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 can thus reflect a balance between adaptation to an environmental optimum and to avoid strong competition. While this has been explored at the local scale, less is known about evolutionary trajectories for competing species in a spatially structured landscape. We developed simulations of quantitative trait evolution using an adaptive dynamics framework for a trait that influences an organism's carrying capacity and its intra- and interspecific competition strength. Species inhabited a three-patch landscape with a gradient of trait optima, and we varied the connectivity level of the species among patches. We also varied the presence and pace of directional environmental change and the strength of competition. Eco-evolutionary dynamics were strongly influenced by the combination of competition strength, dispersal level, and speed of environmental change. Dispersal introduced novel species combinations that altered fitness landscapes, while continuous environmental change introduced strong selection against the maintenance of coexisting competitors. As a consequence, diverse communities that also tracked environmental change were only maintained when strength of competition was strong, at intermediate levels of dispersal and environmental change. When competition was weaker, diverse communities were maintained by a spatial eco-evolutionary feedback loop, where populations from patches with distinct trait values colonized new patches, altered the strength of competition in that new patch, which in turn altered the strength of selection for resident species. These evolved residents then colonize other patches and alter their local distribution of competition strength, completing the feedback loop. Our results thus indicate that understanding biodiversity loss in a changing world will require improved knowledge of both the constraint that competitive interactions place on adaptive potential as well as the opportunity that landscape connectivity can present for introducing novel eco-evolutionary dynamics.

Introduction

Species composition at the scale of local communities and regional metacommunities can reflect a complex array of spatial and environmental processes, as well as biotic interactions and random drift (Holt 1993; Leibold et al. 2004; Leibold & Chase 2017). A matching between species composition and their optimal environmental niche, referred to as species sorting, can arise when dispersal is high enough to allow species to reach favorable environments but low enough to reduce the impacts of mass effects that allow species to persist in unfavorable environments (Chase & Leibold 2003; Cottenie & De Meester 2004; Howeth & Leibold 2010; Leibold 2011). Though dispersal-related mass effects and neutral drift do influence metacommunity structure, species sorting along environmental gradients is a commonly observed pattern in natural communities (Logue et al. 2011; Soininen 2014). In addition to the local environment filtering the regional species pool into an assemblage of species capable of persisting in that environment, biotic interactions play an important role in subsequent community assembly (Boulangeat et al. 2012; HilleResLambers et al. 2012; Kraft et al. 2014). Resident species at a local scale therefore reflect the combination of organisms that are selected for the local environment and for local species interactions (HilleResLambers et al. 2012; Ponisio et al. 2019).

When the environment changes, populations may experience maladaptation and extinction, but may also evolve adaptations that restore positive fitness in the new environment (Gomulkiewicz & Holt 1995; Bell & Gonzalez 2009). However, since fitness in the local environment is also contingent on the network of community interactions, it is therefore important to consider evolutionary responses in the context of the ecological community. For example, evolution-mediated priority effects can occur, where populations that adapt rapidly can exclude other, similarly fit genotypes and species (Lee et al. 2012; De Meester et al. 2016). Species diversity can inhibit local adaptation, because it increases the likelihood that there is another resident species already pre-adapted to the new environment (Fukami et al. 2007; de Mazancourt et al. 2008; but see Holmes et al. 2016). Competition can also slow rates of adaptation to the new environment, because adaptation towards a local environmental optimum can increase the negative impacts of competition as species converge on more similar trait values (Johansson 2008). These studies not only indicate the importance of community-level interactions for evolutionary responses of organisms to environmental change, they also indicate a potential importance for dispersal, landscape connectivity, and metacommunity-scale processes as well. For example, the timing of arrival of immigrant genotypes or species that inhibit local adaptation can depend on organism dispersal rates (Fukami et al. 2007; de Mazancourt et al. 2008; Urban et al. 2008).

The goal of this study was to evaluate how interspecific competition impacts evolutionary trajectories for organisms that inhabit a spatially structured landscape and that are experiencing environmental change. A previous study (Johansson 2008) determined that competition caused a substantial decline in adaptive evolution, because competition both introduces selection against similar trait values and simultaneously decreases population size. However, this study considered dynamics at a single location. de Mazancourt et al. (2008) considered the impacts of

multiple species for evolutionary rates in a multi-patch landscape and found that the presence of other species inhibited adaptive diversification and slowed evolutionary rates. Evolution was also slower when patches were connected, because species were more likely to colonize more suitable patches before local adaptation occurred. However, phenotypic evolution occurred in a trait that impacted growth rate in the local environment and was decoupled from the competition mechanism (i.e. where species competed for recruitment sites). Osmond & de Mazancourt (2013) did consider phenotypic evolution in a quantitative trait that impacted both an organism's carrying capacity in their local environment and their strength of competition (similar to Johansson 2008), and they found that evolutionary rates could be decreased or increased, depending on 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). More generally, Osmond & de Mazancourt (2013) clearly established that evolutionary trajectories will depend on the shapes of the functional curves that link carrying capacities and competition to traits. Building on these findings, an important next step is to consider how spatial structure and species dispersal will impact evolutionary trajectories and community composition, as communities are thus influenced by the changing environment and by the potential establishment of pre-adapted species.

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, and populations can disperse among patches. We monitored metacommunity eco-evolutionary dynamics to evaluate three questions: (1) How does the presence of spatial structure (patches with low and high levels of dispersal connectivity, as compared to isolated patches) influence metacommunity eco-evolutionary dynamics? (2) How do evolving metacommunities respond to directional environmental change at varying rates? And (3) How does the strength of competition influence the evolving metacommunity's response to environmental change? For each question, we evaluated responses by considering local and regional species diversity, measures of stability, and distributions of the quantitative trait over time and across sites.

Metacommunity diversity depends on the degree of site connectivity, spatial scale, and also on the degree of environmental heterogeneity among sites (MacArthur 1965; Moquet & Loreau 2003; Shurin et al. 2004; Tamme et al. 2010), and the degree of species sorting (the matching of species to their optimal environment) depends on site connectivity as well (Chase & Leibold 2003). Previous studies of spatial eco-evolutionary dynamics in evolving metacommunities have found that expected patterns of diversity can be altered when evolution is taken into account. For example, the process of community monopolization, where a species can adaptively respond to a novel environment and exclude other well-adapted species due to their numerical advantage, is more likely at low dispersal rates (Urban et al. 2008; Loeuille & Leibold 2008a; Urban & De Meester 2009; Vanoverbeke et al. 2016). These studies were critical for indicating that traditional community ecological and metacommunity model predictions will change when trait evolution is considered, but they currently do not take into account that trait evolution can be influenced by multiple selection pressures, including both abiotic and biotic ones. In

zooplankton, for example, critical life history traits such as body size are driven by temperature (e.g. Mc Kee & Ebert 1996), but larger body size is also associated both with increased grazing efficiency (and thus an increased competitive ability) and with increased susceptibility to visually hunting predatory fish (Burns 1969; Dodson 1974; Hall et al. 1976). Evolution in traits that represent fitness tradeoffs has been explored in a metacommunity context, but this study evaluates species interactions across trophic levels (Loeuille & Leibold 2008b). The studies of Johansson (2008) and Osmond & de Mazancourt (2013) address trait evolution when fitness is influenced both by adaptation to the local environment and to competitive interactions with other species, and our goal here was to expand study of the effects of competition for trait evolution to the metacommunity scale.

We used previous studies to guide predictions about the impacts of spatial connectivity, rate of environmental change, and competition strength for two types of responses: community diversity at the metacommunity scale and the phenotypic evolutionary trajectories for populations of species. We expected that introducing low levels of dispersal would decrease the total amount of evolutionary change and increase species diversity in the changing environment relative to closed communities, because this would allow species to immigrate to patches with more suitable environments (Urban et al. 2008; de Mazancourt et al. 2008). We also expected species loss and reduced diversity at higher dispersal levels as mass effects would cause homogenization of communities (Moquet & Loreau 2003; Leibold et al. 2004). We expected that increasing the speed of environmental change would increase the total amount of evolution for surviving species but also that fewer species will persist with the highest level of environmental change (and thus overall diversity will decrease as well; Johansson 2008). In treatments with a reduced intensity of competition, we expected to observe a reduced importance of monopolization (where locally adapting species gain a numerical advantage and exclude other colonizing species; e.g. Loeuille & Leibold 2008a; Urban & De Meester 2009; Vanoverbeke et al. 2015) because more species can coexist locally when competition is present but less intense; Geritz et al. 1998; Dieckmann & Doebeli 1999; Kisdi 1999; Doebeli & Dieckmann 2000). We also expected that increased competition strength would slow the overall rate of evolution for species with complete niche overlap, as was observed in Johannsson (2008) and Osmond & de Mazancourt (2013).

