Rate-induced collapse in evolutionary systems

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Abstract

Recent work has highlighted the possibility of "rate-induced tipping", in which a system undergoes an abrupt transition when a perturbation exceeds a critical rate of change. Here we argue that this is widely applicable to evolutionary systems: collapse, or extinction, may occur when external changes occur too fast for evolutionary adaptation to keep up. To bridge existing theoretical frameworks, we develop a minimal evolutionary-ecological model showing that rate-induced extinction and the established notion of "evolutionary rescue" are fundamentally two sides of the same coin: the failure of one implies the other, and vice versa. We compare the minimal model's behavior with that of a more complex model in which the large-scale dynamics emerge from the interactions of many individual agents; in both cases there is a well-defined threshold rate to induce extinction, and a consistent scaling law for that rate as a function of timescale. Due to the fundamental nature of the underlying mechanism, we suggest that a vast range of evolutionary systems should in principle be susceptible to rate-induced collapse. This would include ecosystems on all scales as well as human societies; further research is warranted.

1 Introduction

A wide range of systems — ecological, environmental, and societal — can undergo abrupt transitions when small changes exceed a "tipping point" threshold [Scheffer et al., 2001, Folke et al., 2004, Lenton, 2013, Scheffer, 2020]. The classical view is to consider such tipping point thresholds as fixed (e.g. May [1977], Ashwin et al. [2012]), but recent work has considered "rate-induced tipping", in which the transition is

initiated when a forcing exceeds a critical rate of change [Wieczorek et al., 2010]. Rate-induced tipping has been identified both in models of ecological systems [Scheffer et al., 2008, Vanselow et al., 2019] and of climate [Ashwin et al., 2012, Arnscheidt and Rothman, 2020, Lohmann and Ditlevsen, 2021].

In evolutionary systems, adaptation through natural selection can promote the survival of populations in the face of environmental change. This has long been recognized in the context of individual species [Maynard Smith, 1989]. When evolution allows a species to adapt to conditions that otherwise would have driven it extinct, this is referred to as evolutionary rescue; it has been studied widely in the contexts of conservation biology and medicine [Gonzalez et al., 2013, Carlson et al., 2014, Bell, 2017]. Evolutionary rescue has been demonstrated in laboratory experiments with microbes [Bell and Gonzalez, 2009], and also occurs in nature: antibiotic resistance is one example [Bell, 2017].

On a vastly larger scale, similar ideas have been discussed in the context of mass extinctions. During each of the "Big Five" mass extinctions of the Phanerozoic (542 Ma-present), more than 75% of species were lost, with the end-Permian extinction eliminating as many as 94% [Barnosky et al., 2011]; these are paradigmatic examples of abrupt global state transitions [Barnosky et al., 2012]. Each was accompanied by dramatic environmental change, and it was suggested early on that they were triggered when such change occurred too quickly for evolutionary adaptation (now interpreted on a global scale) to keep up [Newell, 1963]. Recent work has indeed demonstrated a connection between mass extinctions and the exceedance of a critical rate of global carbon cycle change, supporting this hypothesis [Rothman, 2017]. Understanding the detailed conditions under which mass extinctions (or more generally, global biosphere state shifts) occur is especially timely in light of the accelerating modern-day global species losses due to human actions [Ceballos et al., 2015].

In this paper, we synthesize thoughts from across these disparate domains in the following way. We first present a minimal model of a single evolving population, which demonstrates the fundamental relationship between rate-induced tipping towards extinction and the established concept of evolutionary rescue. We identify a well-defined threshold for rate-induced extinction to occur, and obtain a scaling law for the critical rate to induce extinction as a function of timescale; the latter is consistent with prior work in the study of mass extinctions. Next, we test the robustness of these observations in a more complex model in which the interactions of individual reproducing agents are modeled explicitly — finding near-identical behavior. Motivated by these results, we suggest that rate-induced collapse may be a fundamental feature

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of a vast range of evolutionary systems, including ecosystems on all scales as well as human societies.

