Eco-evolutionary dynamics in competitive systems: Rescue or murder?

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Data and code availability statement

Code for reproducing our results is available via Zenodo: https://doi.org/10.5281/zenodo.17982255.

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Author contribution statement

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Title

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Abstract

Rapid evolution in response to changing environments can have beneficial (e.g. evolutionary rescue) or detrimental (e.g. evolutionary suicide) outcomes for the survival of one species. Responses of multi-species systems are even harder to predict, but important to consider. Using a Lotka-Volterra competition model, we simulate eco-evolutionary dynamics in one- and two-species systems, with two traits per species: physiological performance and competitive tolerance. In the single-species system, evolution is consistently beneficial, enabling evolutionary rescue. In contrast, in the two-species system, evolution can be beneficial or detrimental. Notably, when evolution enhances the competitor's persistence, it can result in evolutionary murder of the focal species. Furthermore, the effect sizes of evolution on species' persistence are strongly modulated by whether both traits evolve, and by the shape of ecological and evolutionary trade-offs. Our study enables exploration of eco-evolutionary dynamics in more complex biotic settings, extending understanding of species responses to abiotic and biotic changes.

Keywords

Adaptive dynamics, Biotic interactions, Eco-evolutionary feedback, Environmental change, Extinction, Interspecific competition, Intraspecific competition, Mathematical modeling

1 Introduction

Global change is severely impacting ecosystems and threatening ecosystem functions (Bernhardt et al. 2017; Hooper et al. 2012; Pascual et al. 2022). Understanding how ecosystems respond to these changing conditions will give important insights into maintaining biodiversity and well-functioning ecosystems (Oliveira et al. 2022; Sandifer et al. 2015). Historically, this challenge has been addressed from a purely ecological perspective, which is based on the assumption that ecological and evolutionary processes act on separate timescales. In recent decades, however, increasing evidence has shown that rapid evolutionary responses can occur within just a few generations (Hairston et al. 2005; Koch et al. 2014), especially under fast-changing anthropogenic pressures and disturbances (Hendry et al. 2008; Hoffmann & Sgrò 2011), potentially resulting in eco-evolutionary feedbacks (Hendry 2017; Post & Palkovacs 2009; Schoener 2011). Rapid evolution has been shown to affect ecological dynamics at the population (Yoshida et al. 2003), community (Pantel et al. 2015) and ecosystem (Bassar et al. 2012) level. However, whether rapid evolution and the resulting eco-evolutionary dynamics foster or hinder species persistence in changing environments remains to be fully explored (Pelletier et al. 2009).

Rapid evolution can have beneficial effects for species persistence, e.g., when a given population avoids extinction due to severe external stress through adaptation by natural selection, a process referred to as evolutionary rescue (Bell 2017; Carlson et al. 2014; Gomulkiewicz & Holt 1995). Empirical examples of such evolutionary rescue range from adaptation to water acidification for phytoplankton species to evolution of vertebrate species in response to pesticides and viruses (Bell 2013; Vander Wal et al. 2013). However, several theoretical studies have also shown that evolution can negatively affect population survival, potentially leading to evolutionary suicide, when a viable population evolves traits that

ultimately prevent its persistence (Ferriere & Legendre 2013; Parvinen 2005). Together, these concepts highlight how evolution can also produce detrimental outcomes in altered environments, emphasizing the importance of studying the potential risks of evolution of a species to environmental change.

In multi-species settings, the question of whether evolution is beneficial or detrimental for species persistence is even more complex. Evolutionary rescue can be both direct (as described earlier) or indirect. For example, a non-evolving predator can be rescued from extinction through evolution of its prey, when there exists a defense-growth trade-off in the prey population (Yamamichi & Miner 2015). In small food web modules, indirect rescue of others can even occur more frequently than self-rescue (van Velzen 2023). However, the evolution of a focal species can also lead to the extinction of another, resulting in evolutionary murder (Parvinen 2005). For instance, plants that experience declining pollinator abundances might invest less into attracting those pollinators and more into selfing or vegetative reproduction, which in turn further threatens the already declining pollinator population (Weinbach et al. 2022; Weyerer et al. 2023). Evolutionary murder can also occur between trophic levels, such as in the case of systems where the prey's adaptation affects the persistence of a predator subject to experiencing external disturbance (Shang et al. 2024). We hypothesize that similar scenarios of evolutionary murder could occur in competitive systems. For example, when a competing species can rapidly adapt to changes in the abiotic environment, its resulting high abundances can increase competitive pressure on the focal species. This increased competitive pressure can then accelerate the decline or even extinction of the competing species, especially if their adaptation to the abiotic changes lags behind.

Given that all species are embedded within communities, it is important to consider species interactions when studying species responses to environmental change (De Meester et al. 2019; Loeuille 2019). Indeed, previous studies have shown that biotic interactions can also induce rapid evolutionary changes (Yoshida et al. 2003) as well as alter the evolutionary responses to abiotic environmental change (Govaert et al. 2021; Grainger et al. 2021; Lawrence et al. 2012). Hence, within a community, species experience both biotic and abiotic selective pressures. Trait evolution in response to abiotic or biotic change, or both, often occurs for multiple traits simultaneously (Stoks et al. 2016), and the speed at which such multi-variate trait evolution can occur depends on the underlying genetic variation and constraints of these traits (Lande 1979; Schluter 1996). Traits differ in their genetic variation (Blows & Hoffmann 2005), and evolutionary changes in one trait can aid or hamper evolutionary changes in other traits (Hine et al. 2014). These genetic constraints prevent species from simultaneously optimizing all components of fitness, which can be observed through trade-off relationships between traits (Stearns 1989). Yet, how such genetic trade-offs alter eco-evolutionary outcomes in competitive systems remains an open question.

In this study, we use a two-species Lotka-Volterra competition model to investigate whether the effects of evolution on species persistence are beneficial or detrimental, and under what conditions eco-evolutionary feedbacks speed up or slow down population decline in a changing environment. Specifically, each species in our model has two traits that can evolve: a trait linked to its physiological performance in the abiotic environment and a trait linked to its tolerance to competitive pressure. The abiotic environment deteriorates progressively so that, in the absence of evolution, both species eventually become extinct. The exact time point of extinction, however, depends on how quickly species adapt to the changing abiotic and biotic conditions. The extent to which such adaptation can occur, and

hence the effect of evolution, in turn, depend on evolutionary and ecological constraints. Given its applicability to different competitive systems, our model provides general insights into how the interplay between biotic and abiotic selection pressures shapes species density and trait trajectories and determines whether eco-evolutionary interactions can accelerate or prevent species extinction under environmental change.

2 Model and methods

Our simulation model is inspired by an empirical study system of competing freshwater ciliate species (Govaert & Klauschies 2025; Jiang & Morin 2007). It describes the ecological (i.e., population density) and evolutionary (i.e., trait) dynamics of two competing species. Each species experiences abiotic selection pressure from a changing abiotic environment (e.g., increasing salinity levels) and biotic selection pressure from the competitive interaction with itself and the other species. Correspondingly, each species can evolve two traits, its physiological optimum and its competitive tolerance. We implement an evolutionary trade-off, reflecting underlying genetic trait constraints (Blows & Hoffmann 2005; Hine et al. 2014), as well as an ecological trade-off, representing r/K selection theory (MacArthur & Wilson 1967).

We describe the ecological (Section 2.1) and evolutionary (Section 2.2) dynamics before we explain the design of our simulation scenarios and our choice of parameter values (Section 2.3). Model variables and parameters are summarized in Table 1. Simulations were performed in Python (version 3.11).

2.1 Defining ecological dynamics

For the ecological dynamics, we assume interference competition and use a Lotka-Volterra model. Such models have been applied to freshwater ciliates (Mühlbauer et al. 2020), where interference competition can occur when individuals collide or block access to resources (Holdridge et al. 2016). We denote the two competing species by X and Y and their respective densities at time t by $x(t)$ and $y(t)$ (see Table 1).