Methods

We developed a model of metacommunity evolution with interspecific competition. The landscape contains three patches that vary in their environmental properties (the optimum trait value for resident species; Figure 1). Species in our model are defined as populations with distinct phenotypes that vary along a single trait axis. Population growth follows Lotka-Volterra dynamics with density dependence and interspecific competition, and evolutionary dynamics are implemented using an adaptive dynamics framework. This framework is useful to study effects for 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 to determine 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 we used 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_{it-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}. 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 location on the trait axis can sustain. A population's trait x_i therefore corresponds to its most efficiently used resource, and its carrying capacity $K(x_i)$ is limited by that resource. The population, however, also exploits resources in surrounding regions of the trait axis, resulting in competition when multiple populations are present.

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 ($\alpha_{ii} = 1$).

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

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

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 that drop below 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), and we then created 3 distinct initial metacommunities with three different levels of niche width (σ^2_α = 0.68, 0.86, 1.5), using among-patch environmental overlap δ = 0.5. Local environmental optima in each patch were therefore $E_{1,opt}$ = -0.5, $E_{2,opt}$ = 0, and $E_{3,opt}$ = 0.5. For all of these scenarios, d = Δ = 0, σ_k = 1, r = 1.9, μ = 10^{-5}, σ_μ = 0.05, θ = 2, and ρ = 0.025 (results were qualitatively similar but over longer time scales for lower values of μ and σ_μ). 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 environments independently for 10^6 generations were used as initial patch communities for the evolving metacommunity simulations, depending on the level of niche width (σ^2_α = 0.68, 0.86, 1.5) and $E_{k,opt}$ used in the simulation. For each of the three corresponding metacommunities, we ran simulations 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 community. All simulation were conducted in MATLAB R2017a version.

Metrics for evolutionary and ecological properties

A species l 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: ${}^1D_\alpha = \frac{1}{\sum_{i=1}^{l} p_i^2}$ 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 ${}^1D_\beta = {}^1\overline{D}_\alpha / {}^1D_\gamma$. 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 in individual trait values from the local environmental optimum (calculated for all individuals n within a patch; $SSD_k = \sum_{i=1}^{n} \left(x_i - x_{opt}\right)^2$.

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, $C_t(x) = \sum_{j=1}^{s} \alpha(x, x_j)\, N_{jt-1}$, 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 (only competition with individuals with differing trait values) that an invading mutant with trait x_j would have suffered in generation t. The $K(x)$ curve (which varies with time when there is environmental change) 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, despite the presence of competition (Figure 1b, c). Evolutionary dynamics and consequent species composition in our model is thus determined by the centering 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 carrying capacity 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 σ_α = 0.68, 0.85, and 1.5 (and σ_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 subsequently refer to each distinct phenotypic value persisting at generation 50,000 after the initialization as a unique species.

Spatial structure

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 Δ = 0, σ_α = 0.68, and δ = 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).

The main effect of dispersal was to introduce 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 as well (Figure 2b). These new populations shift the phenotypic distributions in patches on the edges of the metacommunity towards the overall metacommunity $\bar{x}_{opt}$ (in our simulation, the edges are patch 1 with $E_{0,opt}$ = -0.5 and patch 3 with $E_{0,opt}$ = 0.5, and the initial $\bar{x}_{opt}$ = 0) and they also increase phenotypic variance. We evaluated how immigrants influence the phenotypic distribution and consequent fitness landscape by comparing the curves of each patch's $K(x)$ and $C(x)$ (Figure 2b). 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 among-patch phenotypic variation means the density of immigrants increases mass towards the distribution's tails) and inward (towards the direction of immigrant's 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 (K > C) thus can dynamically vary over time, 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 phenotypic distributions in the direction where most immigrants originated, 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 level increased the width (the range of trait values x_{fit}) and depth ($K(x_{fit})$ - $C(x_{fit})$) of this positive growth region. The direction of the shift in the competition curve was determined by whether the population size of immigrants was higher below or above the local optimum trait value x_{opt}, and the magnitude of the shift in the competition curve is proportional to the difference in immigrant population size on either side of x_{opt}. In our simulation the

competition curves $C(x)$ thus shifted towards the metacommunity environmental average $\bar{x}_{opt}$. (i.e. towards increased α_{ij} for individuals with higher trait values in patch 1 and with lower trait values in patch 3). 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, which increases the width of phenotypes away from x_{opt} that experience high carrying capacities (Figure 2b, d = 0.01 and 0.1, patch 2). In the absence of any environmental disturbance, population size and phenotypic distributions are relatively stable and the shifts in phenotypic distributions and $C(x)$ curves in all patches are relatively symmetric with respect to $\bar{x}_{opt}$. As dispersal rate increases, population size of immigrants increases, and the resulting shifts in phenotypic and competitive distributions are larger.

In our stochastic simulation, patches were linked by dispersal at t_0. Introducing novel species led to species replacement and altered local community composition (Figure 2a). In each patch, a resident species was reduced and an immigrant species established with a trait value closer to the local x_{opt} (Figure 2a). 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 under simulation conditions 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

Directional environmental change (increased x_{opt} each generation) has the effect of shifting the carrying capacity curve $K(x)$ to the right at all sites, selecting for individuals with higher trait values. As higher trait values have continually increasing K and also experience less competition, mean trait values at a patch lag behind the local x_{opt} (Johansson 2008; Figure S2). This was reflected in our simulations - with the addition of relatively slow environmental change (d = 0, $\Delta = 10^{-5}$), species evolved trait changes over time in a way that gradually increased with the increase in local environmental optimum (Figure 3a vs. 3b). Mutants with high trait values were better able to persist due to the decreased strength of competition at higher trait values and the increasing K as the changing environmental optimum becomes more favorable over time (Figure S2a). 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 (Figure 3b). Mutants in these populations with increased trait values experience intense competition from other species with similar trait values, and our results thus indicate that

adaptation primarily occurred in the species that occupied niche space where mutants were free from competition (i.e. 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).

Faced 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). The continually increasing x_{opt} creates an even stronger selection pressure for increased trait values closer to this environmental optimum, which also selects more strongly against species with much lower trait values that reduce competition (Figure S2b). Interspecific diversity thus decreases (Figure S5). However, because selection for increased trait values and decreased competition combine to create a large region of positive carrying capacity, many mutants with very different trait values higher than residents can persist in patch 1 and 2 (Figure S2b). As a result the intraspecific diversity for each remaining species is much higher than observed at slow environmental change (Figure S6). The single remaining species in each patch can track the changing environment (though the mean trait value lags behind the optimum), so as the rate of environmental change increases, the overall metacommunity SSD decreases (Figure S7). Metacommunity CV increases as the numerous surviving mutants vary in their population size as the environment continues to change (Figure S8).

Spatial structure and environmental change

Evolutionary trajectories result from the interacting effects of environmental change and introduction of immigrant competitors that alter 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 $\bar{x}_{opt}$. (Figure 4b). The patch-specific shift in $C(x)$ plays a strong role in determining subsequent eco-evolutionary dynamics. In patch 1, environmental selection favors individuals with higher trait values, while the influx of competitors with high trait values favors individuals with lower trait values (i.e. reduced competition). The resulting region where populations experience carrying capacities that exceed competition will thus vary depending on the dispersal rate or speed of evolutionary change. Individuals with lower trait values are strongly selected for 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, both environmental selection and immigration of competitors with low trait values favor individuals with high trait values and these combined selection pressures favor mutants with increasingly high trait values (Figure 4b; Figure S19). There is thus a dynamic feedback loop between evolutionary and ecological dynamics in patch 1 and 3 - dispersal introduces immigrants to patch 3 that contribute to driving evolution for increased trait values, and these patch 3 immigrants with increased trait values then move to patch 1 and increase competition, which then drives evolution for decreased trait values. These patch 1 immigrants then move back to patch 3 to continue the dynamics that select for increased trait values in patch 3 (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.