2   Minimal model of evolutionary rescue and rate-induced extinction

Our first course of action is to outline the fundamental connection between evolutionary rescue and rate-induced tipping towards extinction.

A number of previous studies have considered how evolution can counteract deleterious environmental change [Pease et al., 1989, Lynch and Lande, 1993, Gomulkiewicz and Holt, 1995, Lande and Shannon, 1996, Orr and Unckless, 2008], yet the body of work on rate-induced tipping points has so far developed independently. An exception is the recent work by Vanselow et al. [2021], which shows that rate-induced collapse of a prey population occurring purely due to the ecological dynamics (i.e. even with no evolution) can be indirectly prevented through the evolutionary adaptation of a predator population.

Our focus here is more general. We seek to highlight that *all* instances of unsuccessful evolutionary rescue fundamentally constitute rate-induced tipping (no rate-induced ecological tipping points are necessary), and to derive a model from established assumptions of quantitative genetics that displays this as transparently as possible.

2.1   Model specification

We consider a single population of size n with a single evolving trait whose mean value is x. The population dynamics are given by

$$\frac{dn}{dt} = nr(n, x, t), \tag{1}$$

where r is the population's mean Malthusian fitness (i.e. growth rate). Following standard theory, the mean trait value x evolves according to hill-climbing on the fitness landscape described by r [Lande, 1976]:

$$\frac{dx}{dt} = k\frac{dr(n, x, t)}{dx}H(n). \tag{2}$$

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Here, k is the additive genetic variance; for our purposes, it describes the rate at which evolutionary adaptation can occur, and thus the timescale separation between ecological and evolutionary processes. Since an extinct species cannot evolve, we additionally use a step function $H(n)$ to ensure that there can be no evolution when n is close to 0. We set $H(n)$ to 1 for all $n > \epsilon$ (with $0 < \epsilon \ll 1$), and 0 otherwise; this avoids issues due to $n = 0$ only being approached in the limit $t \to \infty$.

The detailed behavior of the system depends on the fitness function r. We assume that it has a maximum at some value x^*, which we will later vary in time to mimic the effects of environmental change. Following, for example, Lande and Shannon [1996], it is reasonable to approximate the fitness maximum as quadratic and to include density-dependent effects through an additive term $f(n)$:

$$r(n, x, t) = r^* - a(x - x^*)^2 + f(n), \tag{3}$$

where r^* sets the maximum growth rate and a determines how fast fitness declines with distance from x^*. This immediately yields

$$\frac{dx}{dt} = -2ka(x - x^*)H(n), \tag{4}$$

i.e. x decays exponentially towards the optimum value x^*, unless the population is extinct ($n = 0$).

The density dependence $f(n)$ needs to obey two real-world constraints. First, it needs to become negative for large enough n; otherwise, the population could grow indefinitely as long as x permitted it. In other words, $f(n)$ needs to provide an effective carrying capacity: i.e. a stable equilibrium at high n. Second, real populations typically exhibit minimum viable population sizes, and indeed these are required for there to be well-defined extinction "events". This suggests the incorporation of a strong Allee effect: an unstable equilibrium at low n, below which the population collapses (see Stephens and Sutherland [1999] for a review and further discussion). The inclusion of a minimal viable population size is also consistent with previous work on evolutionary rescue [Gomulkiewicz and Holt, 1995].

For ease of analysis, we parametrize all of these effects using the simple quadratic form

$$f(n) = -b + cn - n^2. \tag{5}$$

Here, $b, c > 0$, and $f(n)$ also needs to be negative to avoid effective growth rates larger than r^*. This

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finally yields the population dynamics equation

$$\frac{dn}{dt} = n(r^* - a(x - x^*)^2 - b + cn - n^2). \tag{6}$$

We use the following parameter values: $r^* = 1, a = 1, b = 2, c = 3, x^* = 5, k = 0.001, \epsilon = 10^{-5}$. We make the standard assumption that evolutionary processes occur on a much slower timescale than ecological processes [Roughgarden, 1983, Dieckmann and Law, 1996]. All units, including those of our population n and trait x, are arbitrary. As long as our parameter choices indeed lead to the above timescale separation, our qualitative results will be largely independent of the specific values.

