Title: Eco-evolutionary feedbacks and the maintenance of metacommunity diversity in a changing environment

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Abstract: The presence and strength of resource competition can influence how organisms adaptively respond to environmental change. Selection may thus reflect a balance between two forces, adaptation to an environmental optimum and evolution to avoid strong competition. While this has been explored in single communities, its implications for eco-evolutionary dynamics at the metacommunity scale are unknown. We developed a simulation model of quantitative trait evolution for a trait that influences an organism's carrying capacity and its intra- and interspecific competition strength. Multiple species inhabited a variable three-patch landscape, and we varied the connectivity level of the species among patches, the presence and pace of directional environmental change, and the strength of competition between the species. Our results reflected some patterns previously observed in evolving metacommunity models (e.g. species sorting and community monopolization), although species sorting was more common when competition strength was high and monopolization was observed only when the environmental change was very rapid. We also detected an eco-evolutionary feedback loop between local phenotypic evolution at one site and competition at another site that maintains species diversity in some conditions. The existence of a feedback loop that is maintained by dispersal indicates that eco-evolutionary dynamics in communities operate at a landscape scale.

Introduction

Competition for resources is a critical component structuring biodiversity in nature (Tilman 1994; Hautier et al. 2009). Many ecological theories developed to understand competition, coexistence, and biodiversity treat the traits that influence species interactions as fixed (e.g. Chesson 2000). Recent experimental studies have demonstrated that critical traits - such as the interaction strength of competitors (α) and the minimum resource level required for positive growth (R^*) - are not fixed and can in fact evolve on an ecological timescale (Hart et al. 2019; Bernhardt et al. 2020). Studies have also demonstrated that ecological competition can inhibit or enhance evolutionary diversification and speciation, and can play an important role for understanding biodiversity over a longer macroevolutionary time scale (Gillespie 2004; Losos & Ricklefs 2009; Drury et al. 2016). It is therefore important that theory is developed to predict how coexistence and consequent biodiversity will differ when evolution of traits that influence ecological competition is taken into account (Roughgarden 1972; Lankau 2011). This is especially important as anthropogenic climate change increases or introduces novel selection pressures for organisms (Moran & Alexander 2014).

Theoretical models that evaluate the role of evolution for competition and coexistence in multiple species have been developed at both the local and regional scale, but thus far models at the regional scale have not considered evolution in traits that directly impact competition. Regional models of evolution in multiple species have instead considered evolution in a trait that is selected on by local environmental conditions. These models have found that the degree of adaptive evolution can be slowed when sites are connected, as species are more likely to colonize more suitable patches before local adaptation occurs (de Mazancourt et al. 2008). Another important result is the observation of community monopolization, where a species can adaptively respond to environmental change and prevent the colonization of other well-adapted species due to their numerical advantage (Urban et al. 2008; Loeuille & Leibold 2008; Urban & De Meester 2009; Vanoverbeke et al. 2016). Importantly, these studies indicate that metacommunity composition emerges as a product of environmental heterogeneity, site connectivity (or species dispersal rate), and the speed of adaptive evolution. However, these models do not consider ecological competition explicitly, as individuals with differing traits compete indirectly to occupy microsites within patches (i.e. lottery competition). One study of evolution in metacommunities did model per capita impacts of one species on another (Norberg et al. 2012), and their results do broadly mirror other studies of evolution and competition at the regional scale. However in these studies, trait evolution is influenced only by environmental selection. The measure of fitness (recruitment, survival, or intrinsic rate of population increase) depended only on the local environment and was decoupled from competition.

In nature, trait evolution can be influenced by multiple selection pressures, both abiotic and biotic. In zooplankton, for example, important life history traits, such as body size, are driven not only by temperature (e.g. Mc Kee & Ebert 1996), but also by adaptation for increased grazing efficiency (and thus increased competitive ability) and by risk of susceptibility to visually hunting predatory fish (Burns 1969; Dodson 1974; Hall et al. 1976). Traits in protozoans, such as cell size or population growth rate, can also be influenced by competition and predation (terHorst et al. 2010; terHorst 2011). There are some models where trait evolution is influenced both by the abiotic

environment and by ecological competition as well, but these are only for a single site - multiple connected sites are not considered. These models have produced important findings that may have implications at the regional scale. Competition can slow the rate of evolution, as trait convergence on an adaptive optimum determined by the environment can increase competition strength (Johansson 2008), but it can also increase the rate of evolution in some instances. Osmond & de Mazancourt (2013) found that the degree of niche overlap between competitors (i.e. whether competition selects in the same direction as the new environment or in the opposite direction) determines whether competition slows or accelerates evolution. The goal of our study was to consider the effects of ecological competition on trait evolution at the metacommunity scale. The combination of environmental heterogeneity and spatial connectivity could produce local communities that vary in their degree of niche overlap. When these communities experience a changing environment, their ability to adapt would thus be diminished or accelerated. Spatial structure could play a critical role in the ability of competing species to avoid extinction and adapt to environmental change (evolutionary rescue; Gomulkiewicz & Holt 1995; Bell 2017).

We modeled population growth and competition for multiple species that inhabit a three-patch landscape. Population growth depends on a quantitative trait that determines carrying capacity in the local environment and the degree of intra- and interspecific competition. This trait can evolve (implemented using an adaptive dynamics framework; Metz et al. 1992; Dieckmann & Law 1996) and populations can disperse among patches (Figure 1a). We monitored metacommunity eco-evolutionary dynamics to assess the effects of varying three components of the system: (1) spatial structure (isolated patches and patches with low and high levels of dispersal connectivity), (2) rate of environmental change (none, slow, and fast), and (3) strength of competition (by varying the decay in competition strength with increasing distance between individual trait values; Figure 1b). For each model scenario, we evaluated evolutionary and community dynamics by considering local and regional species diversity, measures of stability, and distributions of the quantitative trait over time and across sites. Because the existing models of evolution and competition at the local and regional scale address some aspects of these components, we focused specifically on two research questions. First, we evaluated whether the degree of niche overlap (which influences the speed of trait evolution) was a fixed property at each site or whether dispersal and environmental change cause the direction of selection by the environment and by competition to vary over space and time. Osmond & de Mazancourt (2008) considered how fixed degrees of niche overlap in communities at a single location influenced the speed of evolution in their model. Johansson (2008) does vary the direction of environmental selection over time, but not the direction of selection for competition. Second, we evaluated whether the findings of existing studies of evolution in metacommunities differed when trait evolution was influenced both by the environment and by competition. We used our evolving metacommunity model to determine whether the match between species traits and their environment (species sorting; Chase & Leibold 2003) observed at low to intermediate dispersal in previous studies is also observed when competition potentially restricts species from adapting to the local environmental optimum, and under what conditions global monopolization emerged.

Methods

Overview

We developed a model of quantitative trait evolution in a metacommunity of species that compete for resources and inhabit a three-patch landscape. Patches vary in their environmental properties (which favor an optimum trait value for resident species; Figure 1). Species in the model are defined as populations with distinct phenotypes that vary along a single trait axis. Although it is important to consider multi-trait evolution, we first consider a single trait axis to expand from the results of existing models of evolution in competing species at the local and regional scale. Our model results will thus be most applicable to systems where a guild of species respond to environmental selection pressures and compete for resources via a shared key trait such as body or beak size (e.g. Goulden et al. 1982; Lamichhaney et al. 2016), or resource uptake rate (e.g. Huston & DeAngelis 1994). Population growth follows Lotka-Volterra dynamics with density dependence and intra- and interspecific competition, and evolutionary dynamics are implemented using an adaptive dynamics framework. This framework is useful to study effects of interactions between species that are linked by dispersal across multiple sites because it links population dynamics directly to evolutionary dynamics (Dieckmann & Law 1996; Brännström et al. 2013), and also because these models can produce trait diversification that resembles distributions of species along niche axes observed in natural populations (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000). The phenotypic trait determines an individual's carrying capacity and the strength of competition with other individuals. We model environmental change as a constant rate of increase in the optimum trait value (the trait value that leads to the highest carrying capacity). We consider the same rate of change for each patch. All individuals of all species have a uniform probability of dispersal and can move equiprobably to the other patches in the landscape. The formulas and model details for ecology, evolution, and dispersal are described below in the sections *Within-patch ecology*, *Evolution*, *Extinction*, *Dispersal*, and *Environmental dynamics*. The details for simulation conditions to address our research questions are described in the sections *Metacommunity initialization* and *Simulation conditions*. Finally, we describe measures to quantify eco-evolutionary properties (e.g. diversity, degree of phenotypic evolution) in the section *Metrics for evolutionary and ecological properties*.

Within-Patch Ecology

Population dynamics are evaluated for all populations i that differ in their trait value x, i.e. each population has its own trait value x_i and population size N_{it} varies over time t. Population size N_{it} is a function of the vectors of trait values **x** for all populations present in the local patch and their population size in the previous generation N_{jt-1}. Population growth depends on trait values **x** in two ways. First, the carrying capacity K of a population with trait value x_i is a Gaussian function of the distance of x_i from x_{opt}, which is the patch-specific optimal trait value:

$$(1)\ K(x_i) = K_{max} * e^{\frac{-(x_{opt} - x_i)2}{2\sigma_K{}^2}}$$

Here x_{opt} is the trait value corresponding to the maximum carrying capacity, K_{max}, and K_{max} is the same for all populations in the patch. Carrying capacity decreases if population traits are distant

from the optimum x_{opt}, and the width of this carrying capacity distribution is determined by the standard deviation term σ_k. $K(x)$ can be interpreted as representing a resource distribution (biotic or abiotic) on a given patch, scaled to equal the total population that the resources at any given position on the trait axis can sustain. A population's trait x_i therefore corresponds to its ability to exploit its most efficiently used resource, and its carrying capacity $K(x_i)$ is limited by that resource.