Observed eco-evolutionary trajectories reflect this underlying balance between the combined selection pressures of environmental change and competition, which varies over time due to dispersal. In the absence of dispersal and at slow environmental change ($\Delta = 10^{-5}$), most adaptive trait shifts occurred in resident species with the highest trait value and species with low trait values declined to extinction (Figure 5a). However when $d > 0$, 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. First of all, species diversity is rapidly lost (Figure 4a; Figure S4). Similar to what was observed when $d = 0$, only the species with the highest trait value adapts, as mutants from this species with increasingly higher trait values have both increased K and decreased C, while mutants from other species suffer from intense competition and are lost to extinction (Figure 4b). When patches are connected by dispersal, patch 3 immigrants do colonize patch 1 and shift the $C(x)$ curve to the right (which decreases the strength of competition for species with lower trait values), but selection against these species by the environment is still stronger than for competition and species with lower trait values are lost to extinction within ~5000 generations (Figure 4b). However, the very broad region in phenotypic space where $K > C$ does create unique evolutionary dynamics. It is possible for mutants with a range of trait values to persist at a range of carrying capacity values in patch 1 (Figure 4b). Though more of these have higher trait values, there is selection to retain individuals with lower trait values for a long period of time, until they are outside the survivable range of $K > C$. As a result, though a single species from patch 3 has now monopolized the entire metacommunity (Figure S5), diverse lineages are able to persist within patch 1 and 2 that maintain an intraspecific competitive hierarchy (Figure 4a; Figure S6). At higher dispersal, the corresponding increased competition effect in patch 3 adds to the selection pressure for higher traits imposed by rapid environmental change (Figure 4b), and this species quickly monopolizes the metacommunity and also 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 (σ_α = 0.85, 1.5) means that mutants with increasingly divergent trait values will face more competition than when σ_α = 0.68, because the decay in competition strength α_{ij} is more gradual with increasing x_i - x_j (Figure 1b). As a result, fewer species exist at a single patch when σ_α^2 = 0.85 and 1.5 (see $d = \Delta = 0$; Figure 5c; Figure S9, Figure S10, S11, S15). However, including dispersal has an important effect of introducing individuals with very different trait values that influence patch eco-evolutionary dynamics. These immigrants have a very strong influence on competition in the patch, and as a result the $C(x)$ curve creates a wide area for more diverse mutants to persist (Figure 5d; Figure S21). In all patches, the intraspecific diversity greatly increased as a result of dispersal (Figure S12, Figure S16), and patches had highest local α diversity at the highest dispersal level (Figure S11, S15).

Species continued to coexist and maintain genetic diversity with slow environmental change, but the number of species that adaptively responded to environmental change depended on competition strength. When σ_α = 1.5, all species were able to adaptively respond to environmental change (Figure S10), but at σ_α = 0.85 species evolution was constrained by competition (Figure S9). At the fast level of environmental change, species diversity was again reduced to a single species (that maintains very high genetic diversity; Figure S9, S10, S12, S16; for SSD see Figures S13 and S17; for CV see Figures S14 and S18).

Discussion

Species do not respond to environmental change in isolation. In addition to evolutionary and population growth dynamics that are influenced by the environment, many species inhabit networks of interactions with other species and also inhabit spatially variable landscapes. These factors interact to structure how biodiversity will respond to environmental change (Urban et al. 2016). For guilds of species that compete for resources and inhabit a shared landscape, competition and spatial structure can alter how species respond to directional environmental change, and we evaluated these factors in a simulation model. We considered evolution in a phenotypic trait that influences both a population's carrying capacity K and also their strength of interaction with other species α_{ij}, in a metacommunity where multiple species with a shared coevolutionary history inhabit a three-patch landscape. We found that competitive interactions played a strong role in species' adaptive responses to directional environmental change, and that dispersal changed the way that species interactions affected fitness in local environments.

Our findings are most directly comparable to two previous studies that model the effects of competition for evolution in response to environmental change, that of Johansson (2008) and Osmond & de Mazancourt 2013. Johansson's (2008) study observed 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 these when patches are not linked by dispersal (Figure 3), and we can see that the mechanism for this is the shift in the fitness landscape due to environmental change that favors only individuals with increased trait

values on each patch (Figure 4, d = 0). However, we found that immigrants persistently introducing competitors also shift 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 a product of the combined changes in fitness due to environmental change and introduced competition. Our findings that evolutionary trajectories, and as a consequence changes in intraspecific and interspecific composition over time, depended on the relative strength of competition and environmental selection are as expected from previous studies of adaptive dynamics and competition when there is environmental change. Osmond and de Mazancourt (2013) importantly determined that whether or not trait evolution is reduced or increased by competition depends on whether or not the environment and competition select in the same direction. Our study introduces dynamic movement of individuals among patches in the landscape, which means that the competition curve is not fixed. It dynamically shifts as a result of environmental change (selecting for increasing trait values globally and also reducing the ability for competitors to persist) and dispersal bringing in immigrants that alter local phenotypic distributions and population size and, as a consequence, competition strength. An important product of our study is thus to begin to characterize how landscape features, connectivity patterns, and metacommunity dynamics determine shifts in fitness landscapes over time.

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 systems (Fronhofer & Altermatt 2015; Legrand et al. 2017). A model for predator-prey interactions in a spatially structured system does address species interactions (Colombo et al. 2018), but eco-evolutionary feedbacks in communities of competitors are less well studied. 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 reduce competition 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 > 0 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 a dynamic feedback between competition and phenotypic evolution.

When the environment experienced directional change, evolution was not sufficient to allow multiple species to adapt and persist. In this instance, the viability of mutants of species with lower trait values is greatly reduced by competition, while mutants with higher trait values arising from the species with the highest trait value were viable. For species with lower trait values, selection in the direction of reduced competition (away from the species with the highest trait

value in patch 3) was as strong or stronger than selection for increased carrying capacity, causing coexisting species' traits to remain mostly stationary through time. The species with the highest trait on patch 3 continued to adapt. The species with lower trait values were more likely to adaptively respond to the environment when dispersal created additional competition pressure that reduced adaptive evolution in species with higher trait values that were more similar to the changing optima. This is most easily observed in the simulation conditions where $\sigma_\alpha = 0.68$ and $\Delta = 10^{-5}$ (Figure 5a and 5b; Figure S19). This result means that dispersal altered the fitness landscape in a way that maintained interspecific diversity over time, as the species that maintained reduced competition would have been more likely to go extinct as the environment changed. These results reflect research demonstrating that novel species interactions introduced when sites are connected can preserve biodiversity (e.g. Wilson 1992; McCann 2000) and also empirical findings that species interactions can influence adaptation in other species that experience environmental disturbance (e.g. Lawrence et al. 2012; Bulleri et al. 2018), and consider the additional perspective that dispersal facilitates novel species interactions that alter coexistence, diversity, and evolutionary trajectories. The number of species adapting to the environment was also determined by the strength of competition, determined here by the term σ_α. While ecological theory has determined that the number of species that can stably coexist is inversely related to the strength of pairwise interactions (May 1972; Allesina & Tang 2015), we instead evaluate the number of species that can stably coexist while tracking the moving environmental optimum through evolution and determined that stronger interaction strength maintained by dispersal among sites can combine with the environmental pressure towards larger trait values to maintain a diverse assemblage (i.e. $\sigma_\alpha = 1.5$; Figure 5d; Figure S21).

Adaptive dynamics theory is well suited to consider 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). The adaptive dynamics framework is used in the studies of competition of Johansson 2008 and Osmond & de Mazancourt 2013, and is also used to study metacommunity eco-evolutionary dynamics of defense traits in a plant-herbivore system (Loeuille & Leibold 2008b). Previous studies have also used adaptive dynamics in a metapopulation setting to consider the evolution of dispersal (Gyllenberg et al. 2002; Parvinen 2007). We used adaptive dynamics to evaluate evolution of a trait that influences resource use and competition in a changing, spatially structured landscape, and our model reproduced some elements observed in previous adaptive dynamics models. For example, the branching process that produces ESS trait values for species generated in our initialization step has deterministic solutions, such as the number of species. The same branching process produced the divergence of populations into multiple coexisting populations within a site in some instances, as can be seen in our results in patch 3 when $d > 0$ and $\Delta = 10^{-5}$ (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', where selection produces mutants with traits that are beyond the extinction boundary to a trait space where the

mutant population cannot persist (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. Though the mutants are eventually lost to extinction, their transitory persistence and growth causes the resident population to shift between the alternate equilibria. In our model, the simulation with the conditions $\sigma_\alpha = 0.68$, $d = 0.1$, and $\Delta = 4\times10^{-4}$ displayed these dynamics (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 lower 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 (Figure S20).

