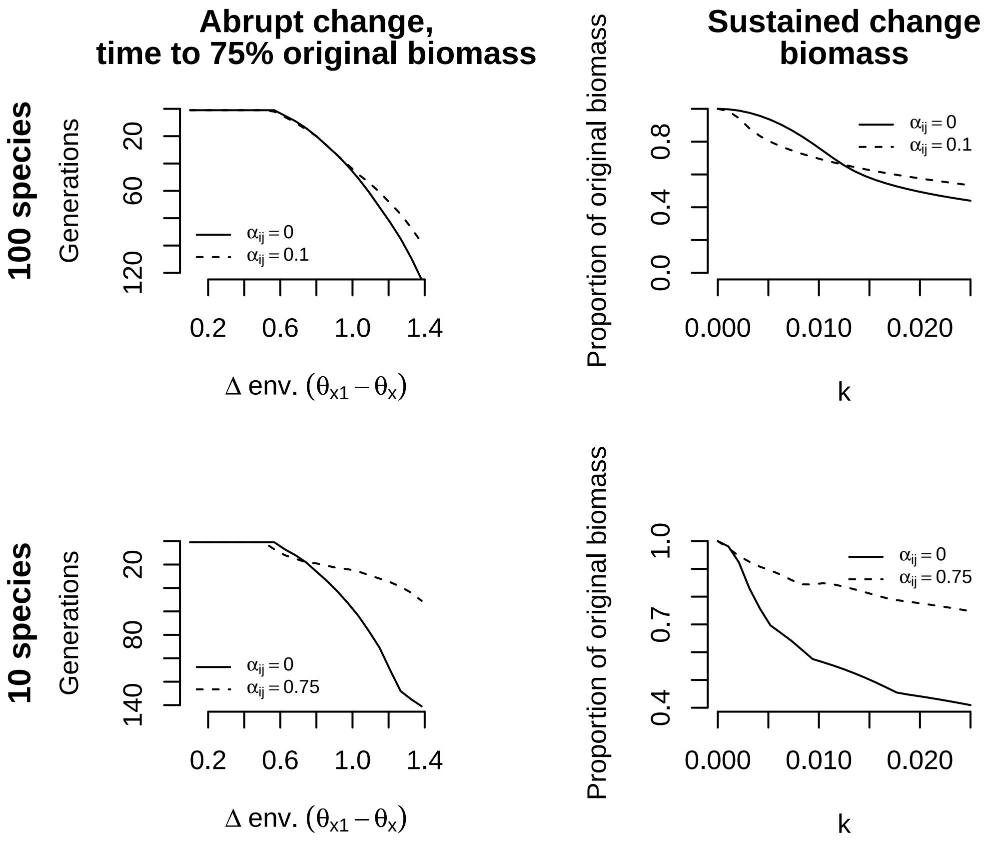

Figure 8: Communities with interspecific competition are more resilient to environmental change, measured in terms of (left panels) time to return to 0.75 of pre-environmental change biomass or (right panels) biomass in 500th generation under sustained linear temporal change. Note that in left panels the y-axis is reversed for comparability with right panels. Biomass is measured as the total number of individuals of all species. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, and $r_m = 0.5$.

2.5 Relationship of eco-evolutionary community turnover to ecological succession

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

Successional community turnover arises as species differ in the rate of population growth (eqn 3) due to interspecific variation in immigration (favoring high σ species) and fitness (favoring low σ species). However, note that the fitness advantage of low σ species is dependent on reproduction by individuals already present, which are few after disturbance. My simulations showed that the more intense the disturbance, the slower the return to community equillibrium (Figure 9), analogous to the slower return following greater abrupt changes in θ (Figure 3). Under a sustained ecological disturbance (constant proportion of individuals lost each generation) ecological community turnover exhibits qualitatively similar patterns to the eco-evolutionary response to sustained change in θ (Figure 9). Specifically, sustained disturbance resulted in consistent dominance by species with intermediate σ, similar to these species being most abundant under sustained change in θ (Figure 6).