Competition between populations is a symmetric function of the difference in their trait values. Competition, the per capita negative effect of a population with trait x_j on a population with trait x_i (α_{ij}) is determined by a decaying symmetric function of the distance between trait values x_i - x_j:

$$(2)\ \alpha(x_i, x_j) = \frac{1}{1 + \frac{(x_i - x_j)^2}{2\sigma_\alpha^2}}$$

where the strength of competition between individuals with differences in trait values is determined by the standard deviation term σ_α (i.e. the niche width). When $x_i = x_j$ the populations are ecologically equivalent and their competitive effect on each other is the same as their intraspecific effect on themselves ($\alpha_{ii} = 1$; otherwise $0 \geq \alpha_{ij} < 1$).

Equations 1 and 2 are incorporated into each population *i*'s growth:

$$(3)\ G_i(\mathbf{x}, N_t) = r\left(1 - \frac{\sum_{j=1}^{m} N_{jt}\alpha(x_i, x_j)}{K(x_i)}\right)$$

Where *r* is the population's intrinsic rate of increase and *m* is the total number of populations present in the patch, across all species present (more on how species are defined in the section *Metacommunity initialization*). We considered discrete population dynamics, so population size from one time step to the next is:

$$(4)\ N_{it+1} = N_{it} * (1 + G_{it})$$

Evolution

A mutation rate μ gives the probability that an individual born in the population has a mutation. In our model, existing populations give birth to rN_{it} individuals every generation. Each mutant born in a population in a given generation ($N_m = \mu r N_{it}$) is treated as a new population (subtracted from the parent population size, with initial population size equal to 1) and they do not encounter competition in the same generation they are generated (which allowed for computational tractability of tracking all mutant populations over time; results with competition in the same generation did not qualitatively differ from those presented here). The trait value of the mutant population x_m, is drawn from a normal distribution centered at the parental trait value x_i with standard deviation σ_μ, $x_m \sim N(x_i, \sigma_\mu^2)$.

Extinction

At the end of each generation t, we remove all populations with $N_{it} < 1$. We also implemented stochastic extinction at low population size: all populations with N_{it} below an extinction threshold θ but above 1 have a probability ρ of being removed from the system.

Dispersal

All patches are equally connected by dispersal. Each generation, all individuals can disperse with probability d. Dispersing individuals from one patch have an equal probability of migrating to any of the other patches.

Environmental dynamics

The metacommunity landscape consists of k patches. The optimal trait values $x_{opt,k}$ are evenly spaced along the trait axis with fixed difference δ, which gives the degree of environmental heterogeneity in the metacommunity. Environmental change was implemented each generation, where the patch optimal trait values $x_{opt,k}$ increase by the same rate Δ on all patches.

Metacommunity initialization

We used equations 1-4 to simulate adaptive dynamics in a single initial population with $N_0 = 500$ and $x_0 = 0$. This initial population was placed in each of $k = 3$ patches that represent the patches used later in the evolving metacommunity simulation (Figure 1a), using among-patch environmental overlap δ = 0.5. Local environmental optima in each patch k ($x_{k,opt}$) were therefore $x_{1,opt} = -0.5$, $x_{2,opt} = 0$, and $x_{3,opt} = 0.5$. For all of these scenarios, $d = \Delta = 0$, $\sigma_k = 1$, $r = 1.9$, $\mu = 10^{-5}$, $\sigma_\mu = 0.05$, $\theta = 2$, and $\rho = 0.025$ (results were qualitatively similar but over longer time scales for lower values of μ and σ_μ). We generated three distinct initial metacommunities, using each of the three different levels of niche width (σ_α = 0.68, 0.86, 1.5). Evolutionary dynamics proceeded for 10^6 generations, to create a community of species that have co-evolved to be well suited for their local environment and for coexistence in competition with the other species (Figure 1c). The adaptive dynamics framework provides a mechanism for emergence of multiple distinct lineages from a single initial trait value (described in more detail in Results, *Initial communities*). The coexisting lineages present at the end of the initialization period were considered unique species (similar to Johansson 2008) and are stochastic approximations of the coevolutionary equilibrium for that set of model conditions.

Simulation conditions

Coevolved communities that evolved from initial conditions in the three patches independently for 10^6 generations were used as initial patch communities for the evolving metacommunity simulations. For each of the three different levels of niche width (σ_α), we ran simulations for each three-patch metacommunity at different dispersal levels (d = 0, 0.01, 0.1) and different rates of environmental change (Δ = 0, 10^{-5}, 4×10^{-4}), maintaining the same level of niche width for that metacommunity. All of the 27 simulations ran for 50,000 generations and all simulation conditions were introduced at t_0. All simulations were conducted in MATLAB R2017a version 9.2.0.556344.

Metrics for evolutionary and ecological properties

A species I is denoted as all populations with distinct trait values at t_0 in the simulation. All populations m that derive from a species are considered sub-populations of that species (and so

individuals with particular trait values can be indexed as x_{lm}). Each generation, we calculated patch alpha diversity using the inverse of Simpson's diversity index: ${}_1D_\alpha = \frac{1}{\sum_{i=1}^{l} \quad p_i^2}$ where l is the number of species present in site k and p_i is the relative proportion of the species at that site (all populations m for a species l are included in this p_i calculation). We calculated gamma diversity ${}_1D_\gamma$ by summing population size of each species across all sites, and we calculated beta diversity ${}_1D_\beta = {}_1\bar{D}_\alpha$ / ${}_1D_\gamma$. We calculated the coefficient of variation in total population size within a patch (i.e. summed across all populations for all species) and the sum of squared deviations of individual trait values from the local environmental optimum (calculated for all individuals n within a patch; $SSD_k = \sum_{i=1}^{n} \quad (x_i - x_{opt})^2$.

To better understand how equations 1 and 2 interacted to structure trait evolutionary trajectories in our evolving metacommunity, we generated approximations of the $C(x)$ and $K(x)$ functions in each patch in each generation (i.e. the curves seen in Figure 1b). The $C(x)$ curve gives the distribution of competitive effect across the trait axis, $C_t(x) = \sum_{j=1}^{s} \quad \alpha(x, x_j) N_{jt-1}$, in time t (calculated at discrete values of x at intervals 0.001 in the range $\{x_{opt,k} - 3, x_{opt,k} + 3\}$). The value for an existing population's trait value (i.e. a population actually present in the patch at that time) in generation t is calculated including both intraspecific (competition with other individuals with the same trait value) and interspecific (competition with individuals with all other trait values, across the same and other species) competition experienced in generation t, and for all other x values in the range it is calculated as the total amount of interspecific competition (i.e. with individuals that have differing trait values) that an invading mutant with trait x_j would have suffered in generation t. The $K(x)$ curve was calculated using equation 1 for the range of x values. Populations with trait values in a region of the trait axis where $K(x) > C(x)$ experience positive population growth in generation t, negative growth when $K(x) < C(x)$, and no population growth at $K(x) = C(x)$ (equation 4). All metrics and figures were made using R version 3.5.0 (2018).

Results

Initial communities

Our model is a stochastic simulation of an adaptive dynamics model (Metz et al. 1992; Dieckmann & Law 1996), and previous studies have found evolutionary branching, where populations with multiple trait values can co-exist despite the presence of a single phenotypic optimum (Geritz et al. 1998; Kisdi 1999). Competition in our model is symmetric, (Christiansen & Loeschcke 1980; Johansson 2008), which means that the ratio between niche width and the width of the resource landscape (σ_α / σ_K) determines when multiple populations stably co-exist in isolation (Figure 1b, c). Evolutionary dynamics and consequent species composition in our model is thus determined by the position of both symmetric functions $C(x)$ and $K(x)$ on the resource optimum x_{opt}, and also the shape of the functional form for $C(x)$.

We used the functional form given in equation 2 described in Johansson (2008), i.e with heavier tails than the Gaussian curve used for $K(x)$. When niche width is smaller than the width of the resource distribution ($\sigma_\alpha < \sigma_K$), there are regions of trait space where $K(x)$ exceeds $C(x)$, and thus

mutants with trait values away from the optimum can have positive population size despite the presence of a resident with $x_i = x_{opt}$. When $\sigma_\alpha > \sigma_K$ mutants cannot persist as the impact of competition exceeds the carrying capacity (Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000; Figure 1b). The resulting ESS (evolutionarily stable strategy) configuration of species is characterized by a balance between two opposing selective forces: one for increased carrying capacity and one for decreased competition. As niche width decreases relative to the width of the resource landscape, the number of stable populations at ESS and the variance of those populations in trait space both increase. We varied niche width in our simulation treatments using $\sigma_\alpha = 0.68$, 0.85, and 1.5 (and $\sigma_K = 1$), which respectively produce 4, 2, and 1 distinct branches as ESS solutions in trait space (Johansson 2008; Figure 1c). Simulations to address our three main research questions subsequently used these communities on each patch for the t_0 metacommunities. We thus refer to each distinct phenotypic value persisting at generation 10_6 after the initialization as a unique species.

Effect of spatial structure for trait evolution and metacommunity diversity

To determine how spatial structure influences metacommunity eco-evolutionary dynamics, we evaluated phenotypic distributions and species composition over time when dispersal $d = 0$, 0.01, and 0.1 for $t = 50{,}000$ generations. To evaluate diverse metacommunities where species can persist in multiple sites, we considered $\Delta = 0$, $\sigma_\alpha = 0.68$, and $\delta = 0.5$ for all results unless otherwise stated (results to address the effects of varying Δ are discussed in section *Environmental change* below and of varying σ_α in the section *Increasing competition strength* below).