The dynamics of species X and Y are described by the differential equations:

$$\begin{cases} \dfrac{dx}{dt} = r_X x \left(w_X - \dfrac{x + a_{XY} y}{K_X} \right), \\ \dfrac{dy}{dt} = r_Y y \left(w_Y - \dfrac{y + a_{YX} x}{K_Y} \right). \end{cases} \tag{1}$$

The species' intrinsic growth rates (r_X, r_Y) are the maximum per capita growth rates under optimal conditions, while the terms in parentheses account for growth limitation due to physiological performance (abiotic environment) and competition (biotic environment).

The physiological performance depends on the difference between the state of the environment, $c = c(t)$ (e.g., salinity level), and the physiological optimum of the species c_X (or c_Y, respectively). It is expressed by the *physiological performance function* w_X (or w_Y, respectively), which, following Little & Seebacher (2021) and Liu et al. (2021), we take to be the Gaussian

$$w_X(c(t)) = \exp\left(-\frac{(c(t) - c_X)^2}{2\,\sigma_{w,X}^2} \right). \tag{2}$$

This function is positive, reaches a maximum of 1 when the physiological optimum (c_X) matches the state of the environment $(c(t))$, and decreases when the distance between c_X and $c(t)$ increases. The parameter $\sigma_{w,X}$ corresponds to the spread of the function, with

smaller values representing a narrower performance curve, and hence a larger cost when the species' trait does not match the state of the abiotic environment.

The second term in parentheses in Equation (1) describes intra- and interspecific competition. It depends on the competitive tolerance trait (K_X, K_Y) and the relative effect of one species on the other (a_{XY} and a_{YX}). When K_X is high, the effect of competition on the growth rate of species X is low, and vice versa. When species Y is absent and the physiological optimum c_X matches the state of the environment c, then K_X is the carrying capacity of species X. The considerations for Y are analogous.

Following r/K selection theory (MacArthur & Wilson 1967), we implement an ecological trade-off between r and K for each species, so that high values of K imply low values of r and vice versa. We let $r_{\max}$ and $K_{\max}$ be the maximal values of those parameters and express the trade-off as

$$\frac{r_X}{r_{\max}} = \left(1 - \left(\frac{K_X}{K_{\max}}\right)^{s_{\text{eco}}}\right)^{\frac{1}{s_{\text{eco}}}} \tag{3}$$

with $s_{\text{eco}} > 0$. The relation is convex, concave, or linear when $s_{\text{eco}} < 1$, $s_{\text{eco}} > 1$ or $s_{\text{eco}} = 1$, respectively (see Figure 1). The formulation for species Y is analogous. Note that, since the intrinsic growth rate r is a scaling factor in Equation (1) governing the ecological dynamics, the r/K trade-off also affects the speed of ecological dynamics. Changing the shape of that ecological trade-off will therefore affect how changes in K will alter the speed of ecological processes.

2.2 Integrating evolutionary dynamics

We model the evolution of our two traits (physiological optimum, c_X, c_Y, and competitive tolerance, K_X, K_Y) via recurrent mutation events. Our approach is inspired by adaptive dynamics (Geritz et al. 1998; Brännström et al. 2013), but we do not assume a strict

separation of ecological and evolutionary timescales because we want to explore the dynamic interplay of both. We therefore explicitly simulate multiple, potentially coexisting types. We denote the different types of species X by X_i $(i = 1, 2, \dots)$, each characterized by its trait values c_{X_i} and K_{X_i}. The total density of species X at time t is then given by the sum of the densities of its types, defined via $\hat{x}(t) := \sum x_i(t)$. Analogous considerations hold for species Y.

After each mutation, the time until the next mutation event is sampled from an exponential distribution with parameter $\mu_X \cdot \hat{x}(t)$, where μ_X is the per-capita mutation rate for species X and $\hat{x}(t)$ is the total population size. At each mutation event, one existing type is selected as "parent" type from which an offspring "mutant" type arises. The probability of a given type to become the parent type is proportional to its relative density within the population. The trait values of the mutant type are sampled from normal distributions around the parent's trait values c_{X_i} and K_{X_i} with standard deviations σ_{c_X} and σ_{K_X}, respectively. Hence, larger values of these standard deviations reflect a larger spread of offspring trait values and hence a potential for faster evolution of this trait. We refer to these parameters as *mutation spread*. In our model, these mutation spreads are fixed parameters, implying that evolutionary strategies are constant over time. We assume that the traits c_{X_i} and K_{X_i} are not independent but constrained by a genetic trade-off (Blows & Hoffmann 2005; Hine et al. 2014): fast evolution of one trait implies slow evolution of the other. We introduce a maximum mutation spread $\sigma_{\max}$ and implement the trade-off as in Equation (3) via

$$\frac{\sigma_{c_X}}{\sigma_{\max}} = \left(1 - \left(\frac{\sigma_{K_X}}{\sigma_{\max}}\right)^{s_{\text{evo}}}\right)^{\frac{1}{s_{\text{evo}}}}, \tag{4}$$

where $s_{\text{evo}} > 0$ determines the shape of the trade-off function (see Figure 1). Once the trait values for the offspring have been determined, the new type is initialized with a density of

p, while the corresponding parent density is reduced by p. The densities of all other types are unchanged in a mutation event. The same process occurs for species Y.

Between two mutation events, the existing types follow the same dynamics as given in Equation (1), modified for multiple types as follows:

$$\begin{cases} \dfrac{dx_i}{dt} = r_{X,i}x_i \left(w_{X,i}(c(t)) - \dfrac{\hat{x} + a_{XY}\hat{y}}{K_{X,i}} \right), \\ \dfrac{dy_j}{dt} = r_{Y,j}y_j \left(w_{Y,j}(c(t)) - \dfrac{\hat{y} + a_{YX}\hat{x}}{K_{Y,j}} \right), \end{cases} \tag{5}$$

where $\hat{x}, \hat{y}$ are the total densities of species X and Y, respectively. Note that the number of types changes after a mutation event and can differ between the two species, depending on how many mutation events have occurred for each species. The parameters are now type-specific as indicated by the subscripts i and j; their meaning is as in Equation (1); see Table 1. We assume that the competitive effect of one species on the other (a_{XY}, a_{YX}) is independent of type. Solutions of the system given in Equation (5) with positive initial conditions remain positive, but the densities of a non-viable type will approach zero. To avoid such unrealistically low densities, we set the densities to zero for all types whose density falls below p, the same density at which new mutants are introduced. With this choice, only mutants with a positive initial growth can enter the system.

Finally, we implement a directional, linearly increasing environmental change $c(t)$ at a rate τ. Consequently, if the physiological optimum of a species $(c_X,\ c_Y)$ is fixed, the difference between the state of the environment and the physiological optimum eventually grows linearly in time. Since the performance function approaches zero as that distance grows (see Equation (2)), the growth rate of the species will eventually be negative and its density will decline. In order to maintain viable densities, the species will have to evolve its physiological optimum trait.

2.3 Designing simulation experiments

To test for the effect of evolution on species survival in our study system, we design three simulation scenarios. In the *ecological scenario*, no evolution can occur. As described above, this will necessarily lead to extinction of the species since the environmental conditions change over time. This scenario will serve as a reference. In the *1-trait evolution scenario*, only the physiological optimum can evolve. In the *2-trait evolution scenario*, both traits can evolve, subject to the trade-off in Equation (4). In the evolution scenarios, extinction may or may not occur.

To quantify the net effect of evolution and the corresponding eco-evolutionary feedback, we follow Weyerer et al. (2023) and calculate the difference in extinction times between the reference (t_{X_R}) and evolutionary (t_X) scenarios, i.e., $\Delta t_X = t_X - t_{X_R}$. Higher absolute values of Δt_X indicate stronger eco-evolutionary feedbacks. Positive values indicate that evolution delays extinction, while negative values indicate an acceleration. When species are not extinct by the end of the simulation, we calculate Δt_X using the final simulation running time as t_X.