3 Discussion

Evolutionary genetic theory is a rich source of hypotheses for how life history impacts evolution. On this rapidly changing planet, understanding and predicting evolutionary responses environmental change will be particularly valuable (Bay et al. 2017; Gienapp et al. 2017). Molecular data are providing a deeper view of the differences among species in population genomic patterns (e.g. Romiguier et al. 2014). The present is ripe for studying how interspecific trait differences impact evolutionary response to environmental change and the consequences for communities and ecosystems. Here, I took existing quantitative genetic models of adaptation (Lynch and Lande 1993; Barton 2001; Polechová et al. 2009) and showed how interspecific trait variation

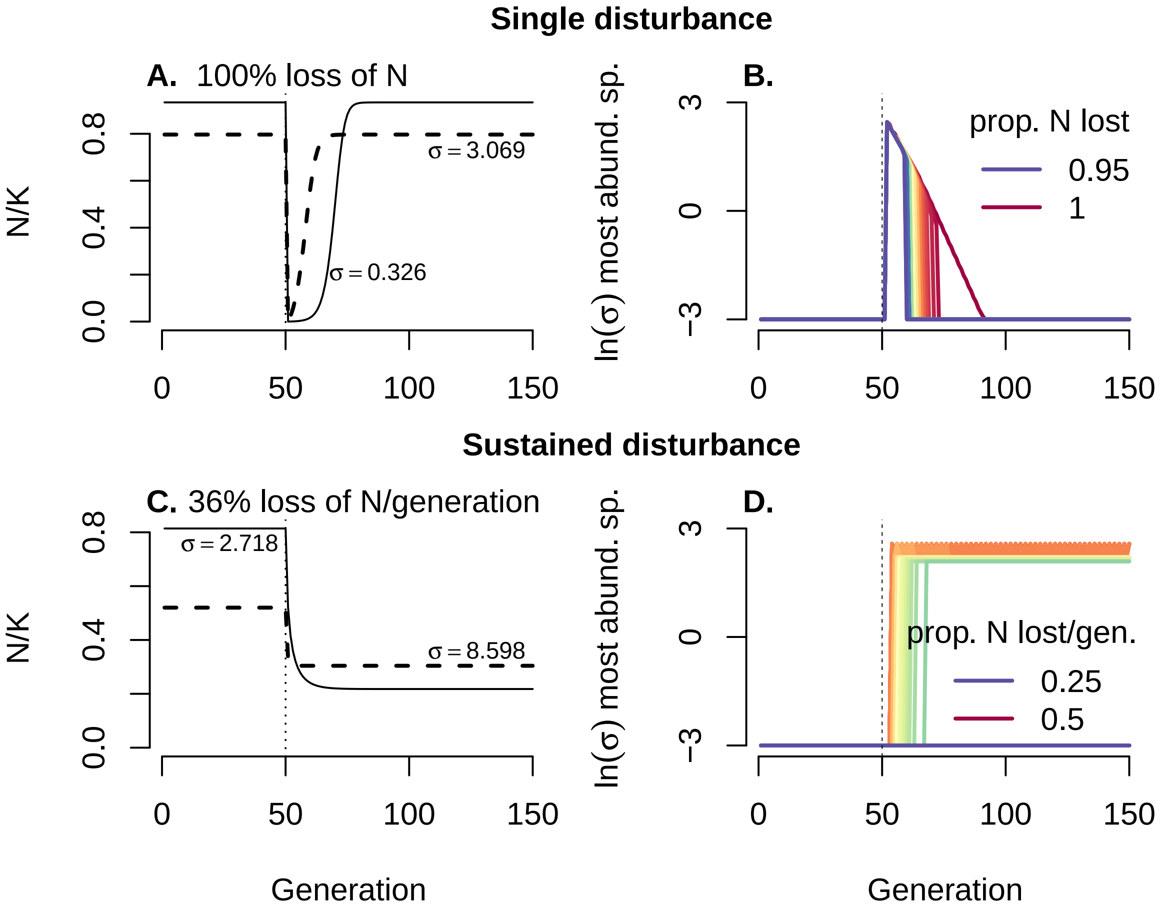

Figure 9: Variation in dispersal (σ) among species determines how communities of locally-adapted populations respond to ecological disturbance. (A-B) A single disturbance removes a large portion of each species' N after generation 50. (C-D) recurring disturbances are imposed in each generation, starting after generation 50. Parameter values (unless otherwise noted) were $b = 0.05$, $V_S = 1$, $V_E = 0.05$, $r_m = 0.5$, and $\frac{\partial^2 N}{\partial x^2} = 5$.

gives rise to differences in genetic diversity with non-monotonic effects on community structure and dynamics. Many previous studies of what is referred to as evolutionary rescue have largely focused on thresholds beyond which populations go extinct under environmental change (Lynch and Lande 1993; Gomulkiewicz and Holt 1995; Bell and Gonzalez 2009; Uecker et al. 2014). Even if populations of most species in a community are able to avoid extinction under environmental change, my results highlight how communities may change drastically in composition and function. Dominant species can become rare and rare species can become dominant (Figure 7). This turnover has important consequences for community diversity and ecosystem function.