2.2   Initial analysis

First, it is instructive to estimate the ecological and evolutionary timescales. From (4), we have an evolutionary timescale $\tau_{\text{ev}} \simeq 1/(2ka)$, i.e. 500 for our default parameter values. Estimating the ecological timescale is more challenging, but one simple option is to define it as the timescale on which the population goes extinct if $x = x^*$ and n is small. From 6, we have

$$\frac{dn}{dt} = n(r^* - b), \tag{7}$$

and so n collapses with a characteristic timescale of $\tau_{\text{ec}} = 1/(b - r^*)$, which is 1 for our default parameter values. We see that ecological and evolutionary timescales are indeed separated by multiple orders of magnitude.

This is an example of a slow-fast dynamical system: the population n adjusts on the faster ecological timescale, while the trait value x adjusts on the slower evolutionary timescale. The dynamics of the system can therefore be well understood by considering the nullclines (where dx/dt and dn/dt equal zero). These are straightforward to solve for explicitly. From (4), $dx/dt = 0$ either when $x = x^*$ or $n < \epsilon$. From (6), $dn/dt = 0$ when $n = 0$ or when

$$n^2 - cn + (b - r^* + a(x - x^*)^2) = 0, \tag{8}$$

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i.e.

$$x = x^* \pm \sqrt{\frac{1}{a}\left(-n^2 + cn - b + r^*\right)}. \tag{9}$$

These nullclines are plotted in Figure 1. Equilibrium states, or fixed points, occur when they intersect: there is one stable fixed point at $x = x^*$ and high n, an unstable saddle point at $x = x^*$ and low n, and a line of stable fixed points at $n = 0$. Because n is driven by the much faster ecological processes, the population rapidly adjusts towards a $dn/dt = 0$ nullcline. This either means reaching the line of fixed points at $n = 0$ (in which case the population goes extinct) or the $dn/dt = 0$ curve at nonzero n, in which case evolutionary adaptation slowly brings the system towards the stable fixed point. The slow dynamics of the system take place very close to these curves. Formally, the dn/dt nullcline defines a "critical manifold" on which all dynamics take place in the limit $k = 0$, and for small enough $k > 0$ the dynamics mostly take place on a very nearby "slow manifold" [Szmolyan and Wechselberger, 2001]. To emphasize their real-world meaning, we refer to the different parts of the $dn/dt = 0$ nullcline separately as the extinct and extant critical manifolds, respectively.
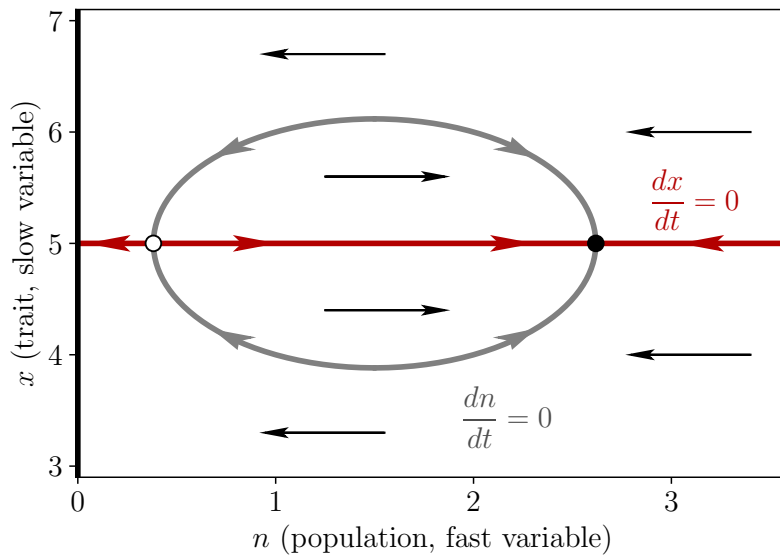

Figure 1: Dynamics of the model (note units of x and n are arbitrary). The black dot and black line at $n = 0$ denote stable fixed points (equilibria), while the white dot denotes an unstable saddle point. The timescale separation means that the system equilibrates rapidly towards the $dn/dt = 0$ nullcline (shown by black arrows), and only then adjusts slowly towards the stable fixed point (if the population is not already extinct).