We first analyze the case of a single species and then use these results to understand the more complex dynamics of two competing species. We explain our choice of parameters and initial conditions in the Supporting Information S1.

3 Results

3.1 Single species system: Two-trait evolution modulates the potential for evolutionary rescue

In the absence of evolution, species eventually go extinct with increasing environmental change, but this extinction can be delayed when species are allowed to evolve (Figure 2). Besides a small region in the convex ecological trade-off (detailed in Supporting Information S2), the curves that show extinction delay as a function of mutation spread of the physiological optimum trait are positive in both the 1-trait (dark, solid lines in Figure 2) and 2-trait (light, dashed lines in Figure 2) evolution scenarios, and across all combinations of ecological and evolutionary trade-off functions. The positive effect of evolution indicates a potential for evolutionary rescue: if the change in the abiotic environment stopped somewhere between the extinction time of the reference (t_{X_R}) and the evolution (t_X) scenarios, then we would observe species extinction in the former but species survival in the latter case.

For the linear ecological and linear evolutionary trade-off (Figure 2e), we find that increasing values of the mutation spread σ_{c_X} increase the delay of the extinction time Δt_X in the 1-trait evolution scenario. This can be explained by the fact that higher values of σ_{c_X} translate into faster adaptation to the abiotic environment and hence longer survival times. We also find that the additional effect of evolving competitive tolerance on extinction delay in the 2-trait evolution scenario depends on the mutation spread: if σ_{c_X} is below some threshold, 2-trait evolution is more beneficial than 1-trait evolution; whereas if σ_{c_X} is above this threshold, 1-trait evolution is more beneficial than 2-trait evolution (solid curve above dashed curve in Figure 2).

To explain this switch in outcome, we compare selected simulation runs with relatively low versus high mutation spread σ_{c_X} (Figure 3a,b). In the 2-trait evolution scenario, we generally find that competitive tolerance K_X evolved to approach its maximum $K_{\max} = 1$ (dashed red lines in Figure 3). This process can be explained through the invasion criteria (detailed in Supporting Information S3). Whether or not the evolution of competitive tolerance is beneficial or detrimental depends on the value of σ_{c_X}. If σ_{c_X} is small (Figure 3a), the rapid evolution to maximum competitive tolerance diminishes the negative effects of competition. This results in an initial higher population density, which then buffers the population against extinction and effectively delays extinction time. However, because of the ecological trade-off, the growth rate (r_X) approaches zero (dashed blue line in Figure 3a) when the competitive tolerance trait approaches its maximum. If σ_{c_X} is large, it is exactly this trade-off that reduces the ability of the species to track environmental change when competitive tolerance evolves (Figure 3b). First, compared to the case of small σ_{c_X}, evolution of competitive tolerance is slower due to the trade-off between σ_{c_X} and σ_{K_X}. Second, since evolution of larger competitive tolerance leads to low growth rates, new types that are better adapted to the environment will not be able to grow fast enough to ensure population persistence. This ultimately results in a too slow evolution of physiological performance, reflected by the dashed line in the third panel in Figure 3b flattening off. Hence, evolution of physiological optimum is beneficial and even required for persistence in the long run, whereas evolution of competitive tolerance has the short-term benefit of increasing population density and the long-term negative cost of inhibiting evolutionary change through the reduction in growth rate.

The value of σ_{c_X} where the 2-trait evolution becomes less beneficial for species survival depends on the specific combination of the ecological and evolutionary trade-off (Figure 2).

For a linear evolutionary trade-off (i.e., panels b, e, h of Figure 2, changing from a linear to convex ecological trade-off, the same initial value of K_X results in a much lower initial value of r_X (Figure 1), and therefore in a much reduced ability of new types with potentially better physiological performance to grow (Figure 3c). Because of the convex ecological trade-off, the rapid evolution to maximum competitive tolerance K_X is only offset by small changes in r_X and does not further slow down the overall evolutionary dynamics. Thus, even small increases in K_X result in large beneficial effects for species survival. By contrast, when that trade-off is concave (Figure 2h), the same initial value of K_X gives a larger value of r_X than in the linear trade-off (Figure 1). Hence, already at smaller values of σ_{c_X}, the population is much better at tracking the abiotic change when only c_X evolves. When both traits can evolve, fast evolution to maximum competitive tolerance is overall detrimental because it effectively slows down evolution of c_X through its effect on lowering r_X.

Similar to the ecological trade-off, the evolutionary trade-off also affects the relative importance of the short-term and long-term benefits of trait evolution. When the trade-off is convex (Figure 2a, d, g), the values of σ_{K_X} for a given σ_{c_X} are much lower than in the linear and concave evolutionary trade-off cases (Figure 1). Hence, even if K_X can evolve, it evolves so slowly that it remains almost constant (Figure 3d), at least when σ_{c_X} is not extremely small. In this case, the invasibility criterion (detailed in Supporting Information S3) becomes primarily determined by the type's physiological optimum, so that new types can only invade when their physiological optimum value is closer to the current state of the environment, largely independent of their competitive tolerance K. Hence, the slow evolution of K_X makes the 2-trait evolution scenario effectively equivalent to the 1-trait scenario. On the other hand, when the evolutionary trade-off is concave, the mutation spread for K_X is much larger for a given σ_{c_X} and K_X again evolves rapidly to its maximum,

which then effectively hinders evolution to the abiotic change through the trade-off effect on r_X, resulting in a large difference between the 1-trait and 2-trait evolution scenario.

In addition, the stochasticity of the timing of mutation events and the trait values of types translated into a large variability between simulation runs for the convex-linear and convex-concave ecological-evolutionary trade-off. This variability primarily arises from differences in the final evolutionary trajectories of the competitive tolerance trait and the associated intrinsic growth rate of the last surviving type, which jointly determine the rate of population decline and hence the extinction time. A detailed explanation of this mechanism is provided in Supporting Information S4.

3.2 Two-species system: competitive interactions can lead to evolutionary murder

In a two-species system, the competitor's interaction and evolution can change how the focal species' evolution affects its extinction time. We therefore study the extinction delay ($\Delta t_X = t_X - t_{X_R}$) of our focal species X as a function of its own mutation spread, σ_{c_X}, and that of its competitor, σ_{c_Y} (Figure 4). In contrast to the single-species case, we find that evolution in the two-species system can be beneficial to the focal species, i.e., delay its extinction ($\Delta t_X > 0$), or detrimental, i.e., accelerate its extinction ($\Delta t_X < 0$). In the latter case, species X goes extinct due to the combined effect of environmental change and evolution of species Y. However, if environmental change stopped somewhere between the two extinction points, contrary to the single-species system, species X would still go extinct due to the evolution of species Y. This is known as evolutionary murder (Parvinen 2005).

In the 1-trait evolution scenario, independent of the ecological trade-off, species X benefits from evolution when its mutation spread is larger than that of its competitor ($\sigma_{c_X} > \sigma_{c_Y}$,

blue region Figure 4a) and suffers when it is smaller ($\sigma_{c_X} < \sigma_{c_Y}$, red region Figure 4a). When σ_{c_X} is larger than σ_{c_Y}, species X adapts faster to the changing environment, maintaining a higher abundance. Therefore, species Y experiences increased abiotic stress and is exposed to biotic pressure for longer, leading to its earlier extinction. The same reasoning holds when σ_{c_X} is lower than σ_{c_Y}, but now results in X going extinct earlier than in the ecological scenario. When $\sigma_{c_X} \approx \sigma_{c_Y}$, the difference in extinction times is close to zero (pale colors along the diagonal, Figure 4a), but the variability in outcomes is high (Figure 4c). With comparable mutation spreads, both species track the environmental change at comparable speeds. Hence, the stochastic timing of mutations and mutant trait values determine which species first gains a significant advantage. For the convex ecological trade-off, the net effect of evolution is less pronounced (i.e., paler red and blue regions) due to lower initial growth rates (Figure 1), which reduce the beneficial effect of evolution.