1. Shifts in direction of selection by environment and competition

Dispersal introduced individuals with distinct trait values (Figure 2), which alters not only the phenotypic distribution of residents within a patch, but also the $C(x)$ curve and thus the selection pressures for phenotypes in the patch. Dispersal increased phenotypic homogenization towards the overall metacommunity $\bar{x}_{opt}$ and increased overall community phenotypic variance (Figure 2a). Immigrants add population density to their region of trait space, which shifts the distribution of competitive effect $C(x)$ in the patch downward (as the patch phenotypic variation increases mass towards the distribution's tails) and inward (towards the direction of immigrant trait values). This is most easily seen in Figure 2b, $d = 0.1$. The region of trait space in each patch where species can have positive realized growth rates (x_{fit}, where $K > C$) can thus vary among patches, increasing with dispersal. Traits evolve in the direction of these high-fitness regions (i.e. populations with trait values in the region where $K - C$ was highest had the highest population sizes; these values approximate the expected trait equilibrium indicated in Osmond and De Mazancourt 2013; Figure 2b). Dispersal shifts local phenotypic distributions in the direction of immigrant trait values, so patch 1 has a high fitness region for lower trait values and patch 3 has a high fitness region for higher trait values (i.e. in the direction where mutants experience less competition). Increasing dispersal increases the width (the range of trait values x_{fit}) and depth ($K(x_{fit}) - C(x_{fit})$) of the positive growth region. The direction of the competition curve in patch 2 does not shift (and thus resident populations with x_{opt} continue to experience the most competition), but immigrants increasing the strength of competition in the right and left tails of the $C(x)$ distribution reduce the height of this competition curve.

2. Phenotypic distributions, diversity, stability, and degree of maladaptation

Introducing novel species via dispersal led to species replacement and altered local community composition (Figure 2a). In each patch, a resident species was replaced by an immigrant species with a trait value closer to the local x_{opt}. These immigrant species occupied a favorable position in trait space that residents did not, combining high carrying capacity close to the environmental optimum with reduced competition. Regional γ diversity decreases because of this species displacement, and local α diversity converges to regional γ diversity as more maladapted sink populations are maintained and the metacommunity becomes more homogenized with increasing *d* (Supplementary Information Figure S1). Very little evolution occurs due to the presence of species that are pre-adapted to their environment and for coexistence, which is expected given that resident communities are at the approximate ESS trait distributions and the environment does not change. Properties of metacommunity stability such as SSD and CV are slightly increased with increasing dispersal (Figure S1). The results reflect the ecological process of species sorting, giving rise to community assemblages that include more species with trait values close to the local environmental optimum (Figure 2a).

Environmental change

1. Shifts in direction of selection by environment and competition

To understand the effects of environmental change, we evaluated simulation results when $d = 0$, $\sigma_\alpha = 0.68$, and $\delta = 0.5$ for varying levels of environmental change $\Delta = 0$, 10^{-5}, and 4.4×10^{-4}. Directional environmental change (increased x_{opt} each generation) shifts the carrying capacity curve $K(x)$ to the right at all sites, selecting for individuals with higher trait values (Figure S2). These individuals experience minimal competition, which increases the overall selection for higher trait values as environmental selection and selection for reduced competition both favor traits in the same direction. This reflects the partial niche overlap discussed in Osmond & de Mazancourt (2013; see their Figure 6a).

2. Phenotypic distributions, diversity, stability, and degree of maladaptation

In our simulations, the addition of relatively slow environmental change ($d = 0$, $\Delta = 10^{-5}$) caused phenotypic distributions to have gradually increasing trait values over time (Figure 3a and b). Species with the lowest trait value in a patch persisted at an increasingly reduced carrying capacity until they were no longer viable in the changing environment and went extinct, as mutants in these populations with increased trait values experience intense competition from other species with similar trait values. Adaptation thus primarily occurred in the species with the highest trait value; Figure 3b). Gradual environmental change thus led to an overall decrease in species diversity due to extinctions, but an increase in intraspecific diversity and decrease in SSD due to local adaptation (Figure S3).

With rapid environmental change ($d = 0$, $\Delta = 4.4\times10^{-4}$) all species in each patch except that with the highest trait value went extinct relatively quickly (Figure 3c; Figure 4a). Though interspecific diversity is lost (Figure S3) due to the stronger selection pressure against species with lower trait values (Figure S2b), intraspecific diversity for the remaining species is much higher than with slow

environmental change (Figure S3). This is because selection for increased trait values and decreased competition combine to create a large region of positive carrying capacity (where $K > C$), and many mutants with very different trait values higher than residents can persist (Figure S2b). As was observed by Johansson (2008), the single remaining species in each patch can track the changing environment and the mean trait value lags behind the optimum (e.g. Figure 4a). As the rate of environmental change increases, the overall metacommunity SSD thus decreases and metacommunity CV increases (because the numerous surviving mutants vary in their population size as the environment continues to change; Figure S3).

Spatial structure and environmental change

1. Shifts in direction of selection by environment and competition

Evolutionary trajectories result from the interacting effects of environmental change and introduction of immigrant competitors that alter local fitness. Environmental change selects for individuals with higher trait values in all patches, and the $K(x)$ curve shifts to the right, while dispersal introduces competitors that increase selection against traits in the direction of the regional mean $\underline{x}_{opt}$. (Figure 4b). The patch-specific shift in $C(x)$ plays a strong role in determining subsequent eco-evolutionary dynamics. In patch 1, the environment selects for individuals with higher trait values, while immigrants with high trait values from patch 2 and 3 lead to reduced competition and increased selection for individuals with lower trait values. The resulting region of trait space where $K > C$ thus varies as a result of dispersal rate and speed of evolutionary change. Individuals with lower trait values are strongly selected for in patch 1 at low speed of environmental change ($\Delta = 10^{-5}$, $d = 0.01$ and $d = 0.1$; Figure S19) and at the combination of rapid environmental change and high dispersal ($\Delta = 4\times10^{-4}$, $d = 0.1$; Figure 4). In patch 3, environmental selection and selection for reduced competition are in the same direction, favoring evolution of increasing trait values (Figure 4b; Figure S19). The phenotypic distribution in patch 2 depends primarily on the speed of environmental change - $\bar{x}_2$ is similar to $x_{2,opt}$ when environmental change is gradual and lags behind at the more rapid speed of environmental change.

Among-site variation in the direction of selection creates a dynamic feedback loop between evolutionary dynamics in Patch 3 and ecological dynamics in patch 1 - the environment selects for individuals with increasingly higher trait values in patch 3, and these individuals immigrate into patch 1 and increase local competition strength for individuals with high trait values. Decreased competition thus favors individuals with lower trait values in patch 1. These individuals then immigrate to patch 3 and combine with environmental change to increase the strength of selection for individuals with higher trait values in patch 3 (Figure 4b; Figure S19).

2. Phenotypic distributions, diversity, stability, and degree of maladaptation

Observed trajectories of evolutionary and ecological properties reflect that fitness landscapes vary in time and space due to the combination of changing environmental selection and competition strength. With slow environmental change in the absence of dispersal ($\Delta = 10^{-5}$, $d = 0$), adaptive trait shifts primarily occurred in resident species with the highest trait value and species with low trait values declined to extinction (Figure 5a). This differed when $d > 0$, as the increased selection for higher trait values in patch 3 creates immigrants that inhibit adaptive diversification in resident

species with high trait values in patch 1 and 2. These immigrants also decrease the strength of competition for species with low trait values, which permits them to persist for longer periods of time and respond to environmental change by evolving increased trait values in some instances (e.g. in patch 1; Figure 5b; Figure S4). As a result, species diversity is not lost with increasing dispersal levels as is the case when $d = 0$ (Figure S5). At the highest dispersal level, adaptive diversification is limited to the species with the highest trait value in patch 3 but a diverse species assemblage persists for the 50,000 generations considered for this study (Figure S4).

Dynamics under rapid environmental change ($d > 0$, $\Delta = 4\times10^{-4}$) differed substantially. Species diversity is rapidly lost (Figure 4a; Figure S4). Only the species in the metacommunity with the highest trait value adapts, as novel mutants from other species experience increased competition and are lost to extinction. Due to dispersal, patch 3 immigrants colonize patch 1 and their competition shifts selection towards favoring individuals with lower trait values. However, selection against these species by the environment is still stronger than for reduced competition and species with lower trait values are lost to extinction within ~5000 generations (Figure 4b).

The very broad region in trait space where $K > C$ creates particular evolutionary dynamics (Figure 4b). Mutants with a broad range of trait values can persist for long periods of time, until they are outside the survivable range of $K > C$. As a result, though a single species from patch 3 monopolizes the entire metacommunity (Figure S5), diverse lineages persist in patch 1 and 2 and maintain an intraspecific competitive hierarchy (Figure 4a; Figure S6). This is observed most strongly at the intermediate dispersal level. With higher dispersal, competition and the environment combine for a strong selection pressure favoring higher trait values in patch 3, and the monopolizing species diminishes the maintenance of genetic diversity in the other patches (though some novel lineages that are favored for transient periods of time with reduced competition develop in patch 1 and 2; Figure 4a; Figure S4; Figure S6). For all levels of environmental change, SSD increased with dispersal and its variance over time increased with rates of environmental change (Figure S7), and rapid environmental change led to strong among-patch variation in CV (Figure S8).

Increasing competition strength

Increasing niche width ($\sigma_\alpha = 0.85, 1.5$) means that mutants with increasingly divergent trait values experience stronger competition than when $\sigma_\alpha = 0.68$ (Figure 1b). As a result, fewer species exist at a single patch when $\sigma_{\alpha 2} = 0.85$ and 1.5 (see $d = \Delta = 0$; Figure 5c; Figure S9, Figure S10, S11, S15). However, dispersal introduces individuals with very different trait values and as a result the $C(x)$ curve has a wider area for more diverse mutants to persist (Figure 5d; Figure S20). Intraspecific diversity increased with dispersal (Figure S12, Figure S16), and patches had highest local α diversity at the highest dispersal level (Figure S11, S15).

Multiple species coexisted and maintained genetic diversity with slow environmental change, but the number of species that adaptively responded to environmental change depended on competition strength. When $\sigma_\alpha = 1.5$, all species were able to adaptively respond to environmental change (Figure S10), but at $\sigma_\alpha = 0.85$ species evolution was constrained by competition (Figure S9). At the fast speed of environmental change, species diversity was again reduced to a single species (that maintains high genetic diversity, with the highest level at the intermediate dispersal

level; Figure S9, S10, S12, S16; for SSD see Figures S13 and S17; for CV see Figures S14 and S18).