2.3 Evolutionary rescue and rate-induced extinction

Perturbations to the system can lead to extinction; Figure 2 shows how. Consider a scenario in which the population was initially at the stable high-n equilibrium, with the trait x at its optimum value x^*, and x^* is then instantaneously increased. Driven by the ecological dynamics, the population size n will rapidly adjust towards $dn/dt = 0$. However, there are two possible outcomes. If x is not too far from x^*, the system will come close to the extant critical manifold and survive long-term — because adaptation saves the population from extinction, this is precisely evolutionary rescue. If x is far enough from x^*, it passes below the local minimum (fold) of the extant critical manifold and becomes extinct. Separating these two cases is a set of trajectories that stay close to the unstable branch of the extant critical manifold, referred to as 'canards' [Benoît et al., 1981, Wieczorek et al., 2010]; they define the (quasi) threshold beyond which a perturbation will lead to extinction.
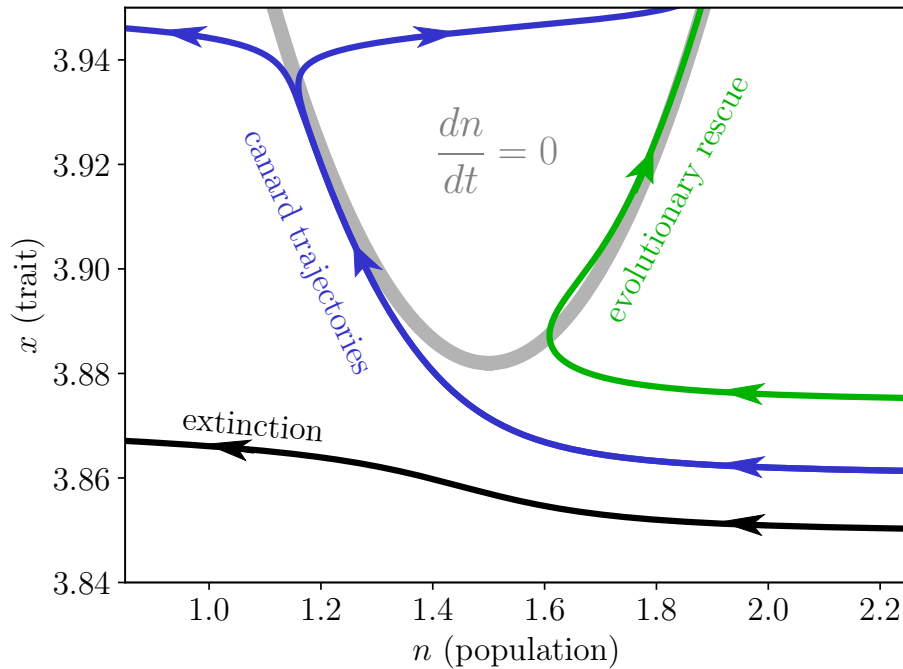
Figure 2: Perturbations to the system can lead to extinction. We assume that the system was initially at the stable high-n equilibrium, and the optimal trait x^* is instantaneously increased. The system will then rapidly adjust towards the neighborhood of $dn/dt = 0$ (the critical manifold). If x is not too far from x^* (green trajectory), the system comes close to the extant critical manifold (gray), and evolutionary rescue occurs: the system recovers back to the high-n stable state. If x is far enough from x^*, the trajectory passes below the local minimum (fold) in the extant critical manifold, and extinction occurs instead. Separating these two cases is a set of 'canard trajectories' that stay close to the unstable branch of the extant critical manifold, towards the low-n saddle point in Figure 1; these can go either towards extinction or recovery, as shown.