Other 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 2008a; Urban & De Meester 2009; Vanoverbeke et al. 2016; across sites and over time: Norberg et al. 2012). Species assemblages generally emerged as a result of environmental heterogeneity and site connectivity or species dispersal, and 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). However, our study and findings differ from these in two critical ways. We modeled competition directly between all individuals (using species interaction coefficients α_{ij}, as in Norberg et al. 2012), instead of using indirect competition for microsites within patches (lottery competition; de Mazancourt et al. 2008; Loeuille & Leibold 2008a; Urban & De Meester 2009; Vanoverbeke et al. 2016). We also modeled 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). Trait evolution in our system thus reflects a balance between selection for increased matching to the environmental optimum and to decrease the strength of competition. This tradeoff represents a realistic way to consider that competing species in natural systems can be both well suited for their environment and can partition niche space to maintain diverse local assemblages. Considering dynamic evolution of traits that influence tradeoffs which 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. The explicit modeling of competition revealed some differences compared to previous studies of evolving metacommunities. Though species did mirror their patch environmental optimum, not all species adapted and so species sorting was diminished over time. This matches the study of Norberg et al. (2012), who found that species extinctions were hastened with increasing dispersal, whereas the study of Loeuille

& Leibold (2008a) found species sorting when dispersal was high relative to evolutionary rates. We also found this pattern depended on the strength of competition (Figure 5), which was not varied in previous models. We did observe global monopolization, but in our system it depended on the speed of environmental change, and thus on the selection pressure. Loeuille & Leibold (2008a) 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 provided a similar effect. 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).

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 can also include species association matrices as well as local adaptation and phenotypic plasticity to map habitat suitability and geographic distributions (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. This result suggests that a possible consequence of habitat fragmentation or loss can be the disruption of these eco-evolutionary feedbacks.

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 that vary in their resource distribution (which leads to a distribution of carrying capacities centered around an environment that favors 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 σ_α / σ_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 σ_α / σ_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 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 xopt 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. 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 rate of environmental change varies from (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. 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 decreasing 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, and rate 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) 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 increases selection for 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 (and the decrease in competition strength with increasing distance between trait values is slower than when σ_α = 0.68; Figure 1b). These species can adapt to slow environmental change (upper row: Δ = 0; lower row: Δ = 10^{-5}) but retain little intraspecific diversity. (d) Dispersal (*d* = 0.1; σ_α = 1.5; upper row: Δ = 0; lower row: Δ = 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-S21.

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Supplementary Code: Code will be made availabl 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 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 populations for 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. 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 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 ($\Delta = 0$, 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 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.

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.

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 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 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 populations across 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.

Figure S20. Competition, carrying capacity, and populations across trait values in a rapidly changing environment. In all plots σ_α = 0.68 and Δ = 4×10^{-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 and vary across levels of dispersal (*d* = 0, 0.01, 0.1).

Figure S21: Competition, carrying capacity, and populations across 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.

References

Allesina, S. & Tang, S. (2015). The stability–complexity relationship at age 40: a random matrix perspective. Popul. Ecol. 57, 63–75.

Bell, G. and Gonzalez, A. (2009). Evolutionary rescue can prevent extinction following environmental change. Ecology Letters, 12: 942-948.

Benito Garzón, M., Robson, T. M., & Hampe, A. (2019). ΔTrait SDMs: species distribution models that account for local adaptation and phenotypic plasticity. New Phytologist, 222(4), 1757-1765.

Bocedi, G., Palmer, S.C., Pe'er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K. and Travis, J.M. (2014), Range Shifter: a platform for modelling spatial eco−evolutionary dynamics and species' responses to environmental changes. Methods Ecol Evol, 5: 388-396.

Boulangeat, I., Gravel, D. and Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters, 15: 584-593.

Brännström, Å., Johansson, J., & von Festenberg, N. (2013). The Hitchhiker's Guide to Adaptive Dynamics. Games, 4(3), 304–328.

Brunner, F. S., Anaya-Rojas, J. M., Matthews, B., & Eizaguirre, C. (2017). Experimental evidence that parasites drive eco-evolutionary feedbacks. Proceedings of the National Academy of Sciences, 114(14), 3678-3683.

Burns, C. W. (1969). Relation between filtering rate, temperature, and body size in four species of Daphnia. Limnology and Oceanography, 14(5), 693-700.

Bulleri F, Eriksson BK, Queirós A, Airoldi L, Arenas F, et al. (2018) Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. PLOS Biology 16(9): e2006852.

Chase, J. M., & Leibold, M. A. (2003). Ecological niches: linking classical and contemporary approaches. University of Chicago Press.

Christiansen, F. B., & Loeschcke, V. (1980). Evolution and intraspecific exploitative competition I. One-locus theory for small additive gene effects. Theoretical Population Biology, 18(3), 297-313.

Colombo, E. H., Martínez-García, R., López, C., & Hernández-García, E. (2019). Spatial eco-evolutionary feedbacks mediate coexistence in prey-predator systems. Scientific Reports, 9(1) 1-15.

Cottenie, K. and De Meester, L. (2004). Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. Ecology, 85: 114-119.

De Mazancourt, C., Johnson, E. and Barraclough, T.G. (2008), Biodiversity inhibits species' evolutionary responses to changing environments. Ecology Letters, 11: 380-388.

De Meester, L., Vanoverbeke, J., Kilsdonk, L. J., & Urban, M. C. (2016). Evolving perspectives on monopolization and priority effects. Trends in Ecology & Evolution, 31(2), 136-146.

Dercole, F., Ferrière, R., & Rinaldi, S. (2002). Ecological bistability and evolutionary reversals under asymmetrical competition. Evolution, 56(6), 1081-1090.

Dieckmann, U., & Doebeli, M. (1999). On the origin of species by sympatric speciation. Nature, 400, 354–357.

Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: A derivation from stochastic ecological processes. Journal of Mathematical Biology, 34(5–6), 579–612.

Dodson, S. I. (1974). Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. Ecology 55:605–613.

Doebeli, M., & Dieckmann, U. (2000). Evolutionary branching and sympatric speciation caused by different types of ecological interactions. The American Naturalist, 156(S4), S77–S101.

Edwards, K. F., Kremer, C. T., Miller, E. T., Osmond, M. M., Litchman, E., & Klausmeier, C. A. (2018). Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity. Ecology Letters, 21(12), 1853-1868.

Ferriere R. (2000). Adaptive responses to environmental threats: evolutionary suicide, insurance, and rescue. (Options Spring 2000), pp. 12–16. Laxenburg, Austria: International Institute for Applied Systems Analysis.

Ferriere, R., & Legendre, S. (2013). Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1610), 20120081.

Fronhofer, E. A., & Altermatt, F. (2015). Eco-evolutionary feedbacks during experimental range expansions. Nature communications, 6, 6844.

Fukami, T., Beaumont, H. J., Zhang, X. X., & Rainey, P. B. (2007). Immigration history controls diversification in experimental adaptive radiation. Nature, 446(7134), 436-439.

Geritz, S. A. H., Kisdi, E., Mesze, G., & Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology, 12(1), 35–57.

Gomulkiewicz, R., & Holt, R. D. (1995). When does evolution by natural selection prevent extinction? Evolution, 49(1), 201–207.

Gyllenberg, M., & Parvinen, K. (2001). Necessary and sufficient conditions for evolutionary suicide. Bulletin of Mathematical Biology, 63(5), 981-993.

Gyllenberg, M., Parvinen, K., & Dieckmann, U. (2002). Evolutionary suicide and evolution of dispersal in structured metapopulations. Journal of Mathematical Biology, 45(2), 79-105.

Hall, D. J., S. T. Threlkeld, C. W. Burns, and P. H. Crowley. (1976). The size-efficiency hypothesis and the size structure of zooplankton communities. Annual Review of Ecology and Systematics 7:177–208.