Discussion

Overview

Species that inhabit changing environments do not live in isolation. Interactions with other species can alter adaptive trajectories (Barraclough 2015), and phenotypic traits that influence fitness in the context of the abiotic environment can also be influenced by biotic interactions (Voje et al. 2015). Incorporating phenotypic evolution, species interactions, and movement in spatially variable landscapes are critical components of models needed to predict how biodiversity will respond to environmental change in the Anthropocene (Urban et al. 2016). We used a simulation model to evaluate how competition and spatial structure influence species responses to directional environmental change. We found three main results. First, spatial structure introduced among-site variation in the direction of selection. In some sites trait evolution towards the adaptive optimum was accelerated as selection from environment and competition was in the same direction, while at other sites competition inhibited local adaptation. Second, metacommunity patterns such as species sorting (the match between species traits and the local environment) and monopolization (where diversity is lost and one genotype or species dominates the landscape) differ from previous models that do not consider phenotype fitness as a function of both the local environment and competition with other individuals. Species sorting can be diminished even at a low dispersal rate, as selection favors species with sub-optimal trait values and reduced competition. Monopolization occurs at a fast rate of environmental change and when competition strength is high, but intraspecific phenotypic diversity was maintained even in this situation and thus genotypic monopolization was not observed. Third, we observed an eco-evolutionary feedback loop between local phenotypic evolution at one site and competition at another site. This feedback loop was maintained by dispersal and indicates that eco-evolutionary dynamics in communities operate at a landscape scale.

Dynamic variation in fitness landscapes over time and space

Our results at the local scale reflect the findings of two previous studies that modeled trait evolution and competition using an adaptive dynamics framework, and builds on them by considering evolution and competition in a spatially structured landscape. Johansson (2008) showed that multiple competing species are retained with slow environmental change and that species are increasingly lost to extinction with fast environmental change. Our results do reflect this when patches are not linked by dispersal (Figure 3), and we show that the fitness landscape shifts caused by rapid environmental change select only for individuals with increasingly higher trait values (and therefore species that experienced decreased competition are lost; Figure 4, d = 0). By introducing movement among variable patches, we found that immigrants persistently introducing competitors also shifts the fitness landscape, in a way that increases selection for individuals with low trait values in patch 1 and high trait values in patch 3 (Figure 4). The dynamics observed at combinations of dispersal > 0 and environmental change rate > 0 are therefore a

product of variation in the fitness landscape over time and space. Osmond & de Mazancourt (2013) explicitly show how the shapes and positions of the carrying capacity function $K(x)$ and the competition function $C(x)$ can vary and how this variation determines the speed and direction of phenotypic evolution. Our results simply introduce spatial structure as one mechanism by which the direction and magnitude of selection can vary among populations. Movement of individuals among patches means that the competition curve is not fixed. It dynamically shifts as dispersal introduces immigrants that alter local phenotypic and population size distributions and, as a consequence, competition strength. Our study presents a first step towards characterizing how landscape features and connectivity patterns can drive eco-evolutionary dynamics in multi-species communities, but it needs more study as the results reflect our among-patch symmetry and degree of environmental heterogeneity.

Metacommunity patterns for trait and species diversity

Previous studies have considered how environmental variation influenced trait evolution in communities of competitors in a spatial landscape. In these studies, phenotypic traits evolved in response to environmental variation (among sites: de Mazancourt et al. 2008; Loeuille & Leibold 2008; Urban & De Meester 2009; Vanoverbeke et al. 2016; across sites and over time: Norberg et al. 2012). Species assemblages emerged as a result of environmental heterogeneity and site connectivity or species dispersal. Maladaptation (a mismatch between species traits and the local environment) could result due to spatial mass effects, low levels of genetic variance reducing adaptive evolution, or combinations of dispersal and amounts of genetic variation (i.e. the 'global monopolization' of one or a few species due to rapid adaptation or evolutionary priority effects). Our study differs from these by modeling competition directly between populations with distinct phenotypes (using species interaction coefficients α_{ij} instead of indirect competition for microsites within patches) and by modeling evolution in a phenotypic trait that influenced both carrying capacity in the local environment and strength of competition (instead of in a trait that influenced only a component of population growth such as recruitment, survival, or growth). Considering evolution of traits that reflect fitness tradeoffs and facilitate coexistence (e.g. Vasseur et al. 2011; Kremer & Klausmeier 2013) is an important step to better understand how trait and species composition in nature differs from expectations in models that do not consider evolution or that consider evolution unconstrained by interactions with other species.

Explicitly modeling competition revealed some differences compared to previous studies of evolving metacommunities. When sites were connected by dispersal, species did mirror their local environmental optimum. However, not all species could adapt and thus species sorting was diminished over time (Figure 3). This matches the results of Norberg et al. (2012), who also modeled competition directly using interaction coefficients. They found that species extinctions were hastened with increasing dispersal and species sorting was diminished, whereas the study of Loeuille & Leibold (2008) found that species sorting was maintained when dispersal was high relative to evolutionary rates (using a lottery competition model). Our study took an additional step of varying the strength of competition (Figure 1b). We found that the inhibition of species sorting depended on competition strength, where metacommunities with stronger effects of competition were more likely to maintain species sorting patterns despite increased dispersal (Figure 5). Like the previous studies of evolution in metacommunities, we did observe global monopolization

where one species dominates the landscape (Loeuille & Leibold 2008; Urban & De Meester 2009; Vanoverbeke et al. 2016), but in our system this depended on the speed of environmental change, and thus on the magnitude of the environmental selection pressure. Loeuille & Leibold (2008) observed global monopolization of one species for the metacommunity at a combination of high dispersal and mutation rates. While we did not vary the mutation rate, it is possible that the rate of environmental change played a similar role. Our results also indicate very high levels of intraspecific phenotypic diversity can be retained by the single species in a way that depends on dispersal rate (Figure 4). In the future, models of evolving metacommunities can benefit from considering additional factors such as the evolution of multiple correlated traits or varying genetic variance (Edwards et al. 2018) and response to multiple environmental stressors (Jackson et al. 2015).

Eco-evolutionary feedback loops and evolutionary suicide

Trait evolution in species that compete for resources and inhabit a metacommunity is influenced by intriguing mechanisms that were previously detailed in the fields of adaptive dynamics and eco-evolutionary dynamics. Eco-evolutionary feedback loops are cyclical interactions between ecology and evolution, where changes in ecological interactions drive evolutionary change in traits that, in turn, feed back to alter the ecological interactions in a continuing process (Post & Palkovacs 2009). These feedback loops have been demonstrated empirically for population, host-parasite and predator-prey, and ecosystem dynamics in closed systems (e.g. Yoshida et al. 2003; Turcotte et al. 2013; Matthews et al. 2016; Brunner et al. 2017) and for evolution of dispersal and metapopulation dynamics in spatially structured populations (Fronhofer & Altermatt 2015; Legrand et al. 2017). There is some evidence that eco-evolutionary feedbacks can facilitate coexistence (terHorst et al. 2018), but these are not well-studied at the metacommunity scale (but see Colombo et al. 2018 for a model of predator-prey interactions in a spatially structured system). We identified an eco-evolutionary feedback loop in our system - evolution in patch 3 selects for individuals with higher trait values, immigrants from patch 3 with high trait values shift competition strength in patch 1 and select for individuals with lower trait values, and then immigrants from patch 1 with lower trait values move to patch 3 where they complete the feedback loop, increasing selection for higher trait values. This was observed at all combinations of dispersal and environmental change rate > 0 but is easiest to visualize at the highest levels of both (Figure 4b). This is a novel mechanism for an eco-evolutionary feedback that involves dispersal maintaining dynamic reinforcement between competition and phenotypic evolution.

Adaptive dynamics theory is well suited to model eco-evolutionary dynamics because the equations explicitly link trait evolution to ecological processes and have been used to understand the process of evolutionary rescue (where initially maladapted populations adapt to the environment and avoid extinction, Gomulkiewicz & Holt 1995; e.g. Ferriere & Legendre 2013). Our simulation model reproduced expected elements observed in previous adaptive dynamics models, such as the branching process that produced ESS trait values for species generated in our initialization step. The same branching process produced the divergence of populations into multiple coexisting sub-populations within a site observed in some conditions, such as in patch 3 when the rate of environmental change is slow and sites are linked by dispersal (final 10,000 generations in Figure 5b; Figure S4). At the highest level of environmental change, when a single

species monopolized the metacommunity, we also observed the process of ‘evolutionary suicide’. Selection can produce mutants with traits that inhabit a trait space beyond the extinction boundary, where the mutant population cannot persist but also can be maintained for long periods of time (Ferriere 2000; Gyllenberg & Parvinen 2001; Gyllenberg et al. 2002). In one adaptive dynamics model with asymmetric competition (Dercole et al. 2002), trait evolution cyclically alternated between two equilibria, one at high and one at low population density. The reversals between these states were driven by selection for mutants that could invade but whose eventual fate was extinction. Our model displayed these evolutionary suicide and alternate equilibria dynamics, for example with the conditions $\sigma_\alpha = 0.68$, $d = 0.1$, and $\Delta = 4\times10^{-4}$ (Figure 4). A primary resident population in patch 3 tracked the local environmental optimum, but immigrant populations from patch 3 shifted the local competition curve on other patches in a way that permitted mutant individuals with a very wide range of trait values to persist for long periods of time before declining to extinction. Figure 4 shows that populations branch from the main resident population and survive, decline to extinction, and the process repeats itself.

Conclusions

As species encounter changing climates, it is critical to understand whether they will adapt, move to more suitable habitats, or instead decline to extinction. Models of species range shifts are increasingly considering genetic variation, evolution, and species interactions (e.g. Bocedi et al. 2014) and species distribution models increasingly include species association matrices as well as local adaptation and phenotypic plasticity (Wisz et al. 2013; Pollock et al. 2014; Benito Garzón et al. 2019). Accurate representations of these more complex processes will be necessary to forecast how biodiversity will track climate change (Urban et al. 2016). Our study considers how trait evolution in metacommunities can respond to environmental change and it adds to previous studies by considering phenotypic evolution in a trait that represents a balance between two selection pressures - the changing environment and the strength of competition with other populations and species consuming a similar range of resources. The placement of the evolving community in a landscape introduced feedbacks between eco-evolutionary processes that are driven by dispersal and that maintain biodiversity despite the increased connectivity of species among sites. One possible consequence of habitat fragmentation or loss may be the disruption of these spatial eco-evolutionary feedbacks and a resulting loss of biodiversity.