In the 2-trait evolution scenarios with linear and concave ecological trade-offs (panels in the middle and bottom row of Figure 4b), the colors are paler than in the 1-trait evolution scenario, indicating long-term costs of rapid evolution to larger values of competitive tolerance. Although a larger mutation spread of the physiological optimum trait improves environmental tracking, this effect is counteracted by evolution to biotic interactions, which favors higher competitive tolerance K at the expense of a lower intrinsic growth rate r. The resulting reduction in r slows down the invasion of fitter types, thereby limiting the adaptive response of both species. As a consequence, species generally struggle to keep pace with environmental change, leading to shorter persistence times than in the 1-trait evolution scenario, although persistence until simulation end was observed in a small number of replicate simulations under convex evolutionary trade-off. These compensatory effects smooth the transition between cases where one or the other species persists longer, replacing the sharp

red–blue boundary of the 1-trait evolution scenario with a more diffuse gradient, and induce more variability when the mutation spread of a species' competitive tolerance strongly differs from that of its competitor (enlarging of the green-blue area observed outside of the diagonal in Figure 4d).

By contrast, a convex ecological trade-off (panels in top row of Figure 4b) reduces the potential for evolutionary murder, strongly diverging from the 1-trait evolution scenario. This reduction is more prominent as the evolutionary trade-off changes from convex to linear and from linear to concave. Under a convex ecological trade-off, initial growth rates are low (Figure 1), and the invasion of better-adapted mutant types is slow, so both species fail to track the shifting environment. The dominant evolutionary change is therefore the increase in competitive tolerance. With a linear evolutionary trade-off, this evolution proceeds rapidly for species X as σ_{c_X} decreases, while under a concave trade-off it occurs rapidly across nearly all σ_{c_X} values. Higher K values temporarily release species X from competitive pressure, allowing an early population increase that delays extinction. Although both populations soon decline as abiotic stress intensifies, the transient competitive release produces overall longer persistence. Even when σ_{K_Y} is large, the additional competition arising from species Y's increase in abundance remains negligible, since both species quickly lose fitness to the changing environment. This mechanism explains the predominantly blue pattern in the upper-right panel of Figure 4b. Note that, for the same reason as in the 1-species system, the combination of convex ecological and concave evolutionary trade-off increases variability in the timing of extinction of species X (detailed Supporting Information S4), explaining the dark green shades observed in the top right panel of Figure 4d.

4 Discussion

Considering both abiotic and biotic changes when studying ecological and evolutionary dynamics is crucial given that both theoretical (Drury et al. 2018; Johansson 2008; Loeuille 2019; Wang et al. 2025) and empirical studies (Govaert et al. 2021; Grainger et al. 2021; Hart et al. 2019; Yoshida et al. 2003) have shown that biotic interactions can induce rapid evolution and alter evolutionary trajectories of species in response to abiotic change. In general, considering ecological and evolutionary dynamics simultaneously is important given the vast evidence of dynamical interactions between ecology and evolution (Hairston et al. 2005; Hendry 2017; Schoener 2011). However, whether evolution will be beneficial or detrimental in a multi-species setting is not straightforward. Our eco-evolutionary competition model tracked the ecological densities and evolutionary trait dynamics of two species exposed to a directional abiotic environmental change. Using this model, we show that evolution is beneficial in the 1-species system, while it holds potential for evolutionary murder in a 2-species system. Overall, our study highlights the importance of considering multiple species and multiple traits to understand whether trait evolution will be beneficial for species survival exposed to changing environmental conditions.

The outcomes of our study can be understood through three eco-evolutionary feedbacks identified in our model. First, evolution to abiotic stress directly enhances environmental tracking, reducing abiotic stress and sustaining higher population densities, which in turn fosters evolution. Second, evolution to biotic stress initially increases population size through a higher competitive tolerance K, raising mutation frequency and thereby promoting further evolution; these first two feedbacks are therefore self-reinforcing. Third, over longer timescales, evolution of competitive tolerance lowers the intrinsic growth rate r, which on the one hand slows down adaptation, but on the other hand delays extinction

by reducing the rate of population decline. The extent to which these feedbacks result in beneficial or detrimental effects on species extinction then depends on the mutation spread of each trait and on whether species evolve alone or in presence of a competitor.

In the single-species model, 1-trait and 2-trait evolution were overall beneficial for species survival, although the extent of extinction delay depended on the number of evolving traits and on the shape of the ecological and evolutionary trade-offs. When only the physiological optimum trait evolved, increasing the mutation spread progressively delayed extinction. This result is in line with previous work on evolutionary rescue (Carlson et al. 2014; Gomulkiewicz & Holt 1995), demonstrating that larger genetic diversity (e.g., in microbial species *Pseudomonas fluorescens*; Ramsayer et al. (2013)) and greater population size (e.g., in yeast *Saccharomyces cerevisiae*; Bell & Gonzalez (2009)) increase the potential for evolutionary rescue. The shape of the ecological trade-off modulated the effect of evolution to abiotic pressure: linear and concave ecological trade-offs resulted in a larger extinction delay than the convex one, because the same initial competitive tolerance (K) yielded a higher intrinsic growth rate (r), facilitating the growth of better adapted types. When multiple traits can evolve, their evolution is often restricted by genetic or evolutionary constraints (Hine et al. 2014), and hence does not necessarily increase the potential for evolutionary rescue (Campbell et al. 2025). In contrast to the 1-trait evolution scenario, concave and linear ecological trade-offs led to smaller extinction delays when both traits could evolve, as competitive tolerance (K) rapidly evolved to high values that lowered population growth (r). However, when a convex ecological trade-off was combined with a linear or concave evolutionary trade-off, 2-trait evolution provided a strong survival advantage, since rapid evolution of reduced competitive tolerance increased initial population density and buffered the population against extinction.

These results emphasize that ecological and evolutionary trade-offs are important for eco-evolutionary dynamics. For example, the ecological growth-defense trade-off in different strains of the alga *Chlorella vulgaris* resulted in rapid evolution in response to predation by the rotifer *Brachionus calyciflorus*, giving rise to predator-prey dynamics oscillating out of phase (Yoshida et al. 2003). At the community level, the shape of the growth–defense trade-off strongly influences whether communities respond to environmental change through rapid frequency shifts among coexisting resident species with different trait combinations or through slower species turnover with immigration of new species, with important implications for diversity and ecosystem functioning (Ehrlich et al. 2025). In addition, evolutionary trade-offs can give rise to different eco-evolutionary dynamics (Kasada et al. 2014). Our study corroborates that eco-evolutionary dynamics are influenced by both types of trade-offs. While previous work often focuses on ecological or evolutionary trade-offs alone, we in addition show that it is also the combination of ecological and evolutionary trade-offs that can determine these dynamics. Hence, our study highlights the need to incorporate both ecological and evolutionary processes, as well as trade-offs, into a single modeling framework.

Contrary to the single-species setting, evolution was not always beneficial in the two-species system and even led to cases of evolutionary murder. Evolutionary murder occurred when the competitor species could rapidly track the environmental change, establishing high population densities. This then increased competitive pressure on the focal species, reducing its density and its evolutionary potential to track the environmental change, thereby accelerating its decline. In the two-species system, the aforementioned feedback loops interact in a way that affects these outcomes. Evolution to biotic pressure in the 2-species system becomes more beneficial than in the single-species system because increases in competitive tolerance release both intra- and interspecific competitive pressures. Consequently,

two-trait evolution can become more advantageous than one-trait evolution in conditions where it was not beneficial in the single-species system. This is particularly true for concave ecological trade-offs, where 2-trait evolution was almost never as beneficial as 1-trait evolution in the 1-species system, while in the 2-species system it led to comparatively reduced species extinction. Research on evolutionary murder remains remarkably scarce since its introduction by Parvinen (2005), although it did receive some attention in the context of mutualistic (Weinbach et al. 2022; Weyerer et al. 2023) and antagonistic systems (Shang et al. 2024). By demonstrating that such evolutionary murder can also occur in a competitive two-species system, our work represents an important step in investigating how the interaction of ecological and evolutionary processes can shape conditions under which evolution becomes detrimental between competing species.