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. Annual Review of Ecology, Evolution, and Systematics, 43, 227-248.

Holmes, C. J., Figary, S., Schulz, K. L., & Cáceres, C. E. (2016). Effects of diversity on community assembly in newly formed pond communities. Ecosphere, 7(7), e01377.

Holt, R.D. (1993) Ecology at the mesoscale: the influence of regional processes on local communities. Species Diversity in Ecological Communities (eds R.E. Ricklefs & D. Schluter), pp. 77–88. University of Chicago Press, Chicago.

Howeth, J. G., & Leibold, M. A. (2010). Prey dispersal rate affects prey species composition and trait diversity in response to multiple predators in metacommunities. Journal of Animal Ecology, 79(5), 1000-1011.

Jackson, M. C., Loewen, C. J., Vinebrooke, R. D., & Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: a meta−analysis. Global change biology, 22(1), 180-189.

Johansson, J. (2008). Evolutionary responses to environmental changes: how does competition affect adaptation?. Evolution 62(2), 421-435.

Kisdi, É. (1999). Evolutionary branching under asymmetric competition. Journal of Theoretical Biology, 197(2), 149–162.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. and Levine, J.M. (2015). Community assembly, coexistence and the environmental filtering metaphor. Functional Ecology 29: 592-599.

Kremer, C. T., & Klausmeier, C. A. (2013). Coexistence in a variable environment: eco-evolutionary perspectives. Journal of theoretical biology, 339, 14-25.

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J. G., Phillimore, A. B., Bell, T., & Barraclough, T. G. (2012). Species interactions alter evolutionary responses to a novel environment. PLoS Biology, 10(5), e1001330.

Lee, W. G., Tanentzap, A. J., & Heenan, P. B. (2012). Plant radiation history affects community assembly: evidence from the New Zealand alpine. Biology Letters, 8(4), 558-561.

Legrand, D., Cote, J., Fronhofer, E. A., Holt, R. D., Ronce, O., Schtickzelle, N., Travis, J.M. and Clobert, J. & Clobert, J. (2017). Eco−evolutionary dynamics in fragmented landscapes. Ecography, 40(1), 9-25.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D. and Loreau, M. (2004). The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M.A. (2011) The metacommunity concept and its theoretical underpinnings.The Theory of Ecology (eds S.M. Scheiner & M.R. Willig), pp. 163–184. Chicago University Press, Chicago, IL, USA

Leibold, M. A., & Chase, J. M. (2017). Metacommunity Ecology, Volume 59. Princeton University Press.

Loeuille, N., & Leibold, M. A. (2008a). Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. The American Naturalist, 171(6), 788-799.

Loeuille, N., & Leibold, M. A. (2008b). Ecological consequences of evolution in plant defenses in a metacommunity. Theoretical population biology, 74(1), 34-45.

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H., & Metacommunity Working Group. (2011). Empirical approaches to metacommunities: a review and comparison with theory. Trends in ecology & evolution, 26(9), 482-491.

MacArthur, R. H. (1965). Patterns of species diversity. Biological Reviews, 40(4), 510-533.

Matthews, B., Aebischer, T., Sullam, K. E., Lundsgaard-Hansen, B., & Seehausen, O. (2016). Experimental evidence of an eco-evolutionary feedback during adaptive divergence. Current Biology, 26(4), 483-489.

May, R. M. Will a large complex system be stable? Nature 238, 413–414 (1972).

McCann, K. S. (2000). The diversity–stability debate. Nature, 405(6783), 228-233.

McKee, D., & Ebert, D. (1996). The effect of temperature on maturation threshold body-length in Daphnia magna. Oecologia, 108(4), 627-630.

Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define ‘fitness’ for general ecological scenarios? Trends in Ecology & Evolution, 7(6), 198–202.

Mouquet, N., & Loreau, M. (2003). Community patterns in source-sink metacommunities. American Naturalist, 162(5), 544–557.

Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change, 2(10), 747-751.

Osmond, M. M., & de Mazancourt, C. (2013). How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society B: Biological Sciences, 368(1610), 20120085.

Parvinen, K. (2007). Evolutionary suicide in a discrete-time metapopulation model. Evolutionary Ecology Research, 9(4), 619-633.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A. and McCarthy, M.A. (2014), Understanding co−occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods Ecol Evol, 5: 397-406.

Ponisio, Lauren C., Fernanda Valdovinos, Korrinna T. Allhoff, Marília Gaiarsa, Allison Barner, Paulo Guimarães, David H. Hembry, Beth Morrison, and Rosemary Gillespie. (2019). A network perspective for community assembly. Frontiers in Ecology and Evolution 7: 103.

Post, D. M., & Palkovacs, E. P. (2009). Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Philosophical Transactions of the Royal Society B: Biological Sciences, 364(1523), 1629-1640.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Shurin, J. B., Amarasekare, P., Chase, J. M., Holt, R. D., Hoopes, M. F., & Leibold, M. A. (2004). Alternative stable states and regional community structure. Journal of Theoretical Biology, 227(3), 359-368.

Soininen, J. (2014). A quantitative analysis of species sorting across organisms and ecosystems. Ecology, 95(12), 3284-3292.

Tamme, R., Hiiesalu, I., Laanisto, L., Szava‐Kovats, R. and Pärtel, M. (2010), Environmental heterogeneity, species diversity and co‐existence at different spatial scales. Journal of Vegetation Science, 21: 796-801.

Turcotte, M. M., Reznick, D. N., & Daniel Hare, J. (2013). Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. The American Naturalist, 181(S1), S46-S57.

Urban, M.C., Leibold, M.A., Amarasekare, P., De Meester, L., Gomulkiewicz, R., Hochberg, M.E., Klausmeier, C.A., Loeuille, N., De Mazancourt, C., Norberg, J., Pantel, J.H., Strauss, S.Y., Vellend, M., and M.J. Wade. 2008. The evolutionary ecology of metacommunities. Trends in Ecology & Evolution, 23(6): 311-317.

Urban, M. C., & De Meester, L. (2009). Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. Proceedings of the Royal Society B: Biological Sciences, 276(1676), 4129-4138.

Urban, M. C., G. Bocedi, A.P. Hendry, J.-B. Mihoub, G. Pe'er, A. Singer, J.R. Bridle, L.G. Crozier, L. De Meester, W. Godsoe, A. Gonzalez, J.J. Hellmann, R.D. Holt, A. Huth, K. Johst, C.B. Krug, P.W. Leadley, S.C.F. Palmer, J.H. Pantel, A. Schmitz, P.A. Zollner, and J.M.J. Travis (2016). Improving the forecast for biodiversity under climate change. Science, 353(6304).

Vanoverbeke, J., Urban, M.C. and De Meester, L. (2016), Community assembly is a race between immigration and adaptation: eco‐evolutionary interactions across spatial scales. Ecography, 39: 858-870.

Vasseur, D. A., Amarasekare, P., Rudolf, V. H., & Levine, J. M. (2011). Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. The American Naturalist, 178(5), E96-E109.

Wisz, Mary Susanne, Julien Pottier, W. Daniel Kissling, Loïc Pellissier, Jonathan Lenoir, Christian F. Damgaard, Carsten F. Dormann et al. "The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling." Biological reviews 88, no. 1 (2013): 15-30.

Wilson, D. S. (1992). Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology, 73(6), 1984-2000.

Yoshida T., Jones L.E., Ellner S.P., Fussmann G.F. & Hairston N.G. (2003). Rapid evolution drives ecological dynamics in a predator–prey system. Nature. 424, 303–306.