Figures

Figure 1. Model of metacommunity eco-evolutionary dynamics for species that compete for resources in a changing environment. (a) Communities inhabit a three-patch landscape with sites that vary in their resource distribution (which yields a distribution of carrying capacities centered around a maximum value with an optimal trait value x_{opt}) and are connected at three levels of dispersal (d = 0, 0.01, 0.1 are the grey, thin black, and thick black lines respectively). (b) Simulations in the metacommunity were conducted using three different values for competition strength (σ_α = 0.68, 0.85, 1.5). Resident communities for the simulations were generated from modeling long-term coevolution in each patch (no dispersal) in a constant environment. The communities that emerge depend on the relationships between two functions that depend on a phenotype x. The competition function $C(x)$ (red line) is proportional to the difference in trait values between two populations, and is a distribution with a standard deviation σ_α. The carrying capacity function $K(x)$ (black line) depends on the distance of a population's trait from the local environmental optimum, can be interpreted as different resources that species can utilize at various efficiencies, and is a distribution with a standard deviation σ_K (equal to 1 in simulations). (c) The evolutionary history of the initial communities used in the simulation are shown. Species can coexist in a stable competitive hierarchy that evolves from a single initial population using a stochastic simulation of adaptive dynamics. The number of species (all unique populations in existence after 10_6 generations) is determined by the ratio of the niche width to the width of the resource distribution (σ_α / σ_K). An initial mutant population can evolve into multiple stable populations when when $\sigma_\alpha / \sigma_K < 1$ (corresponding to σ_α = 0.68 and 0.85 in this model), as a region of trait space exists where new mutants with trait values that differ from the local optimum still have a carrying capacity that exceeds the impact of competition (where the black line is above the red line). When $\sigma_\alpha / \sigma_K > 1$ (σ_α = 1.5 in this model), a single population is maintained with a trait value at the local optimum.

Figure 2. Trait evolution and competition for multiple species in communities over time in an unchanging environment (Δ = 0, σ_α = 0.68, d = 0, 0.01, and 0.1). (a) Time series of phenotypic distributions. Density plots of trait values (x-axis) weighted by relative abundance (height of density curve) are shown over 5,000 generations (y-axis; the time series was thinned for visualization, so density plots along the y-axis are shown every 250 generations). Simulations were run for 50,000 generations but the dynamics are clear within the first 5,000 generations. The solid black line in each plot indicates the local optimum trait value over time. Dispersal introduces new species with favorable x values that are closer to the resource optimum x_{opt} but still experience reduced levels of competition, and in some instances resident species are replaced. (b) Competition strength and carrying capacity as a function of trait value for d = 0, 0.01, and 0.1 (left to right) in three patches (left to right are patch 1, 2, and 3). Plots on the top row show competition ($C(x)$, red) and carrying capacity ($K(x)$, black) as a function of trait value x (x-axis) and are calculated as average values from 121 sampled generations spaced evenly from generation 20,000 to 50,000. Black points show the phenotypic distribution in each patch and their corresponding population size (y-axis). The left and right-most points are the average trait values (across the 121 generations considered from time 20,000 to 50,000) of the species with the lowest and highest trait values and the middle point is the average trait value of the species

with the highest population size. The patch's average x_{opt} (short-dashed black line), mean x (blue solid line, averaged across the sampled 121 time points, weighted by population size), and points where the carrying capacity and impact of competition are equal to one another (long-dashed black line) are shown as well. The plots on the bottom row are zoomed in to better see distinctions between the $C(x)$ and $K(x)$ functions.

Figure 3. Trait distributions in communities over time across a range of environmental change rates. In all plots, $\sigma_\alpha = 0.68$ and $d = 0$, and the rate of environmental change varies: (a) $\Delta = 0$, (b) $\Delta = 10^{-5}$, and (c) $\Delta = 4\times10^{-4}$. Communities in patches 1, 2, 3 are shown (from left to right) and features of the trait density plots are as described in Figure 2a (except that the time series are thinned to show every 800 generations). In (b), the species with the highest trait value in each patch is less constrained by competition than other species and experiences the most adaptive trait change. Species with lower trait values are gradually lost to extinction. In (c), all species are lost within 5000 generations and the species with the initially highest trait values persists and adapts over time.

Figure 4. Trait evolution and competition for multi-species communities over time in a rapidly changing environment ($\Delta = 4\times10^{-4}$, $\sigma_\alpha = 0.68$, $d = 0$, 0.01, and 0.1). (a) Distributions of phenotypes in populations and communities over 10,000 generations of the evolving metacommunity simulation. At all levels of dispersal, all but a single species went extinct within ~6000 generations. When $d > 0$, competition with new mutant populations leads to periodic selection for divergent trait values but these are then lost to extinction as the environment continues to change. This intraspecific diversity is always highest in patch 1, where selection for increasing traits is driven by environmental change but immigration from the other patches creates increased selection pressure for lower competition strength and thus lower trait values. (b) Competition strength ($C(x)$, red line) and carrying capacity ($K(x)$, black line) as a function of trait values (x-axis). Without dispersal, the changing environment selects for individuals with higher trait values in all patches. When patches are linked by dispersal, immigrants are introduced and in patch 1, these increase the fitness of individuals with lower trait values that experience less competition than individuals with higher trait values. These mutant populations arise periodically then become extinct as the environment continues to change. Features of all plots are as described in Figure 2.

Figure 5. Impacts of competition strength, dispersal rate, and speed of environmental change for community trait distributions over time. Plots give phenotypic distributions (x-axis is trait value, height of density plots is relative abundance of individuals with that trait value, y-axis is time; the time series are thinned to show every 250 generations) and the solid black line in each plot indicates the local optimum trait value over time. (a) When competition strength is low ($\sigma_\alpha = 0.68$) and in the absence of dispersal ($d = 0$), slow environmental change (upper row: $\Delta = 0$; lower row: $\Delta = 10^{-5}$) leads to adaptation only in species in the community with the highest trait value and species with lower trait values are gradually lost to extinction. (b) Dispersal ($d = 0.01$) introduces competitors for the resident species with the highest trait value, which favors individuals with lower trait values that experience weaker competition (upper row: $\Delta = 0$; lower row: $\Delta = 10^{-5}$). As a result, an increased number of species show adaptive responses to the environment. (c) When competition strength is high ($\sigma_\alpha = 1.5$), in the absence of dispersal ($d = 0$) fewer species exist

because individuals with similar trait values face strong competition. These species can adapt to slow environmental change (upper row: $\Delta = 0$; lower row: $\Delta = 10^{-5}$) but retain little intraspecific diversity. (d) Dispersal ($d = 0.1$; $\sigma_\alpha = 1.5$; upper row: $\Delta = 0$; lower row: $\Delta = 10^{-5}$) not only introduces more interspecific diversity (as species from other patches have distinct enough trait values that they can persist in other patches but at lower population sizes), it also increases the amount of intraspecific diversity, as competition with other species increases the range of viable mutants that can persist with positive population size away from the local environmental optimum.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Supplementary Information, Figure S1-S20.

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Supplementary Code: Code will be made available on the GitHub page of J.H. Pantel at time of publication.

Supplementary Information for Eco-evolutionary feedbacks and the maintenance of metacommunity diversity in a changing environment

Figure S1. Inter- and intraspecific diversity, deviation from optimum trait value, and coefficient of variation over time in an unchanging environment ($\Delta = 0$, $\sigma_\alpha = 0.68$, $d = 0$, 0.01, and 0.1). Row 1 is interspecific diversity (grey: α, black: γ, orange: β). Row 2 is intraspecific diversity, where every color is a species. Row 3 is the sum of squared deviations of trait values from the local environmental optimum trait value for all individuals in a patch (black: patch 1, red: patch 2, blue: patch 3). Row 4 is the coefficient of variation of total population size across all species at the local (patch 1: grey, patch 2: light blue, patch 3: orange) and metacommunity (black) level.

Figure S2. Competition, carrying capacity, and population trait values in a changing environment. In both plots $\sigma_\alpha = 0.68$ and $d = 0$, in (a) $\Delta = 10^{-5}$, and in (b) $\Delta = 4\times10^{-4}$. Competition functions ($C(x)$, red), carrying capacity functions ($K(x)$, black), population (black points), and all other features are as given in Figure 2.

Figure S3. Inter- and intraspecific diversity, deviation from optimum trait value, and coefficient of variation over time in a slowly changing environment ($\Delta = 10^{-5}$, $\sigma_\alpha = 0.68$) across a range of dispersal levels (from left to right, $d = 0$, 0.01, and 0.1). Features of all plots are as described in Figure S1.

Figure S4. Phenotypic distributions over time when competition strength is low ($\sigma_\alpha = 0.68$) across a range of dispersal levels and rates of environmental change, for 50,000 generations (the time series are thinned to show every 800 generations). Rows of results correspond to increasing rate of environmental change ($\Delta = 0$, 10^{-5}, and 4×10^{-4} from top to bottom) and columns represent three patches across dispersal levels ($d = 0$, 0.01, and 0.1 from left to right). Features of plots are as described in Figure 2.

Figure S5. Interspecific diversity over time when competition strength is low ($\sigma_\alpha = 0.68$) across a range of dispersal levels and rates of environmental change (grey: α diversity, black: γ diversity, orange: β diversity). Rows are increasing levels of environmental change ($\Delta = 0$, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal ($d = 0$, 0.01, and 0.1 from left to right).

Figure S6. Intraspecific diversity over time when competition strength is low ($\sigma_\alpha = 0.68$) across a range of dispersal levels and rates of environmental change. Each color represents genetic diversity of a different species. Rows are increasing levels of environmental change ($\Delta = 0$, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal ($d = 0$, 0.01, and 0.1 from left to right).