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 adaptability to environmental change. In my model, 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 has a major influence on the rate of adaptation, but other traits, such as generation time, vary among species in communities and may also result in eco-evolutionary community turnover. For example, parasites may have shorter generation time than hosts, allowing parasites to adapt faster to abiotic environmental change. Both vertebrate hosts (Fraser 2013) and their parasites (Sternberg and Thomas 2014) can be locally-adapted along temperature gradients, though parasites might adapt to climate change 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 (Polechová et al. 2009; 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). 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). I did not investigate interspecific variation in phenotypic plasticity, which may supplant local adaptation as a response 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 changing environments may cause complex community change. 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 functional 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; Polechová et al. 2009). 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 my results demonstrate how diverse forms of environmental change may cause complex dynamics in nature.

Though I modeled community turnover in a single local population, all communities in my model are equivalent and the processes I described would occur across species ranges. This suggests that there is a large potential spatial extent of eco-evolutionary responses to rapid environmental change, resulting in community change across large regions. In nature b is non-linear and rugged, a feature worthy of study in future simulation of response to temporal environmental change. Furthermore, multiple traits may be under simultaneous spatially-varying selection (Guillaume 2011; Duputié et al. 2012; 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 relative abundance for species differing in σ.

The model studied here was simple and thus it is challenging to determine how important my results are in natural systems. However, gene flow across spatial selective gradients is likely a major source of within-population genetic variation in traits under selection (Yeaman and Jarvis 2006; Paul et al. 2011; Farkas et al. 2013). Findings on ponderosa pine suggest that greater b can cause greater V_G (Yeaman and Jarvis 2006). Less is known, however, of how adaptability or V_G are related to interspecific variation in census population size (abundance). The negative relationship between these two quantities is the key to community turnover following environmental change in my results. One problem with empirically studying the processes I described there is often a substantial lag before better dispersing species dominate communities (Figures 3 & 6). Thus researchers may overlook empirical population changes caused by environmental change.

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

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

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 complexity in eco-evolutionary community change. Future research could improve our ability to predict responses to environmental change in nature by learning more about the genetics and ecology of adaptation in addition to theoretical investigation of more complex scenarios.

3.2 Acknowledgments

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4 Appendix

4.1 Impacts on community-mean traits

Interspecific variation in adaptation following environmental change will likely have impacts on the distribution of traits in a community, which is often of interest to community and ecosystem ecologists (Muscarella and Uriarte 2016; Šímová et al. 2018). For example, ecosystem function may be influenced by the mass-averaged functional traits in a community (Grime 1998). Under the scenario of abrupt environmental change, the slow adaptation and return to equillibrium abundance of species that dominate communities may have interesting effects on changes in community-weighted mean (CWM) traits. Indeed, following abrupt environmental change, initially there is a very rapid phase of change in CWM driven by fast-adapting high σ species (Figure 10). However, there is an abrupt slow-down in change in CWM as most high σ species have adapted but low σ species remain maladapted. Nevertheless, the low migration load of these low σ species contributes to their fitness and abundance and hence influence over CWM traits. By contrast, when there is sustained change in θ over time, species exhibit marked variation in their ability to adapt to the moving optimum. Although the highest σ species are able to maintain $\bar{z}$ close to the optimum, they are less abundant than intermediate σ species due to migration load (equation 10, Figure 6). Thus the CWM exhibits a substantial and stable lag behind the optimum.