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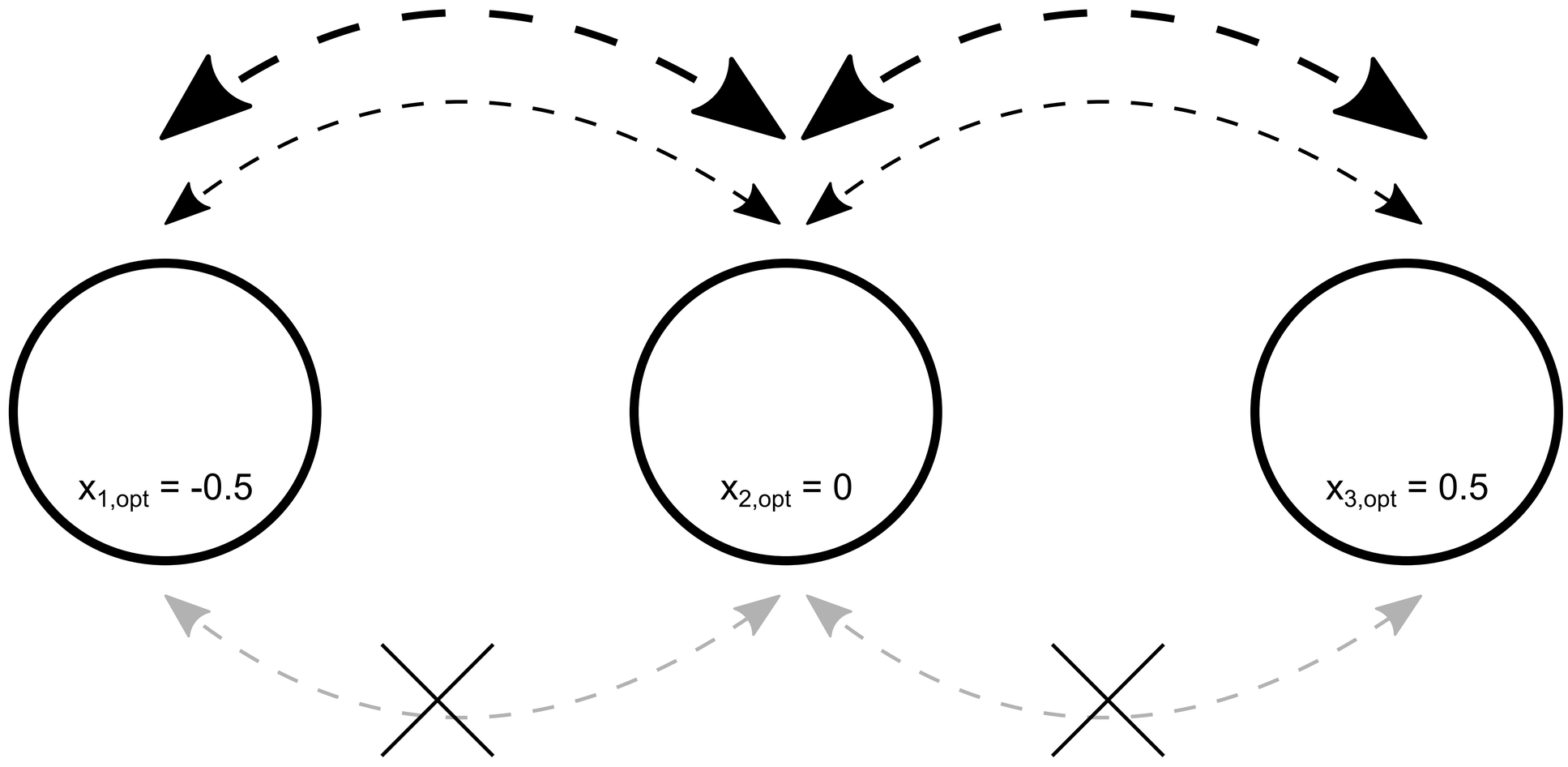

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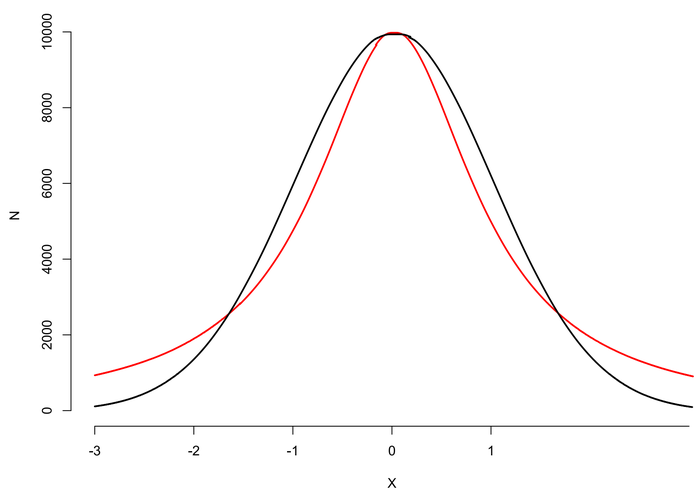

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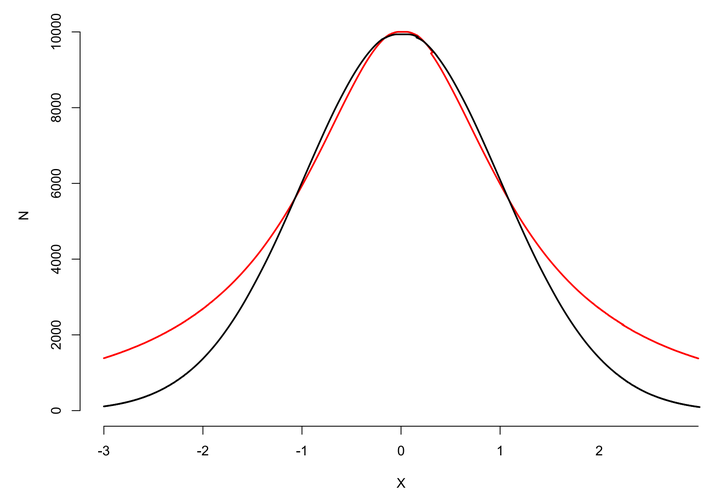

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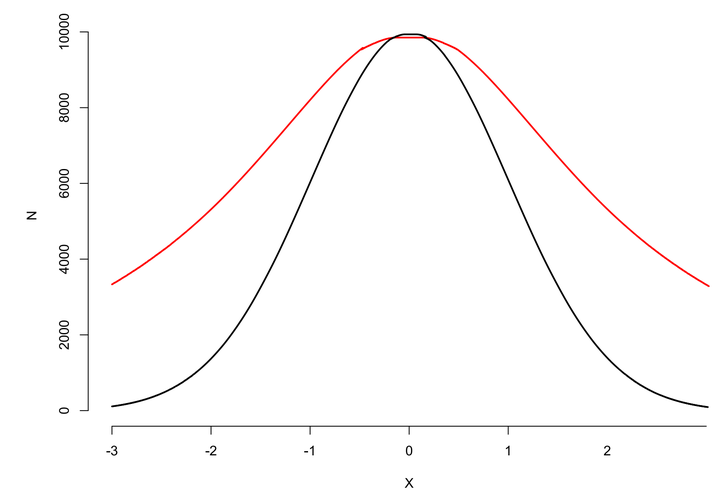

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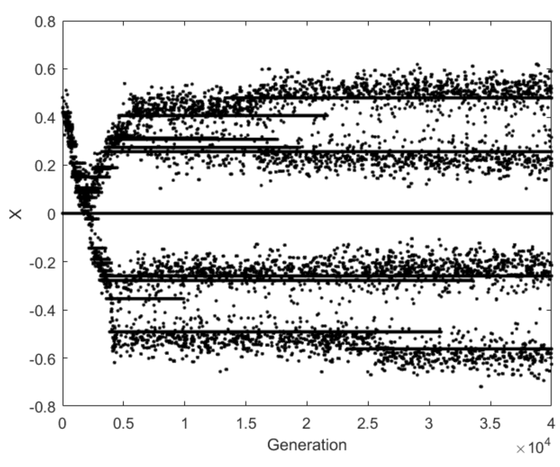