Figure S7. Sum of squared deviations of trait values from local environmental optimum trait value for all individuals in patches over time when competition strength is low ($\sigma_\alpha = 0.68$), across a range of dispersal levels and rates of environmental change (black: patch 1, red: patch 2, blue:

patch 3). Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S8. Coefficient of variation of total population size across all species at the local (patch 1: grey, patch 2: light blue, patch 3: orange) and metacommunity (black) level over time when competition strength is low (σ_α = 0.68), across a range of dispersal levels and rates of environmental change. Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S9. Phenotypic distributions over time when competition strength is intermediate (σ_α = 0.85) across a range of dispersal levels and rates of environmental change. Rows of results correspond to increasing rate of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns represent three patches across dispersal levels (*d* = 0, 0.01, and 0.1 from left to right). Features of plots are as described in Figure 2 (except that the time series are thinned to show every 800 generations).

Figure S10. Phenotypic distributions over time when competition strength is high (σ_α = 1.5) across a range of dispersal levels and rates of environmental change. Rows of results correspond to increasing rate of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns represent three patches across dispersal levels (*d* = 0, 0.01, and 0.1 from left to right). Features of plots are as described in Figure 2 (except that the time series are thinned to show every 800 generations).

Figure S11. Interspecific diversity over time when competition strength is intermediate (σ_α = 0.85) across a range of dispersal levels and rates of environmental change (grey: α diversity, black: γ diversity, orange: β diversity). Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S12. Intraspecific diversity over time when competition strength is intermediate (σ_α = 0.85) across a range of dispersal levels and rates of environmental change. Each color represents genetic diversity of a different species. Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S13. Sum of squared deviations of trait values from local environmental optimum trait value for all individuals in a patch over time when competition strength is intermediate (σ_α = 0.85), across a range of dispersal levels and rates of environmental change (black: patch 1, red: patch 2, blue: patch 3). Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S14. Coefficient of variation of total population size across all species at the local (patch 1: grey, patch 2: light blue, patch 3: orange) and metacommunity (black) level over time when competition strength is intermediate (σ_α = 0.85), across a range of dispersal levels and rates of environmental change. Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S15. Interspecific diversity over time when competition strength is high (σ_α = 1.5) across a range of dispersal levels and rates of environmental change (grey: α diversity, black: γ diversity, orange: β diversity). Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S16. Intraspecific diversity over time when competition strength is high (σ_α = 1.5) across a range of dispersal levels and rates of environmental change. Each color represents genetic diversity of a different species. Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S17. Sum of squared deviations of trait values from local environmental optimum trait value for all individuals in a patch over time when competition strength is high (σ_α = 1.5), across a range of dispersal levels and rates of environmental change (black: patch 1, red: patch 2, blue: patch 3). Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S18. Coefficient of variation of total population size across all species at the local (patch 1: grey, patch 2: light blue, patch 3: orange) and metacommunity (black) level over time when competition strength is high (σ_α = 1.5), across a range of dispersal levels and rates of environmental change. Rows are increasing levels of environmental change (Δ = 0, 10^{-5}, and 4×10^{-4} from top to bottom) and columns are increasing levels of dispersal (*d* = 0, 0.01, and 0.1 from left to right).

Figure S19: Competition, carrying capacity, and population trait values in a slowly changing environment. In all plots σ_α = 0.68 and Δ = 10^{-5}. Competition functions ($C(x)$, red), carrying capacity functions ($K(x)$, black), population (black points), and all other features are as given in Figure 2 and vary across levels of dispersal (*d* = 0, 0.01, 0.1).

Figure S20: Competition, carrying capacity, and population trait values in an unchanging environment. In all plots σ_α = 1.5 and Δ = 0. Competition functions ($C(x)$, red), carrying capacity functions ($K(x)$, black), population (black points), and all other features are as given in Figure 2 and vary across levels of dispersal (*d* = 0, 0.01, 0.1).

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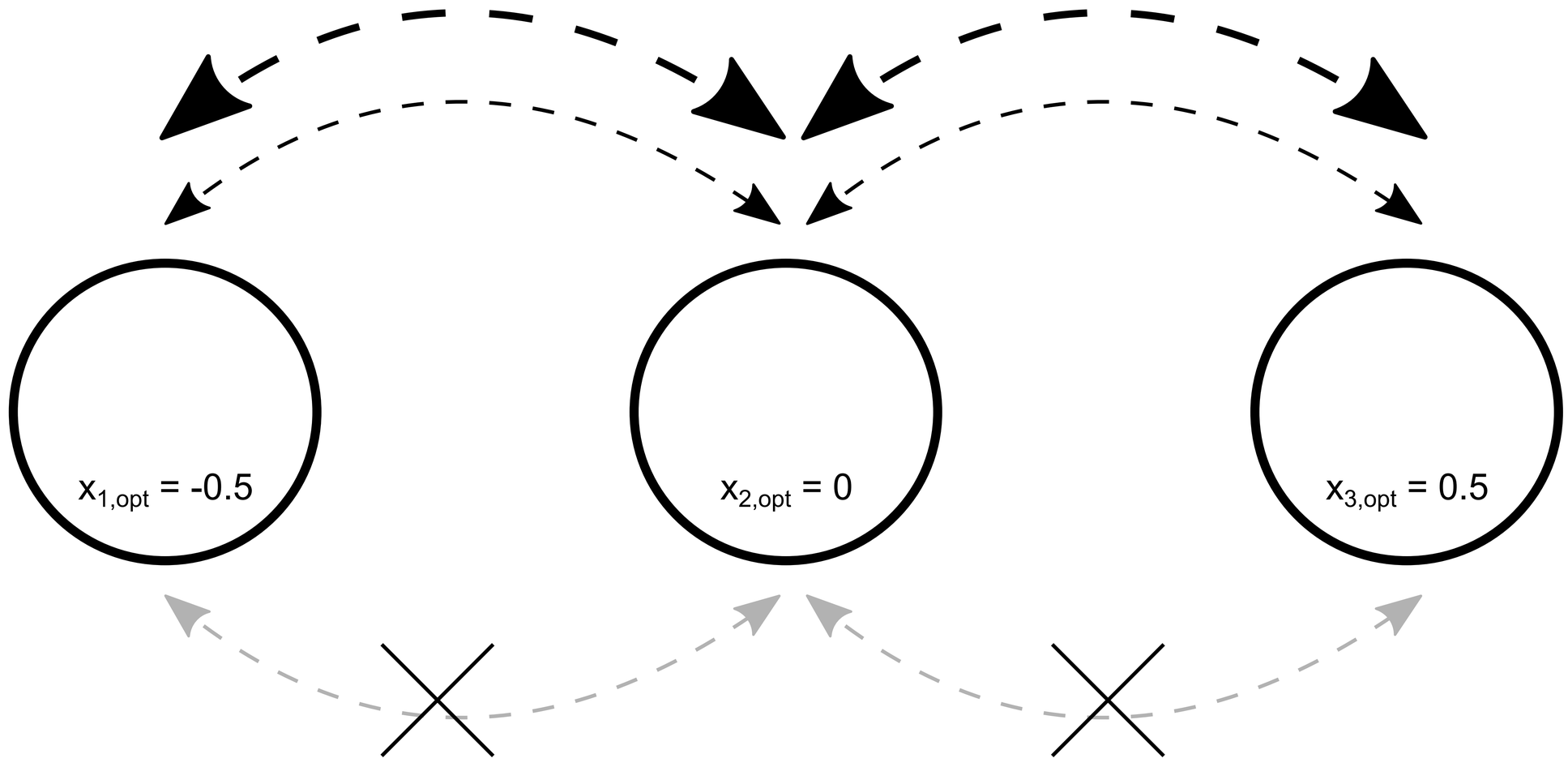

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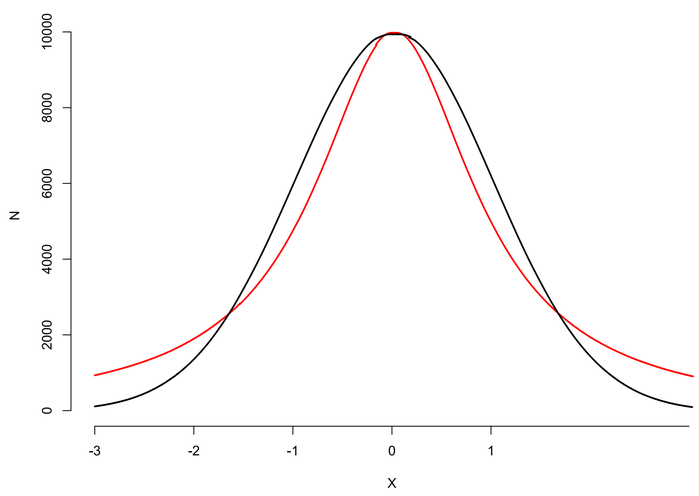

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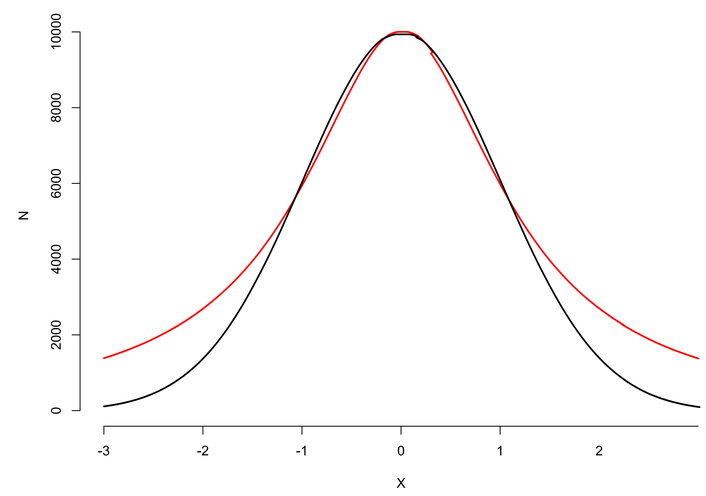