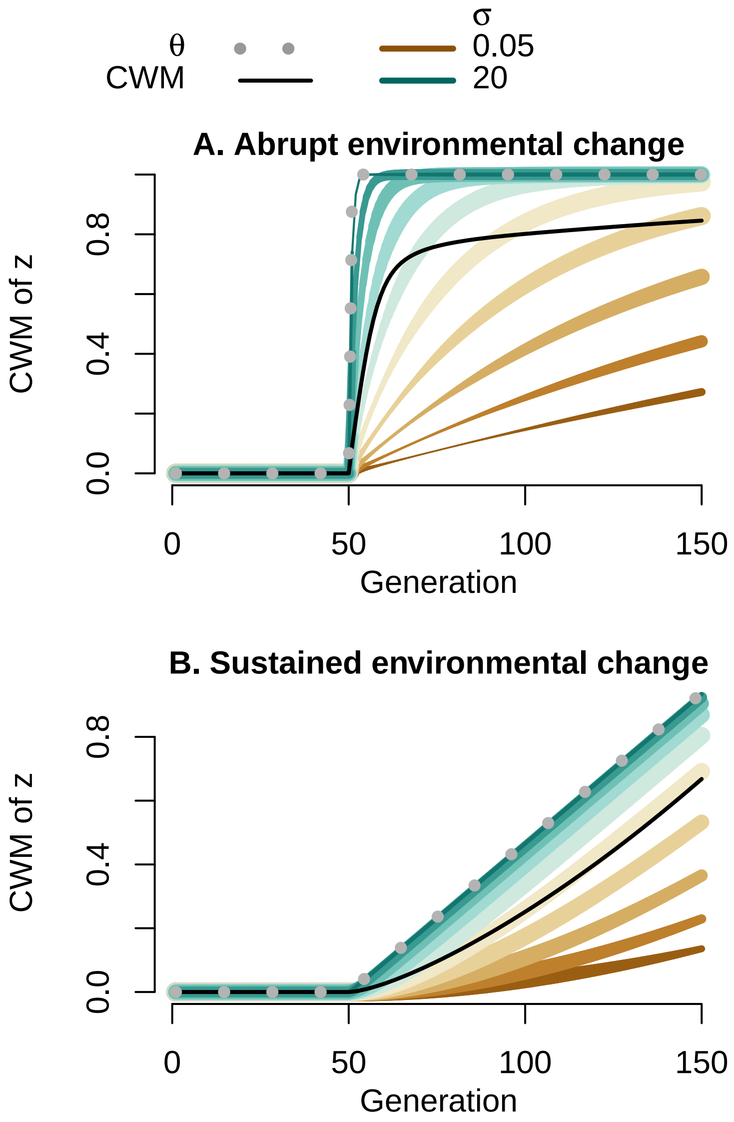

Figure 10: Effects of environmental change on community-weighted mean (CWM) traits under selection due to eco-evolutionary responses. Example species with a range of σ values are shown (colors), with line thickness indicating relative abundance. As in earlier presented simulations, communities were composed 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), $\theta_{x1} - \theta_x = 1$. For (B), $k = 0.009$.

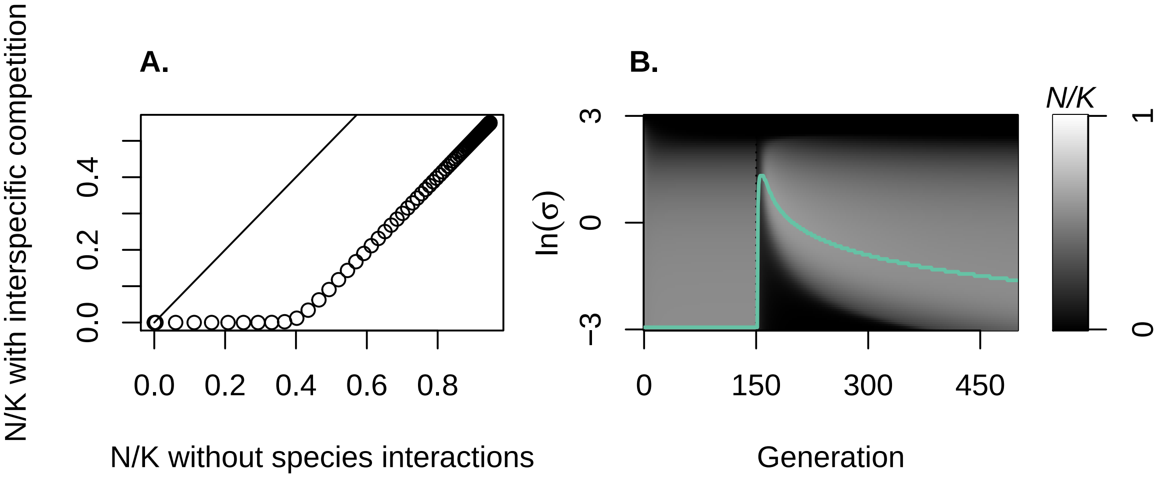

Figure 11: Community turnover under abrupt environmental change, with interspecific competition. (A) Comparing approximate equilibrium species' N for scenarios differing in presence of interspecific competition. Black circles show species in a diverse (100 species) community with weak interactions ($\alpha_{ij} = 0.01$). 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 $\theta_{x1} - \theta_x = 1$.