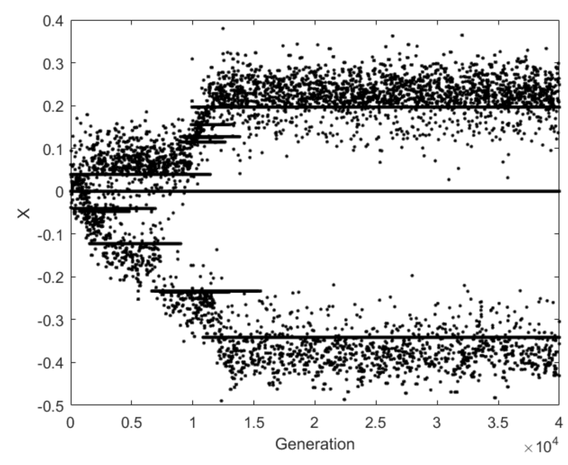

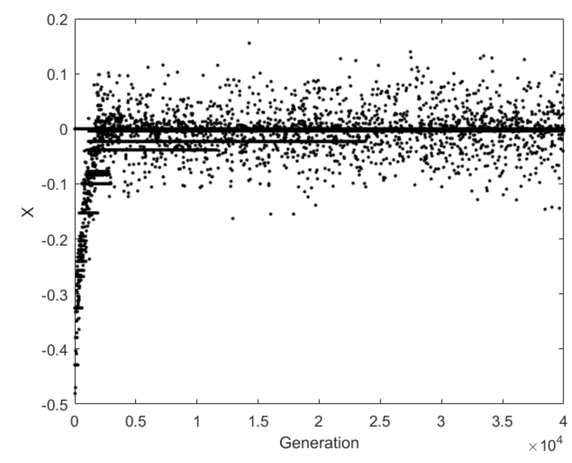

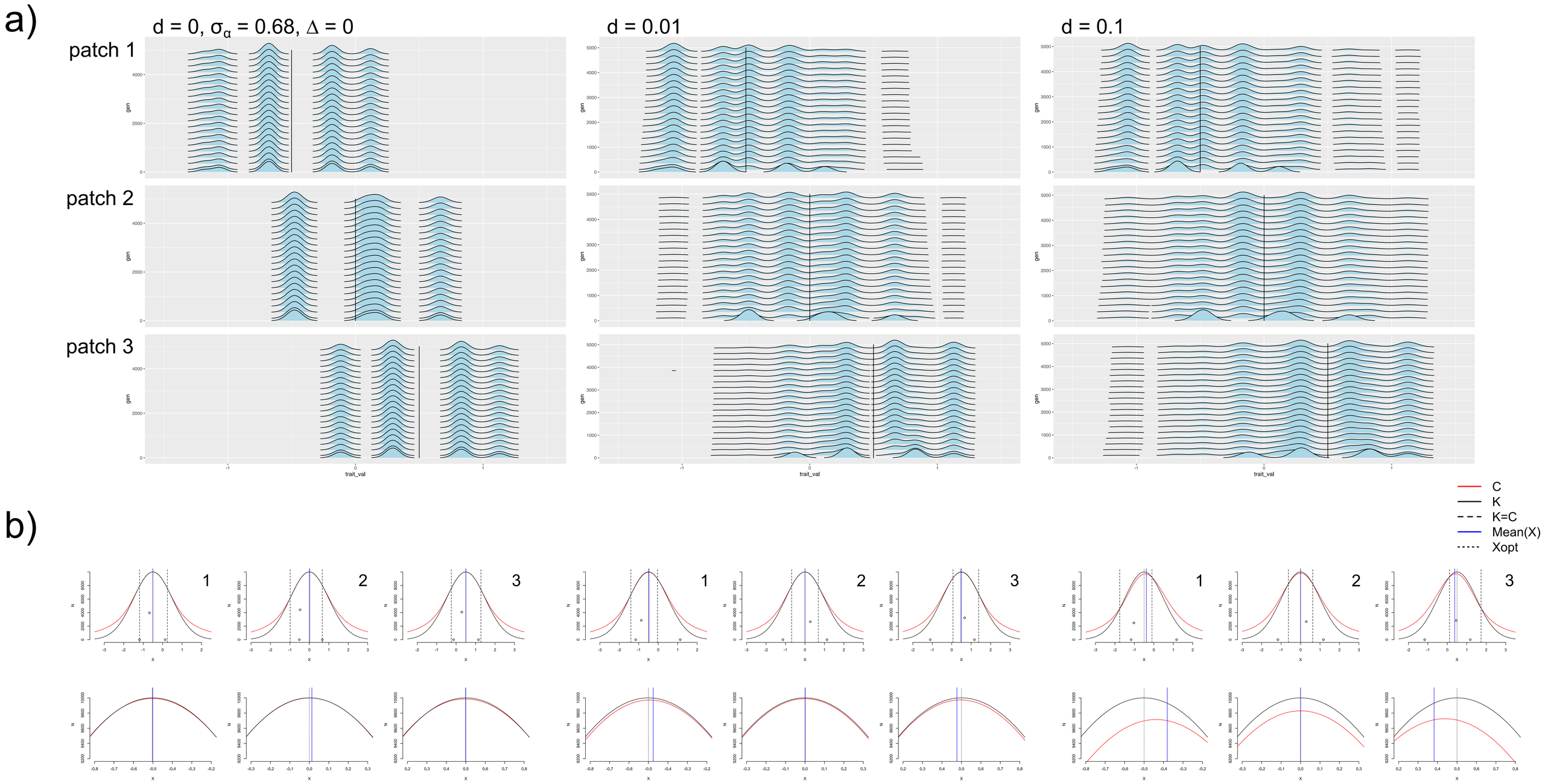
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d = 0.1
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patch 2
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trait_val
b)
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K=C
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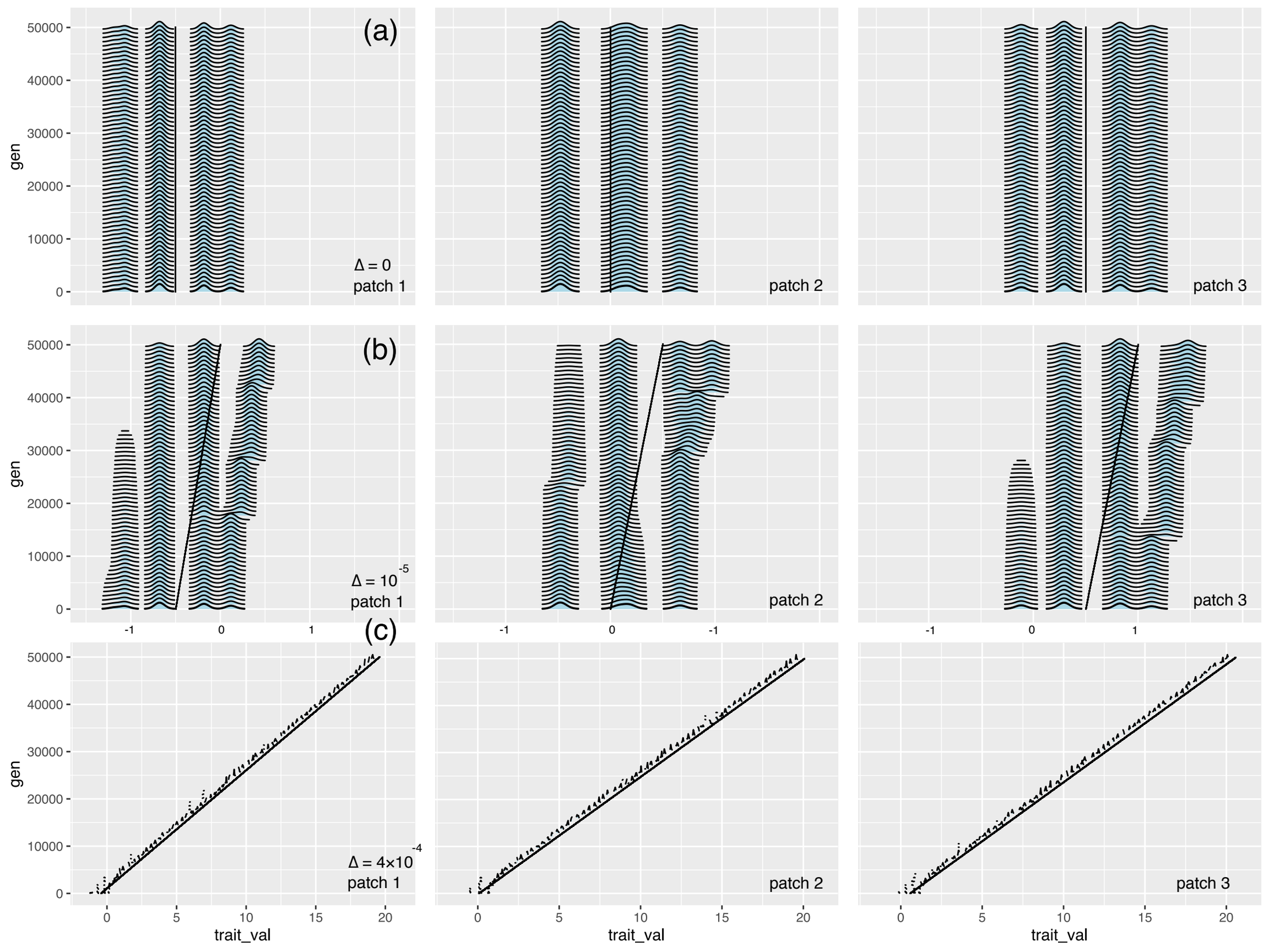
x