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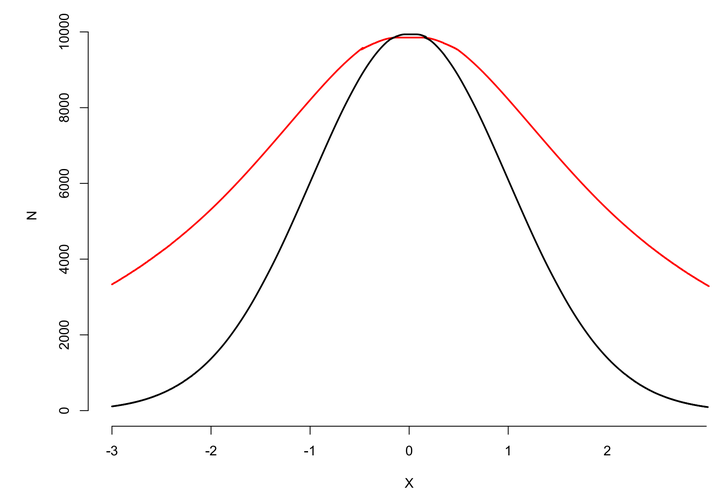

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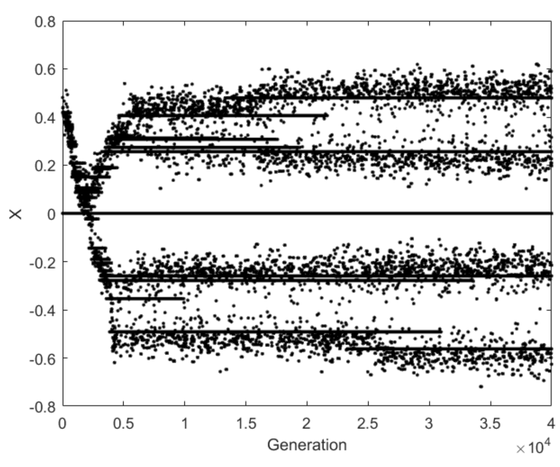
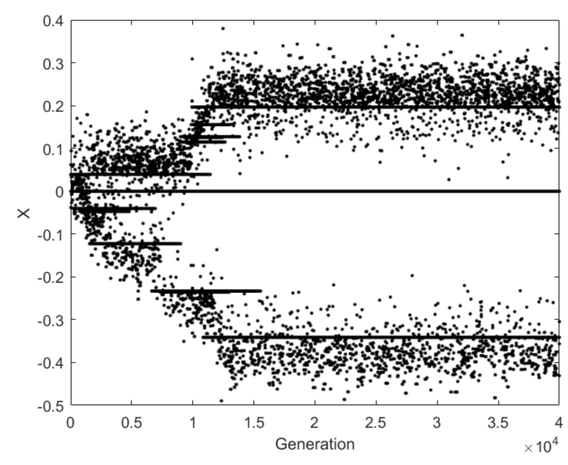
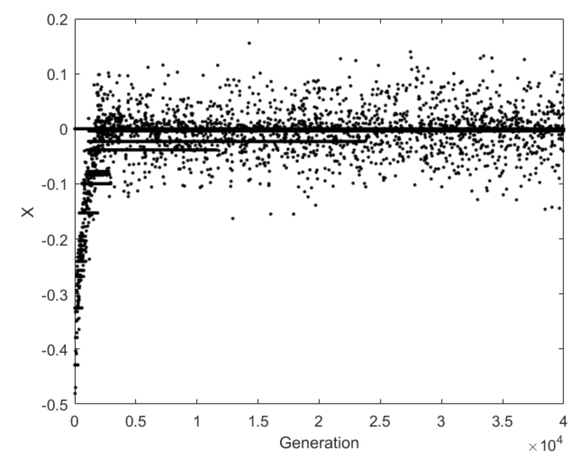
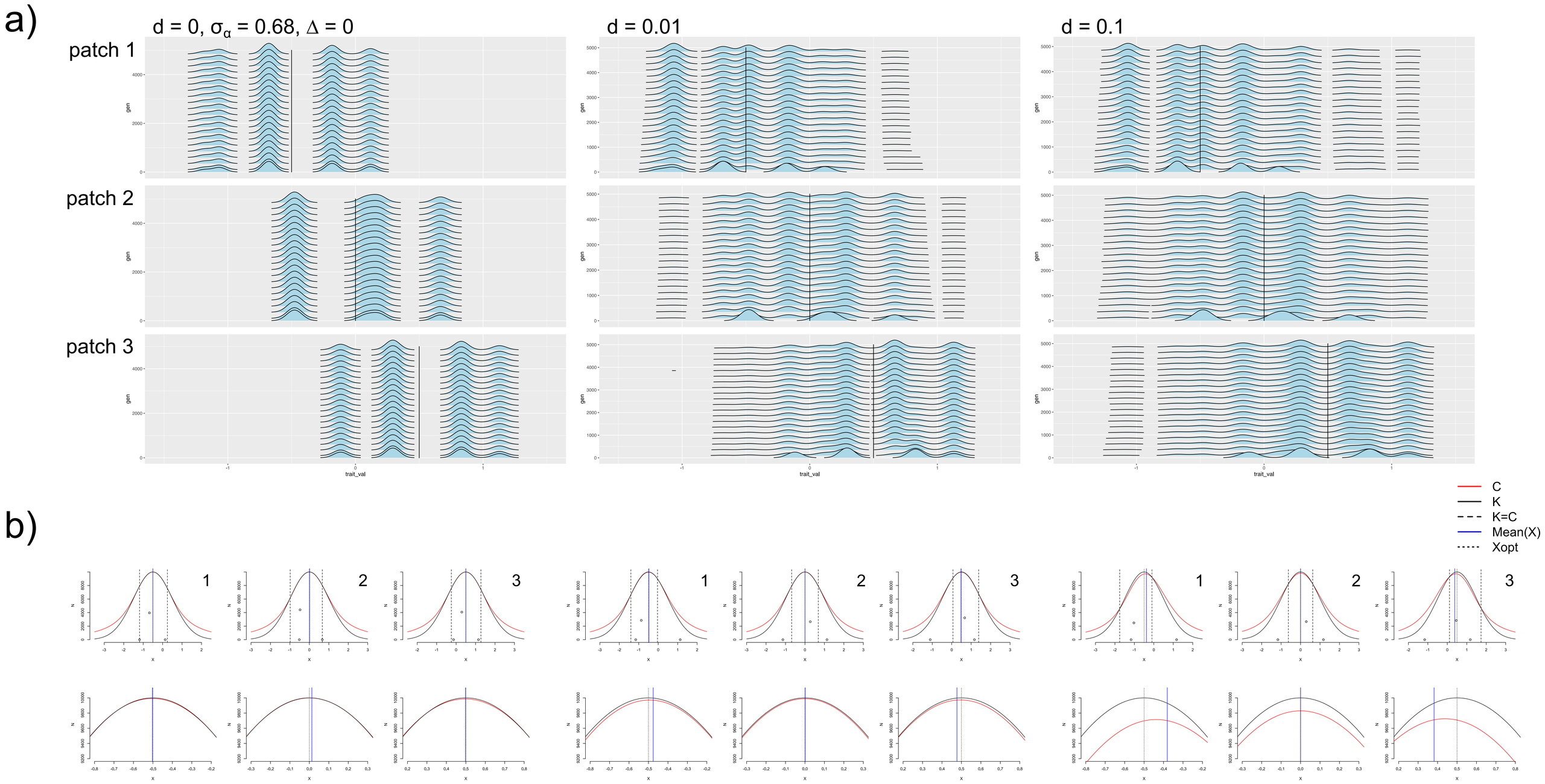
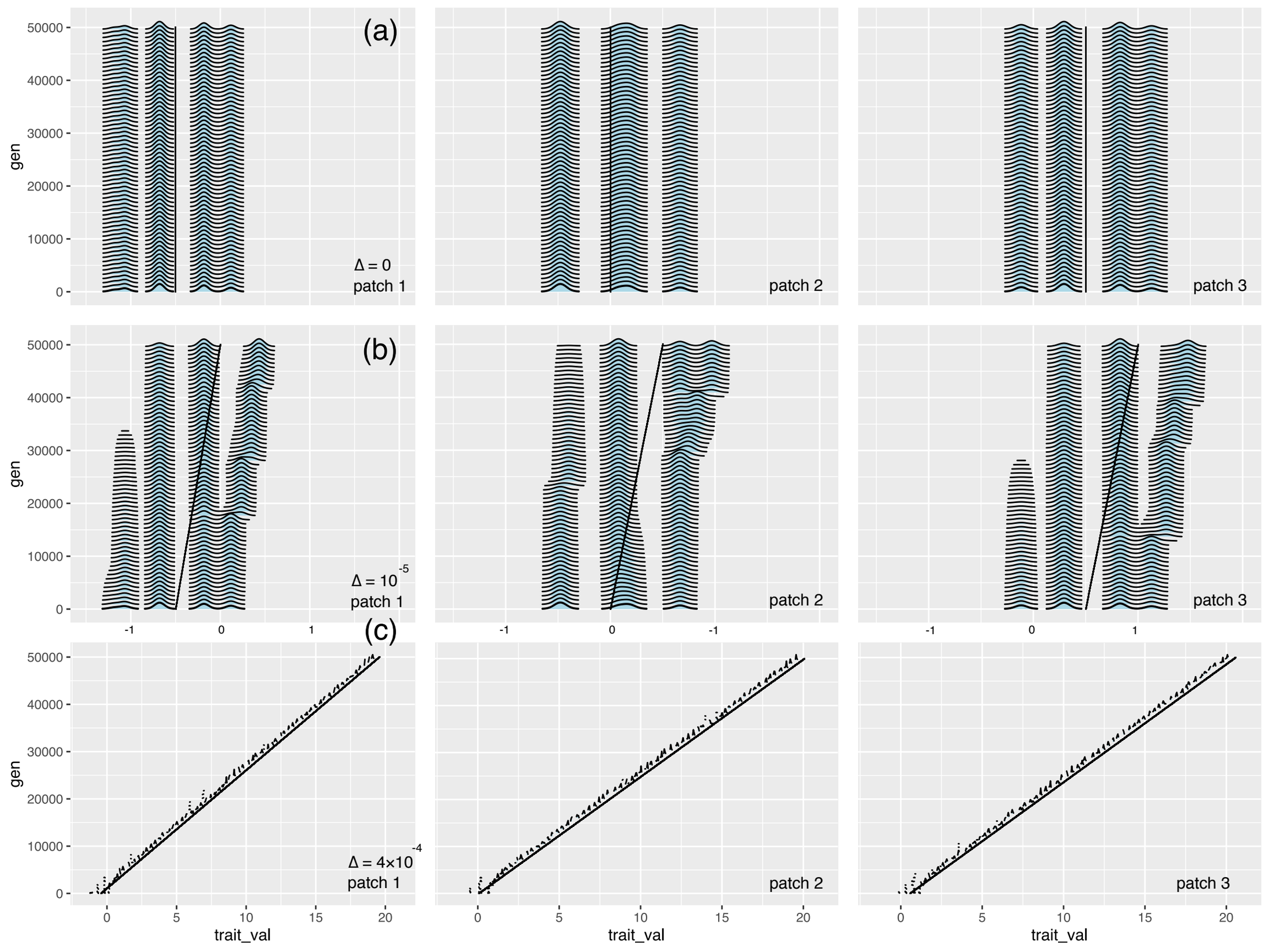