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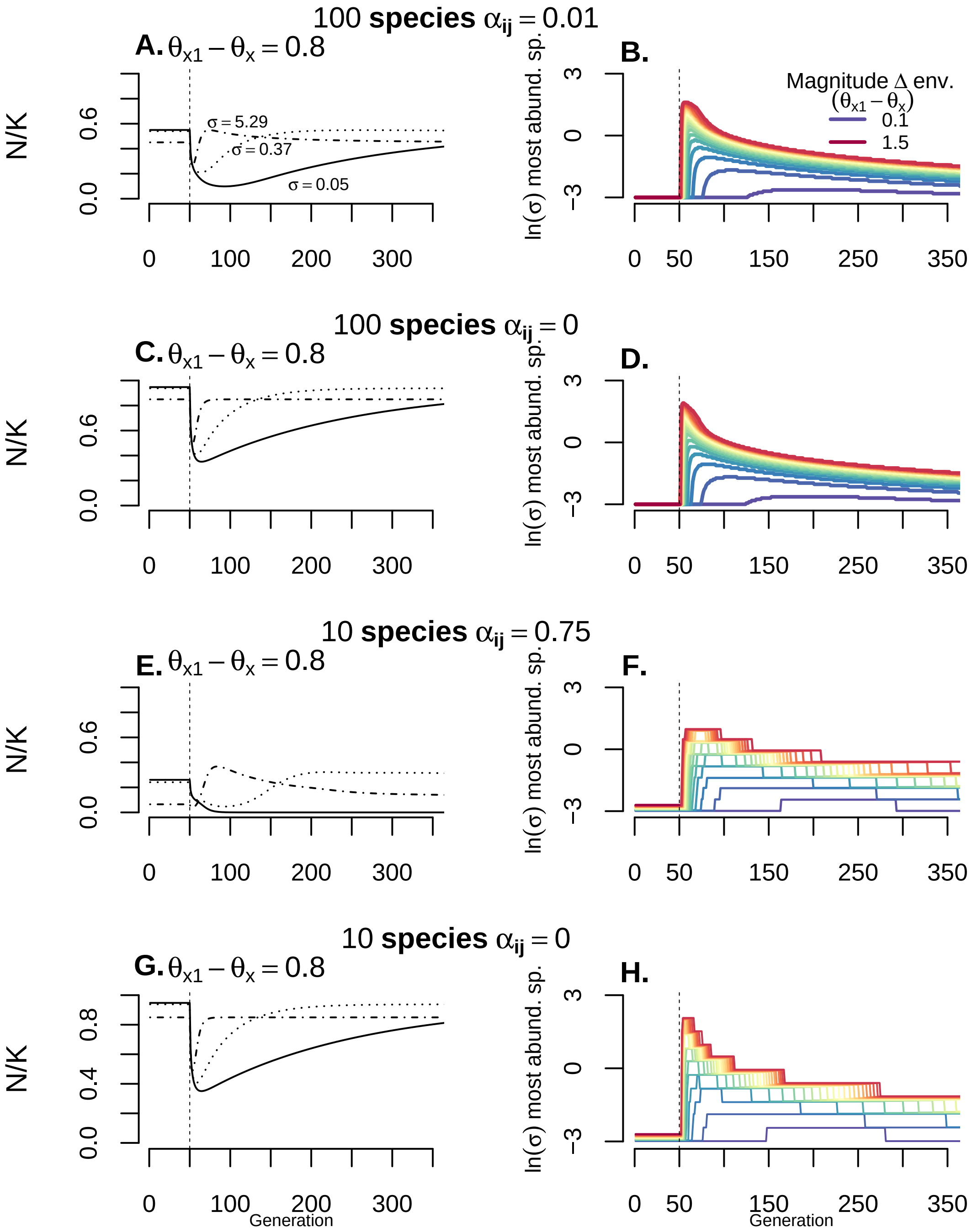

Figure 12: How the magnitude of environmental shift and interspecific competition affects community turnover. Left panels show the same three representative species of varying σ under different scenarios of interspecific competition. Right panels show which species are most abundant at any point in time, under different levels of abrupt environmental change. Populations are at approximate equilibrium and adapted to θ_x for the first 50 generations, when an instantaneous environmental change to θ_{x1} occurs. 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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