Indirect evolutionary rescue and evolutionary murder have mainly been demonstrated in theoretical studies (Shang et al. 2024; van Velzen 2023; Weinbach et al. 2022; Weyerer et al. 2023; Yamamichi & Miner 2015). Our study contributes to those theoretical studies. However, we also suggest that some of our model predictions could be tested experimentally by combining evolved with non-evolved populations of competitors to demonstrate indirect evolutionary effects, either rescue or murder. Possible experimental model systems include ciliates (Govaert et al. 2021), phytoplankton (Réveillon & Becks 2024), zooplankton (Vanvelk et al. 2024), duckweed (Hart et al. 2019) and plant weeds (Alexander et al. 2015). Alternatively, experimental practices to halt evolution, such as replacing evolving populations by ancestral individuals repeatedly throughout an experiment (Hart et al. 2019), could also reveal patterns of indirect evolutionary rescue or murder. Lastly, combining such eco-evolutionary experiments using genotypes or clonal lines with different ecological trade-

offs (rotifer-algal system; Yoshida et al. (2003)) could showcase the importance of different ecological and evolutionary trade-offs within an experimental system.

Finally, our results have important implications for larger systems. Several recent studies suggest that the concept of evolutionary rescue can be extended towards multi-species systems (e.g., Bell et al. 2019; Fugère et al. 2020; Fussmann & Gonzalez 2013; Low-Décarie et al. 2015; van Velzen 2023; Yacine et al. 2021; Yamamichi & Miner 2015). Interestingly, a large proportion of these studies focuses on trophic interactions, demonstrating for example that prey adaptation to external stressors can enable predator survival (van Velzen 2023; Yamamichi & Miner 2015). Empirical evidence from phytoplankton communities furthermore demonstrates that trophic structure modulates so-called community rescue, e.g., when predator and prey species experience and evolve to different levels of external stressors (Bell et al. 2019). By contrast, our model predicts that biotic interactions within multi-species systems can not only reduce the potential for evolutionary rescue, they can also enable evolutionary murder. This result is in line with insights from the predator-prey food web model by van Velzen (2023), where evolutionary murder could occur within trophic levels, that is, between species that interact indirectly via resource competition (sharing the same prey) or apparent competition (sharing the same predator). Our results are also consistent with a spatially explicit eco-evolutionary model of multi-species responses to climate change, which predicted that competitive interactions can lead to extinction debts, even long after climate stabilization (Norberg et al. 2012). These studies and our results suggest that whether or not evolution is beneficial or detrimental for species persistence in multi-species ecological networks could depend on the type of biotic interaction dominating these networks. Evolution in antagonistic systems can lead to both beneficial and detrimental effects on species persistence depending on the mechanism of adaptation. By contrast, in competitive (or

mutualistic, see Weinbach et al. (2022)) systems, we might expect to see more evolutionary murder, and hence partial network collapse, due to self-reinforcing feedbacks arising from pairwise interactions. We argue that further empirical and theoretical research is needed to test how networks composed of multiple interaction types, as conceptually outlined by Fontaine et al. (2011), can help us understand and forecast eco-evolutionary responses in more realistic systems.

References

Alexander, J. M., J. M. Diez & J. M. Levine (2015). "Novel competitors shape species' responses to climate change". In: *Nature* 525.7570, pp. 515–518.

Bassar, R. D., R. Ferriere, A. Lopez-Sepulcre, M. C. Marshall, J. Travis, C. M. Pringle, et al. (2012). "Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (Poecilia reticulata)". In: *Am. Nat.* 180.2, pp. 167–185.

Bell, G. (2013). "Evolutionary rescue and the limits of adaptation". In: *Philos. Trans. R. Soc. B Biol. Sci.* 368.1610, p. 20120080.

— (2017). "Evolutionary rescue". In: *Ecology* 48.1, pp. 605–627.

Bell, G., V. Fugère, R. Barrett, B. Beisner, M. Cristescu, G. Fussmann, et al. (2019). "Trophic structure modulates community rescue following acidification". In: *Proceedings of the Royal Society B* 286.1904, p. 20190856.

Bell, G. & A. Gonzalez (2009). "Evolutionary rescue can prevent extinction following environmental change". In: *Ecol. Lett.* 12.9, pp. 942–948.

Bernhardt, E. S., E. J. Rosi & M. O. Gessner (2017). "Synthetic chemicals as agents of global change". In: *Front. Ecol. Environ.* 15.2, pp. 84–90.

Blows, M. W. & A. A. Hoffmann (2005). “A reassessment of genetic limits to evolutionary change”. In: *Ecology* 86.6, pp. 1371–1384.

Brännström, Å., J. Johansson & N. Von Festenberg (2013). “The hitchhiker’s guide to adaptive dynamics”. In: *Games* 4.3, pp. 304–328.

Campbell, D. R., J. M. Powers & J. Kipness (2025). “Predicting the contribution of single trait evolution to rescuing a plant population from demographic impacts of climate change”. In: *Evolution*, qraf019.

Carlson, S. M., C. J. Cunningham & P. A. Westley (2014). “Evolutionary rescue in a changing world”. In: *Ecology* 29.9, pp. 521–530.

De Meester, L., K. I. Brans, L. Govaert, C. Souffreau, S. Mukherjee, H. Vanvelk, et al. (2019). “Analysing eco-evolutionary dynamics—The challenging complexity of the real world”. In: *Ecology* 33.1, pp. 43–59.

Drury, J. P., J. A. Tobias, K. J. Burns, N. A. Mason, A. J. Shultz & H. Morlon (2018). “Contrasting impacts of competition on ecological and social trait evolution in songbirds”. In: *PLOS Biology* 16.1, e2003563.

Ehrlich, E., G. Adje & U. Gaedke (2025). “The role of trade-off shapes for community adaptation and maintenance of ecosystem functions under environmental change”. In: *Ecology* 106.8, e70156.

Ferriere, R. & S. Legendre (2013). “Eco-evolutionary feedbacks, adaptive dynamics and evolutionary rescue theory”. In: *Philos. Trans. R. Soc. B Biol. Sci.* 368.1610, p. 20120081.

Fontaine, C., P. R. Guimarães Jr, S. Kéfi, N. Loeuille, J. Memmott, W. H. van Der Putten, et al. (2011). “The ecological and evolutionary implications of merging different types of networks”. In: *Ecol. Lett.* 14.11, pp. 1170–1181.

Fugère, V., M.-P. Hébert, N. B. Da Costa, C. C. Xu, R. D. Barrett, B. E. Beisner, et al. (2020). "Community rescue in experimental phytoplankton communities facing severe herbicide pollution". In: *Ecology* 4.4, pp. 578–588.

Fussmann, G. F. & A. Gonzalez (2013). "Evolutionary rescue can maintain an oscillating community undergoing environmental change". In: *Interface Focus* 3.6, p. 20130036.

Geritz, S. A., E. Kisdi, G. Meszéna & J. A. Metz (1998). "Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree". In: *Ecology* 12, pp. 35–57.

Gomulkiewicz, R. & R. D. Holt (1995). "When does evolution by natural selection prevent extinction?" In: *Evolution*, pp. 201–207.

Govaert, L., L. J. Gilarranz & F. Altermatt (2021). "Competition alters species' plastic and genetic response to environmental change". In: *Scientific Reports* 11.1, p. 23518.