(a)
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Δ = 4×10^-4
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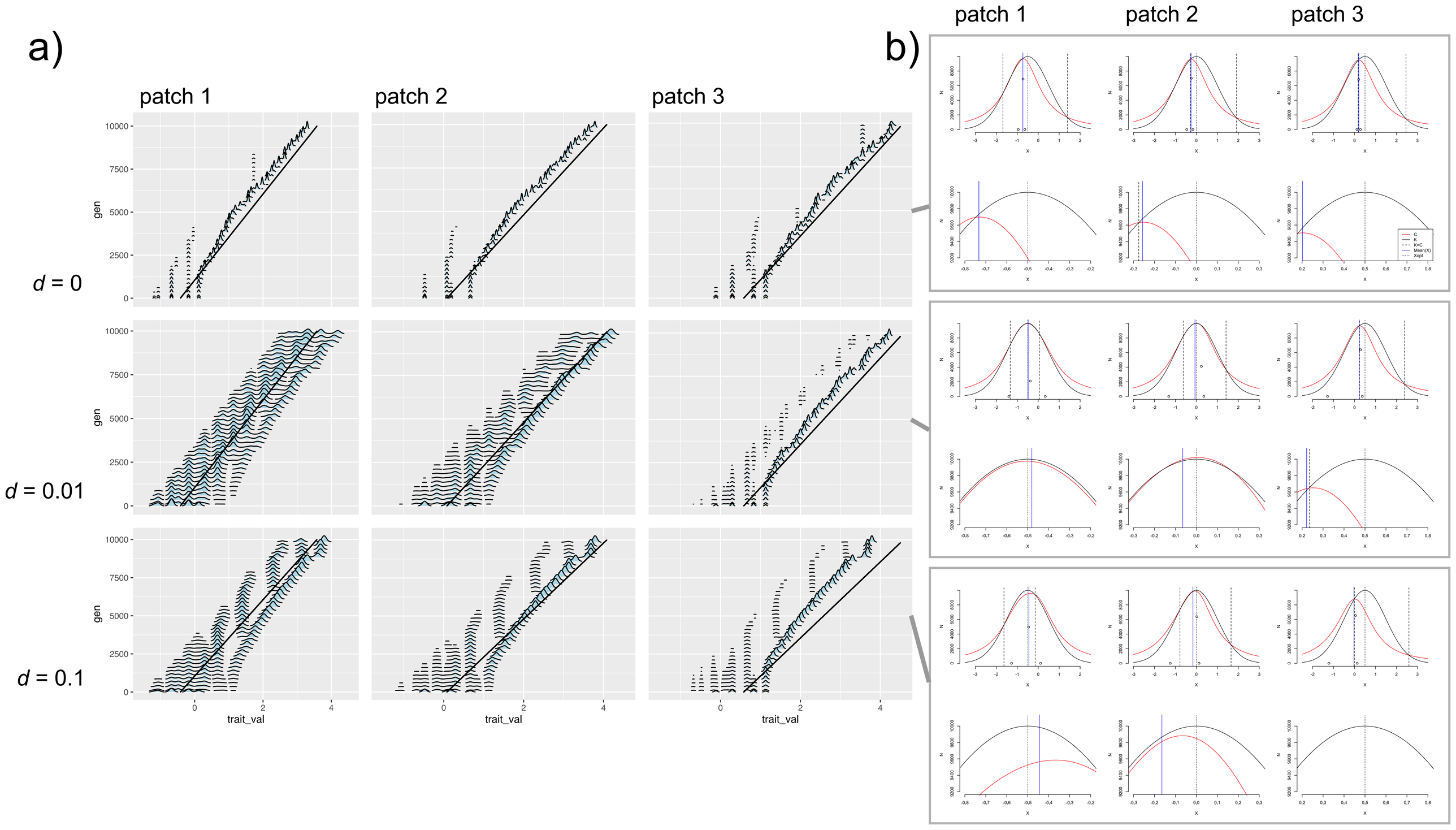
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patch 3
C
K
K=C
Mean(X)
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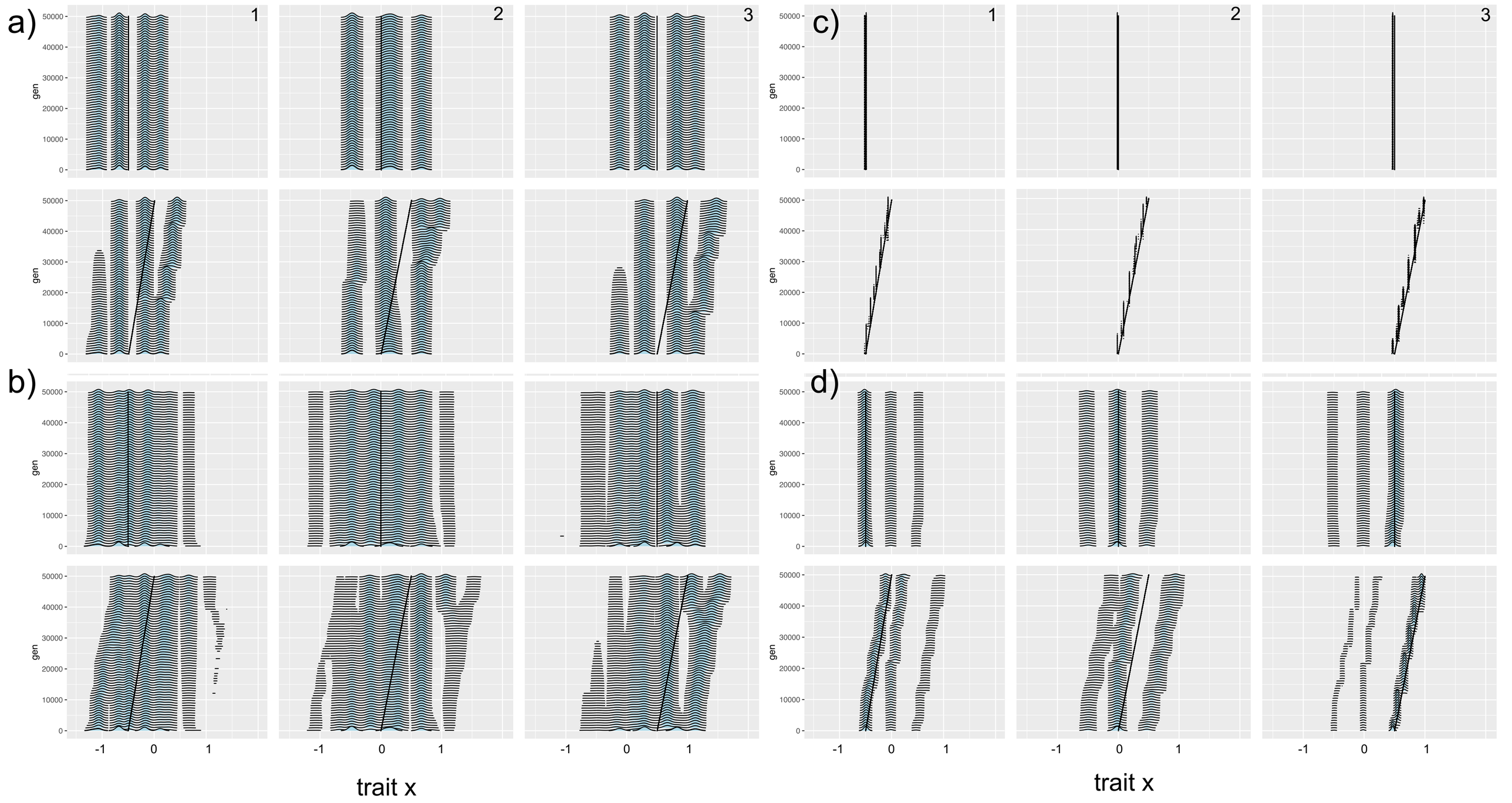
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