a)
d = 0, σα = 0.68, Δ = 0
d = 0.01
d = 0.1
patch 1
patch 2
patch 3
gen
trait_val
b)
C
K
K=C
Mean(X)
Xopt
1
2
3
N
x


(a)
(b)
(c)
gen
trait_val
Δ = 0
Δ = 10^-5
Δ = 4×10^-4
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patch 3
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10000
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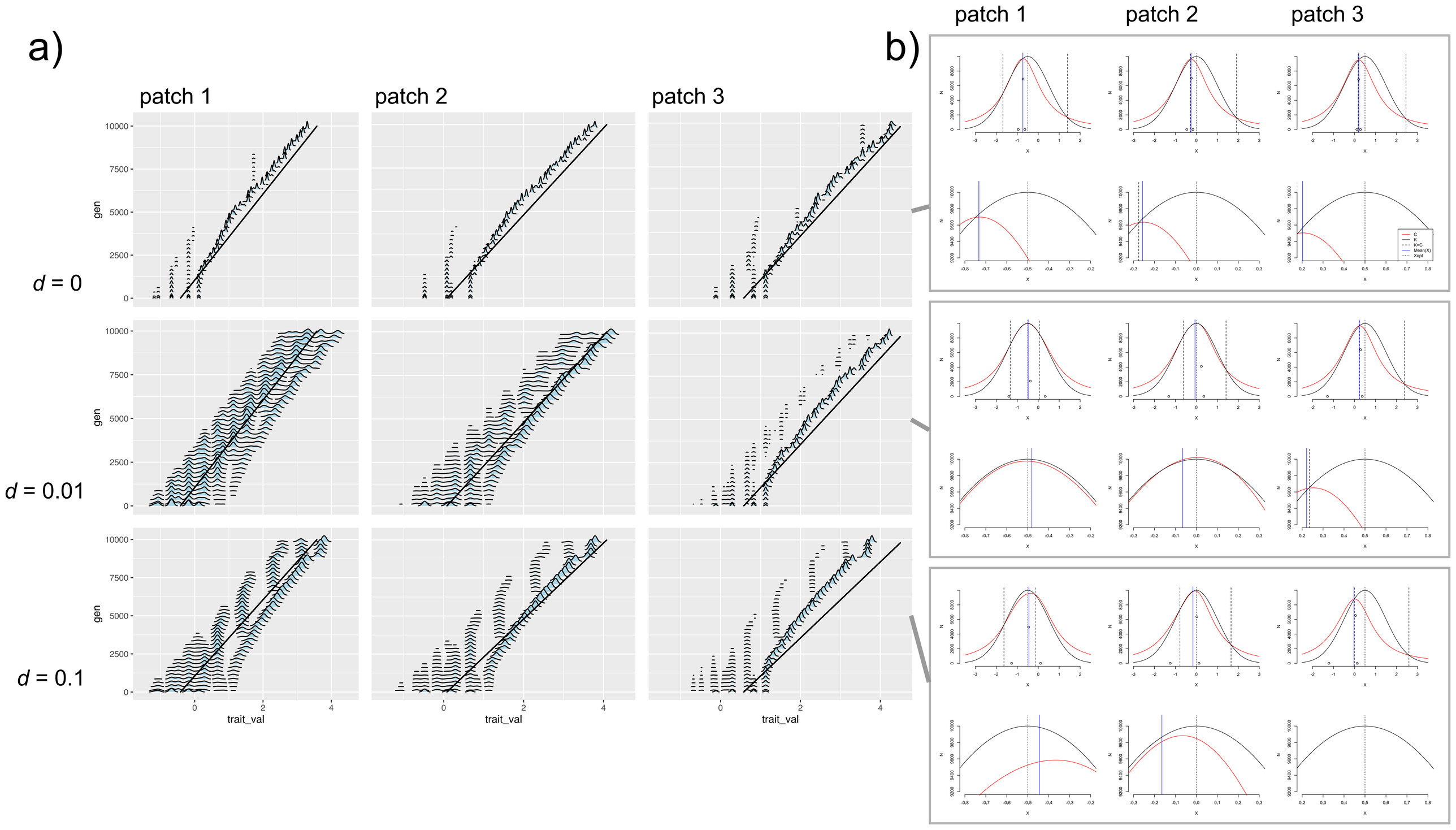
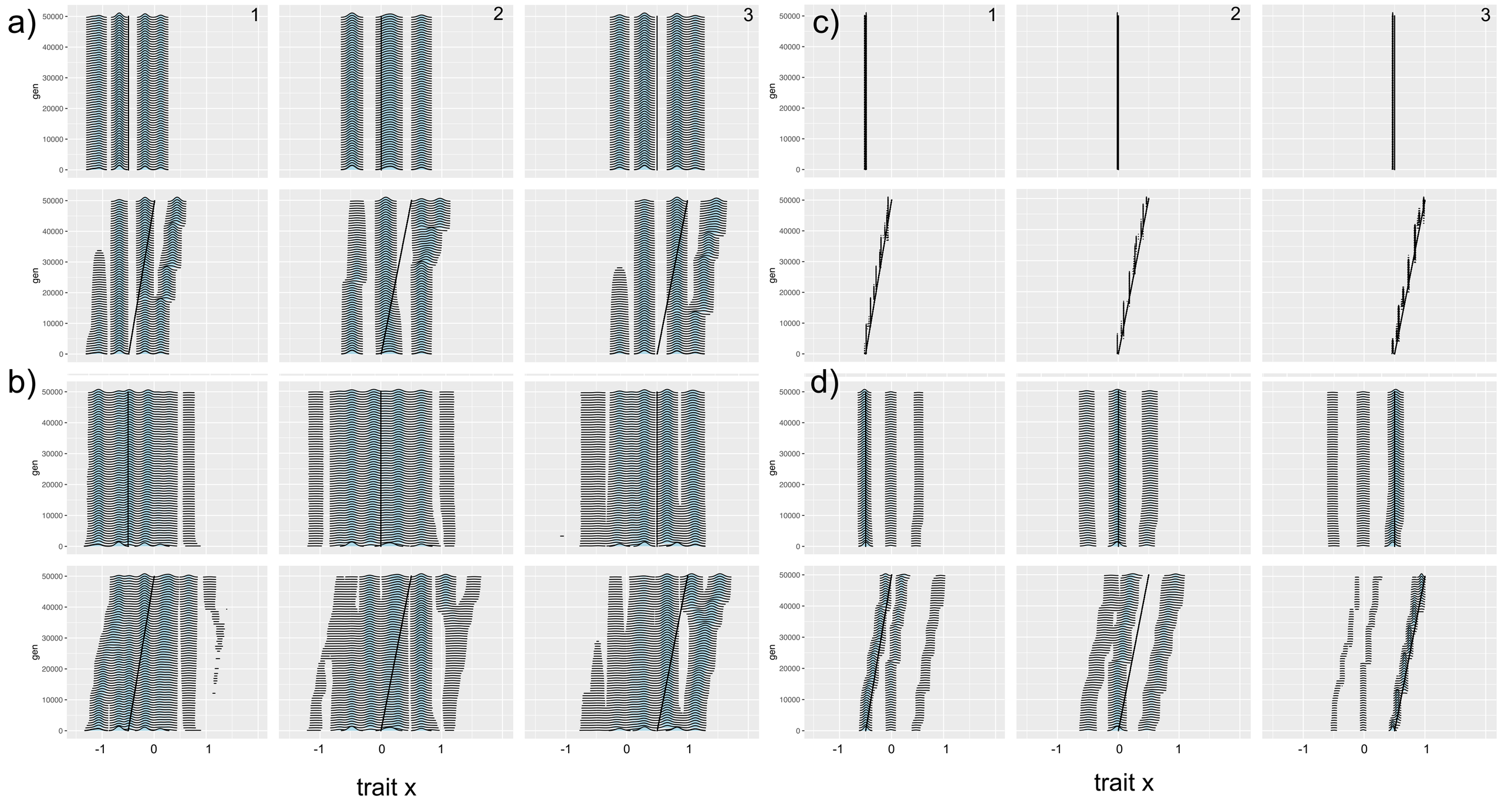
30000
40000
50000
-1
0
1
0
5
10
15
20


a)
patch 1
patch 2
patch 3
d = 0
d = 0.01
d = 0.1
gen
trait_val
b)
patch 1
patch 2
patch 3
C
K
K=C
Mean(X)
Xopt


a)
b)
c)
d)
1
2
3
gen
50000
40000
30000
20000
10000
0
-1
0
1
trait x