Govaert, L. & T. Klauschies (2025). "Eco-phenotypic feedback loops differ in multistressor environments". In: *Ecology* 106.1, e4480.

Grainger, T. N., S. M. Rudman, P. Schmidt & J. M. Levine (2021). "Competitive history shapes rapid evolution in a seasonal climate". In: *Proc. Natl. Acad. Sci. U.S.A.* 118.6, e2015772118.

Hairston, N. G., S. P. Ellner, M. A. Geber, T. Yoshida & J. A. Fox (2005). "Rapid evolution and the convergence of ecological and evolutionary time". In: *Ecol. Lett.* 8.10, pp. 1114–1127.

Hart, S. P., M. M. Turcotte & J. M. Levine (2019). "Effects of rapid evolution on species coexistence". In: *Proc. Natl. Acad. Sci. U.S.A.* 116.6, pp. 2112–2117.

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton University Press.

Hendry, A. P., T. J. Farrugia & M. T. Kinnison (2008). "Human influences on rates of phenotypic change in wild animal populations". In: *Ecology* 17.1, pp. 20–29.

Hine, E., K. McGuigan & M. W. Blows (2014). "Evolutionary constraints in high-dimensional trait sets". In: *Am. Nat.* 184.1, pp. 119–131.

Hoffmann, A. A. & C. M. Sgrò (2011). "Climate change and evolutionary adaptation". In: *Nature* 470.7335, pp. 479–485.

Holdridge, E. M., C. Cuellar-Gempeler & C. P. terHorst (2016). "A shift from exploitation to interference competition with increasing density affects population and community dynamics". In: *Ecology* 6.15, pp. 5333–5341.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. Byrnes, B. A. Hungate, K. L. Matulich, et al. (2012). "A global synthesis reveals biodiversity loss as a major driver of ecosystem change". In: *Nature* 486.7401, pp. 105–108.

Jiang, L. & P. J. Morin (2007). "Temperature fluctuation facilitates coexistence of competing species in experimental microbial communities". In: *J. Anim. Ecol.* 76.4, pp. 660–668.

Johansson, J. (2008). "Evolutionary responses to environmental changes: How does competition affect adaptation?" In: *Evolution* 62.2, pp. 421–435.

Kasada, M., M. Yamamichi & T. Yoshida (2014). "Form of an evolutionary tradeoff affects eco-evolutionary dynamics in a predator–prey system". In: *Proc. Natl. Acad. Sci. U.S.A.* 111.45, pp. 16035–16040.

Koch, H., J. Frickel, M. Valiadi & L. Becks (2014). "Why rapid, adaptive evolution matters for community dynamics". In: *Ecology* 2, p. 17.

Lande, R. (1979). "Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry". In: *Evolution*, pp. 402–416.

Lawrence, D., F. Fiegna, V. Behrends, J. G. Bundy, A. B. Phillimore, T. Bell, et al. (2012). "Species interactions alter evolutionary responses to a novel environment". In: *PLoS biology* 10.5, e1001330.

Little, A. G. & F. Seebacher (2021). "Physiological Performance Curves: When Are They Useful?" In: *Frontiers in Physiology* 12.

Liu, M., D. R. Rubenstein, S. A. Cheong & S.-F. Shen (2021). "Antagonistic effects of long- and short-term environmental variation on species coexistence". In: *Science* 288.1958, p. 20211491.

Loeuille, N. (2019). "Eco-evolutionary dynamics in a disturbed world: implications for the maintenance of ecological networks". In: *F1000Research* 8, F1000–Faculty.

Low-Décarie, E., M. Kolber, P. Homme, A. Lofano, A. Dumbrell, A. Gonzalez, et al. (2015). "Community rescue in experimental metacommunities". In: *Proc. Natl. Acad. Sci. U.S.A.* 112.46, pp. 14307–14312.

MacArthur, R. H. & E. O. Wilson (1967). *The theory of island biogeography*. Princeton University Press.

Mühlbauer, L. K., M. Schulze, W. S. Harpole & A. T. Clark (2020). "gauseR: Simple methods for fitting Lotka-Volterra models describing Gause's "Struggle for Existence"". In: *Ecology* 10.23, pp. 13275–13283.

Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier & N. Loeuille (2012). "Eco-evolutionary responses of biodiversity to climate change". In: *Nature* 2.10, pp. 747–751.

Oliveira, B. F., F. C. Moore & X. Dong (2022). "Biodiversity mediates ecosystem sensitivity to climate variability". In: *Communications Biology* 5.1, p. 628.

Pantel, J. H., C. Duvivier & L. D. Meester (2015). "Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms". In: *Ecol. Lett.* 18.10, pp. 992–1000.

Parvinen, K. (2005). "Evolutionary suicide". In: *Acta biotheoretica* 53.3, pp. 241–264.

Pascual, L. S., C. Segarra-Medina, A. Gómez-Cadenas, M. F. López-Climent, V. Vives-Peris & S. I. Zandalinas (2022). "Climate change-associated multifactorial stress combination: A present challenge for our ecosystems". In: *Journal of Plant Physiology* 276, p. 153764.

Pelletier, F., D. Garant & A. Hendry (2009). "Eco-evolutionary dynamics". In: *Philos. Trans. R. Soc. B Biol. Sci.* 364.1523, pp. 1483–1489.

Post, D. M. & E. P. Palkovacs (2009). "Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play". In: *Philos. Trans. R. Soc. B Biol. Sci.* 364.1523, pp. 1629–1640.

Ramsayer, J., O. Kaltz & M. E. Hochberg (2013). "Evolutionary rescue in populations of Pseudomonas fluorescens across an antibiotic gradient". In: *Evol. Appl.* 6.4, pp. 608–616.

Réveillon, T. & L. Becks (2024). "Trade-offs between defense and competitive traits in a planktonic predator–prey system". In: *Ecology* 105.12, e4456.

Sandifer, P. A., A. E. Sutton-Grier & B. P. Ward (2015). "Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation". In: *Ecosystem services* 12, pp. 1–15.

Schluter, D. (1996). "Adaptive radiation along genetic lines of least resistance". In: *Evolution* 50.5, pp. 1766–1774.

Schoener, T. W. (2011). "The newest synthesis: understanding the interplay of evolutionary and ecological dynamics". In: *Science* 331.6016, pp. 426–429.

Shang, Y., M. Kasada & M. Kondoh (2024). “Rescue or murder? The effect of prey adaptation to the predator subjected to fisheries”. In: *Ecology* 14.12, e70336.

Stearns, S. C. (1989). “Trade-offs in life-history evolution”. In: *Ecology* 3.3, pp. 259–268.

Stoks, R., L. Govaert, K. Pauwels, B. Jansen & L. De Meester (2016). “Resurrecting complexity: the interplay of plasticity and rapid evolution in the multiple trait response to strong changes in predation pressure in the water flea Daphnia magna”. In: *Ecol. Lett.* 19.2, pp. 180–190.

Van Velzen, E. (2023). “High importance of indirect evolutionary rescue in a small food web”. In: *Ecol. Lett.* 26.12, pp. 2110–2121.

Vander Wal, E., D. Garant, M. Festa-Bianchet & F. Pelletier (2013). “Evolutionary rescue in vertebrates: evidence, applications and uncertainty”. In: *Philos. Trans. R. Soc. B Biol. Sci.* 368.1610, p. 20120090.

Vanvelk, H., L. Govaert, E. M. van den Berg & L. De Meester (2024). “Eco-Evolutionary Interactions With Multiple Evolving Species Reveal Both Antagonistic and Additive Effects”. In: *Ecol. Lett.* 27.11.

Wang, S., R. Agarwal, K. A. Segraves & D. M. Althoff (2025). “Trait and plasticity evolution under competition and mutualism in evolving pairwise yeast communities”. In: *PLOS ONE* 20.1, e0311674.

Weinbach, A., N. Loeuille & R. P. Rohr (2022). “Eco-evolutionary dynamics further weakens mutualistic interaction and coexistence under population decline”. In: *Ecology* 36.3, pp. 373–387.

Weyerer, F., A. Weinbach, C. Zarfl & K. T. Allhoff (2023). “Eco-evolutionary dynamics in two-species mutualistic systems: One-sided population decline triggers joint interaction disinvestment”. In: *Ecology* 37.6, pp. 981–999.

Yacine, Y., K. T. Allhoff, A. Weinbach & N. Loeuille (2021). “Collapse and rescue of evolutionary food webs under global warming”. In: *Ecology* 90.3, pp. 710–722.

Yamamichi, M. & B. E. Miner (2015). “Indirect evolutionary rescue: prey adapts, predator avoids extinction”. In: *Evol. Appl.* 8.8, pp. 787–795.

Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann & N. G. Hairston Jr (2003). “Rapid evolution drives ecological dynamics in a predator–prey system”. In: *Nature* 424.6946, pp. 303–306.

Tables

Table 1: Summary of state variables and model parameters, their description, units and (initial) values. We indicate species-specific parameters with subscripts X and Y, respectively. 33

Table 1: Summary of state variables and model parameters, their description, units and (initial) values. We indicate species-specific parameters with subscripts X and Y, respectively.

Symbol	Name	Unit	Value
$x_i(t), y_j(t)$	population density of type i of species X, type j of species Y at time t	L^{-1}	0.05
$c(t)$	state of the environment at time t	[1]	1
$c_{X,i}, c_{Y,j}$	physiological optimum trait	[1]	1
$K_{X,i}, K_{Y,j}$ ($K_{\max}$)	competitive tolerance trait (maximum)	L^{-1}	0.8 (1)
$r_{X,i}, r_{Y,j}$ ($r_{\max}$)	intrinsic growth rate (maximum)	t^{-1}	determined by Equation (3) (1)
a_{XY} (a_{YX})	competitive effect of Y on X (X on Y)	[1]	0.8
p	initial mutant density / extinction threshold	L^{-1}	$1 \cdot 10^{-3}$
$\sigma_{c_X}, \sigma_{c_Y}$	mutation spread of physiological optimum	[1]	$[0, \sigma_{\max}]$
$\sigma_{K_X}, \sigma_{K_Y}$	mutation spread of competitive tolerance	[1]	$[0, \sigma_{\max}]$
$\sigma_{\max}$	maximum mutation spread	[1]	0.03
$\sigma_{w,X}, \sigma_{w,Y}$	spread of physiological performance	gL^{-1}	0.85
μ_X, μ_Y	per-capita mutation rate	t^{-1}	$5 \cdot 10^{-4}$
s_{eco} (s_{evo})	ecological (evolutionary) trade-off shape	[1]	$\{0.5, 1, 2\}$
τ	experiencing external disturbance rate of abiotic environmental change	t^{-1}	$2 \cdot 10^{-6}$

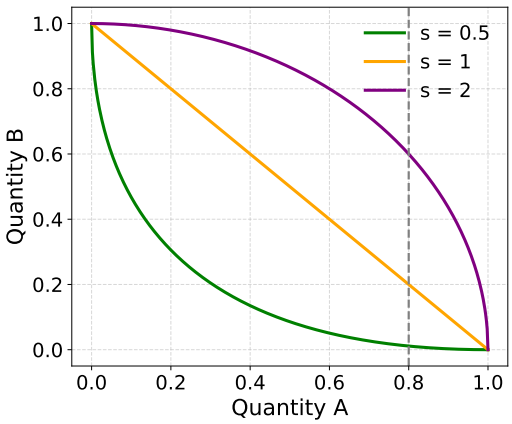
Figures

Figure 1: Visualization of the trade-off functions from Equations (3) and (4). For the ecological trade-off, quantity A denotes $K/K_{\max}$ and quantity B denotes $r/r_{\max}$. For the evolutionary trade-off, quantity A denotes $\sigma_c/\sigma_{c_{\max}}$ and quantity B denotes $\sigma_K/\sigma_{K_{\max}}$. The dashed line indicates the different initial values of $r/r_{\max}$ for the fixed initial value $K/K_{\max} = 0.8$ depending on the ecological trade-off shape. 36

Figure 2: Net effect of evolution and corresponding eco-evolutionary feedback on the extinction time of a single population. The curves represent the mean delay of extinction ($\Delta t_X = t_X - t_{X_R}$) as a function of mutation spread σ_{c_X} over 10 simulation runs; the shaded areas represent 95% confidence intervals. The dark solid curves represent the extinction delay for the 1-trait evolution scenario. The lighter dashed curves represent the extinction delay for the 2-trait evolution scenario. Red vertical lines indicate simulation scenarios displayed in Figure 3. Unless otherwise noted, parameter values are as in Table 1. 37

Figure 3: Selected simulations under low $(\sigma_{c_X}/\sigma_{\max}) = 0.15$ (a, c) and high $(\sigma_{c_X}/\sigma_{\max}) = 0.65$ (b, d) mutation spread of the physiological optimum trait, with linear-linear (a, b), convex-linear (c), and linear-convex (d) ecological-evolutionary trade-off shapes. In each of these four subfigures, panels show population density (top panel), competitive tolerance (red line) and growth rate (blue line) (middle panel), and environmental state (yellow) and physiological optimum (black line) (bottom panel). Solid (dashed) lines: 1-trait (2-trait) evolution; gray colors: ecological reference. Solid (dashed) horizontal arrows: extinction time delays under 1-trait (2-trait) evolution relative to the reference. 38

Figure 4: Extinction delay Δt_X (i.e., difference in extinction time between evolutionary and ecological scenarios) for species X in the 1-trait (a) and 2-trait (b) evolution scenario, and variability thereof over 10 replicates (c, d). In (a) and (c), given that only one trait evolves, no evolutionary trade-off exists, so only one heatmap is shown for each ecological trade-off shape. Colors represent (a, b) mean or (c, d) standard deviation of Δt_X across 10 replicated simulation runs. Positive Δt_X values (blue colors in a, b) indicate that evolution delays the extinction of species X, whereas negative values (red colors in a, b) indicate that evolution accelerates extinction. 39



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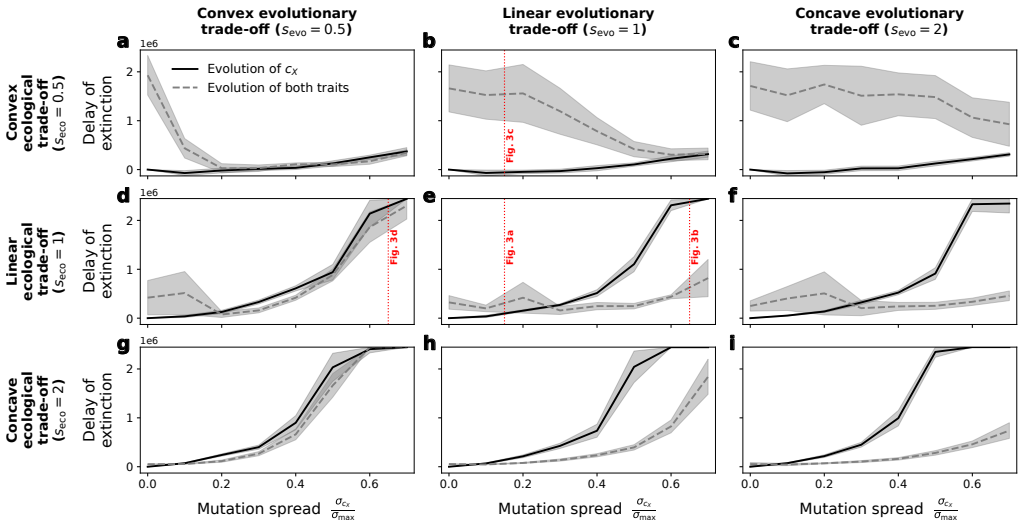

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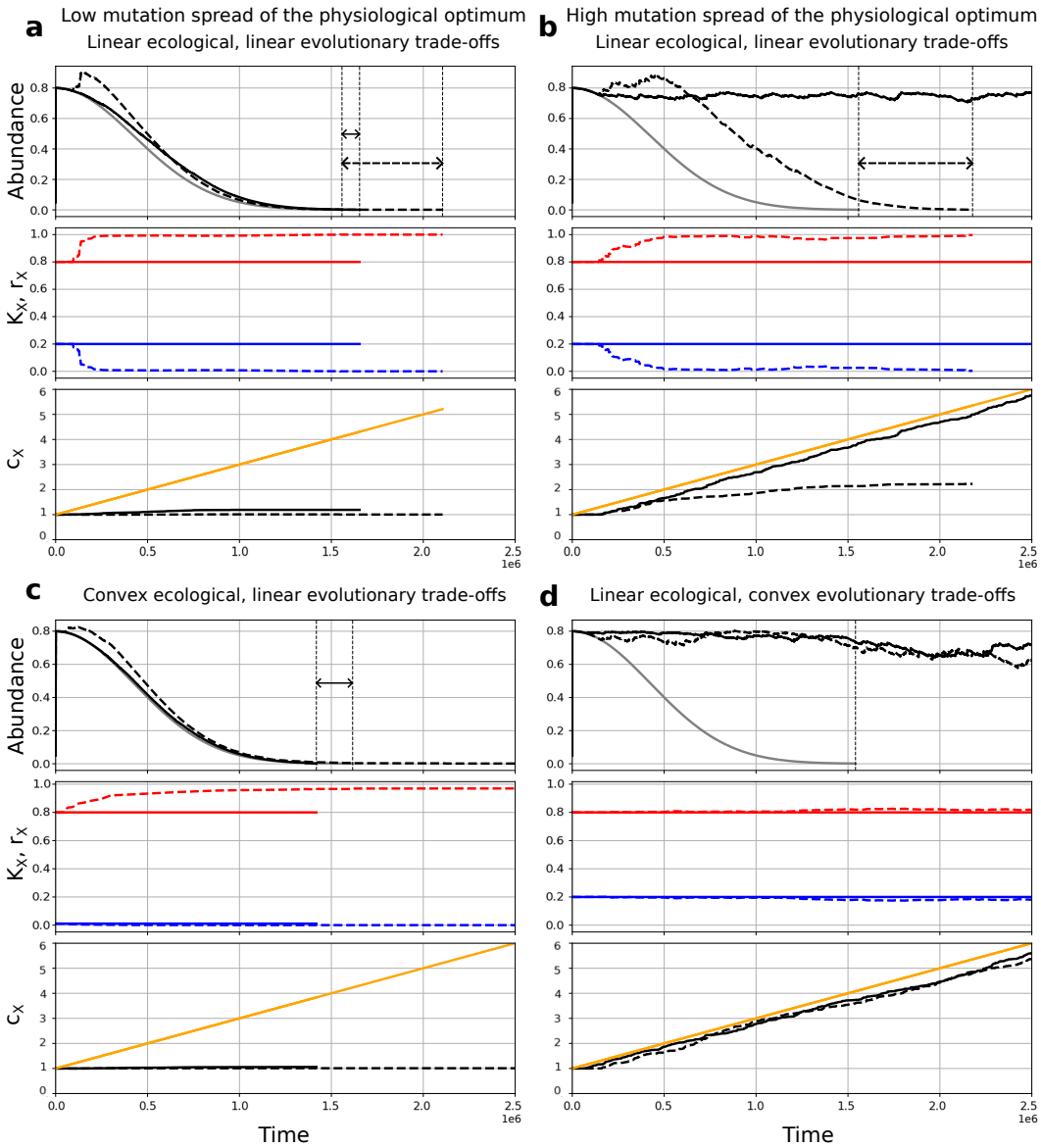

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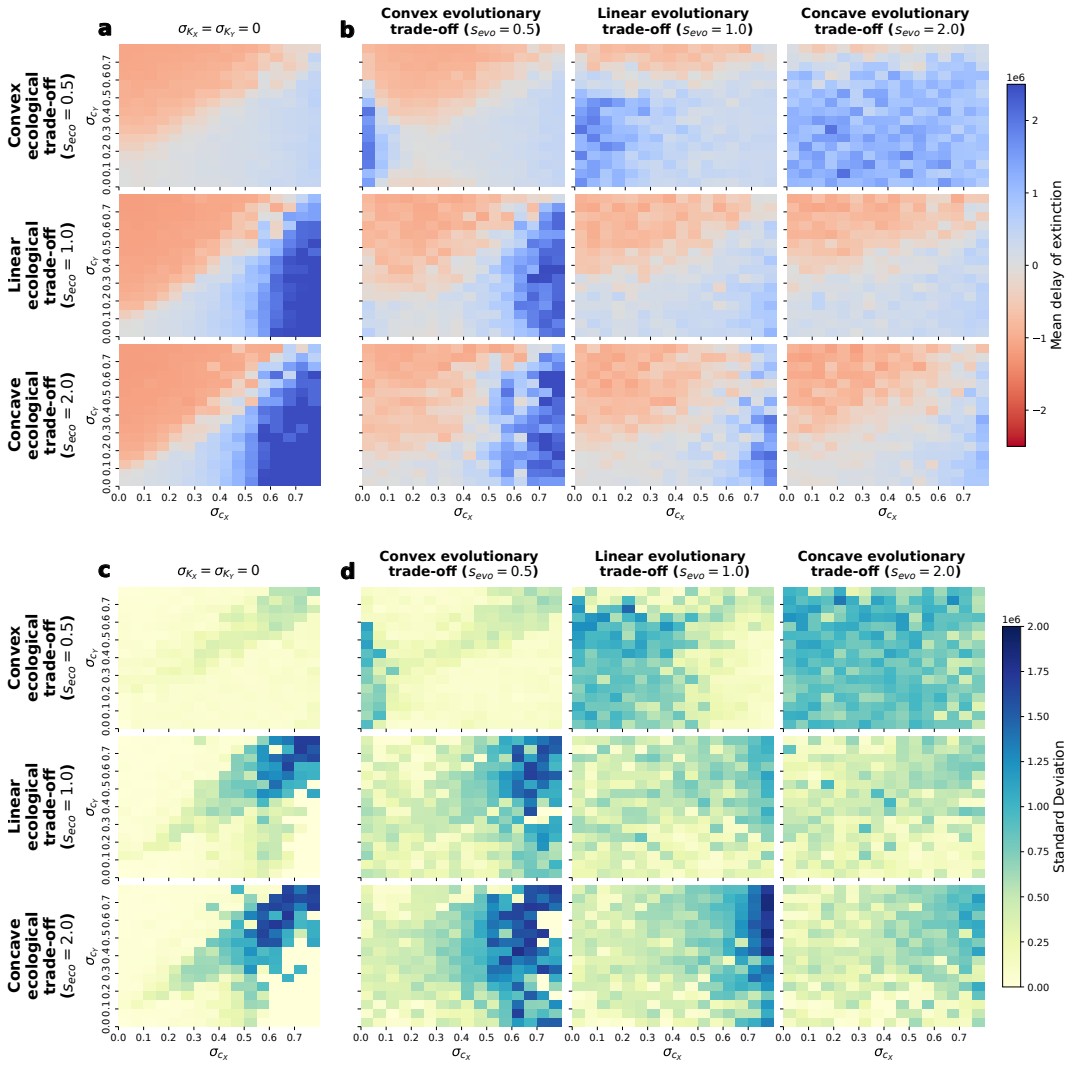

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