It is worth noting that the high-n equilibrium does not need to lose its stability for extinction to occur: in other words, the collapse is not a consequence of a bifurcation. This distinction is significant because tipping points have long been primarily associated with bifurcations (e.g. Scheffer et al. [2001]), and because bifurcations imply that tipping occurs when forcings exceed fixed thresholds. Rather, this collapse is an instance of rate-induced tipping [Wieczorek et al., 2010, Ashwin et al., 2012], where a transition occurs when the system is forced beyond a critical rate of change. The dynamical mechanism of a threshold set of canard trajectories (as demonstrated in Figure 2) is exactly that given by Wieczorek et al. [2010]; the generality of our model suggests that this pathway to rate-induced tipping may be widely applicable across evolutionary systems.

The exquisite sensitivity to the rate of change of the forcing is further demonstrated in Figure 3. Here,

we ramp the optimal trait value x^* linearly (i.e. $dx^*/dt = $ const.) from 5 to 8 over two slightly different timescales: 1200 and 1000 timesteps, respectively. In the slower case, the population is able to recover and evolutionary rescue occurs. In the faster case, the population is driven to extinction. Following previous work (e.g. Wieczorek et al. [2010], Ashwin et al. [2012], Arnscheidt and Rothman [2020]), it is instructive to consider the trajectories in the three-dimensional space of the two variables (n, x) and the time-varying forcing parameter (x^*). Now, the extant critical manifold becomes a three-dimensional surface; we reverse the x-axis to visualize the fold more clearly. For both the slower and faster perturbations the trajectories initially stay close to the extant critical manifold. However, when perturbed more quickly the system crosses the fold, and rapidly heads towards extinction.
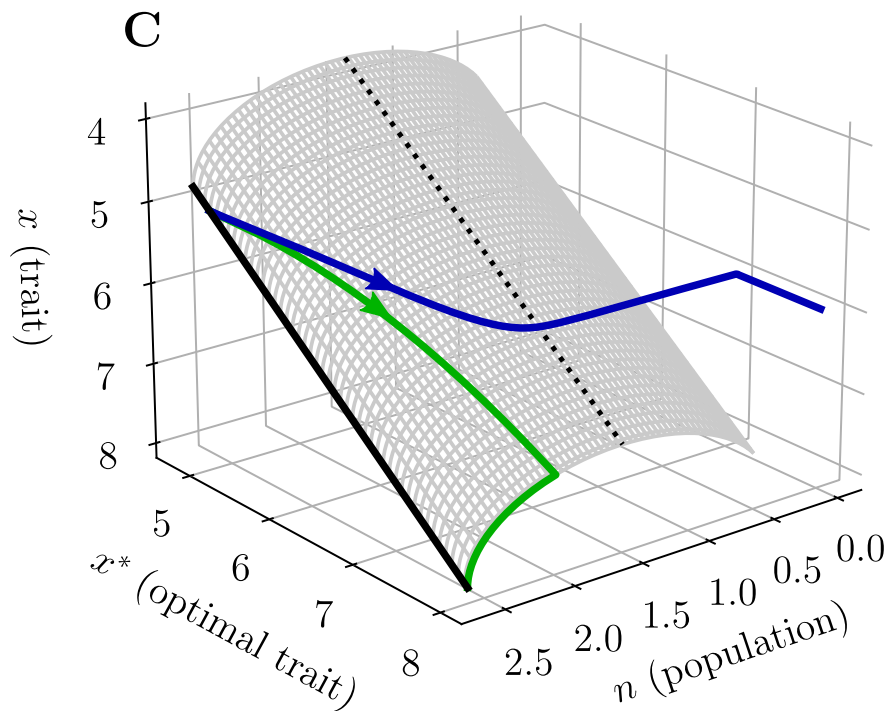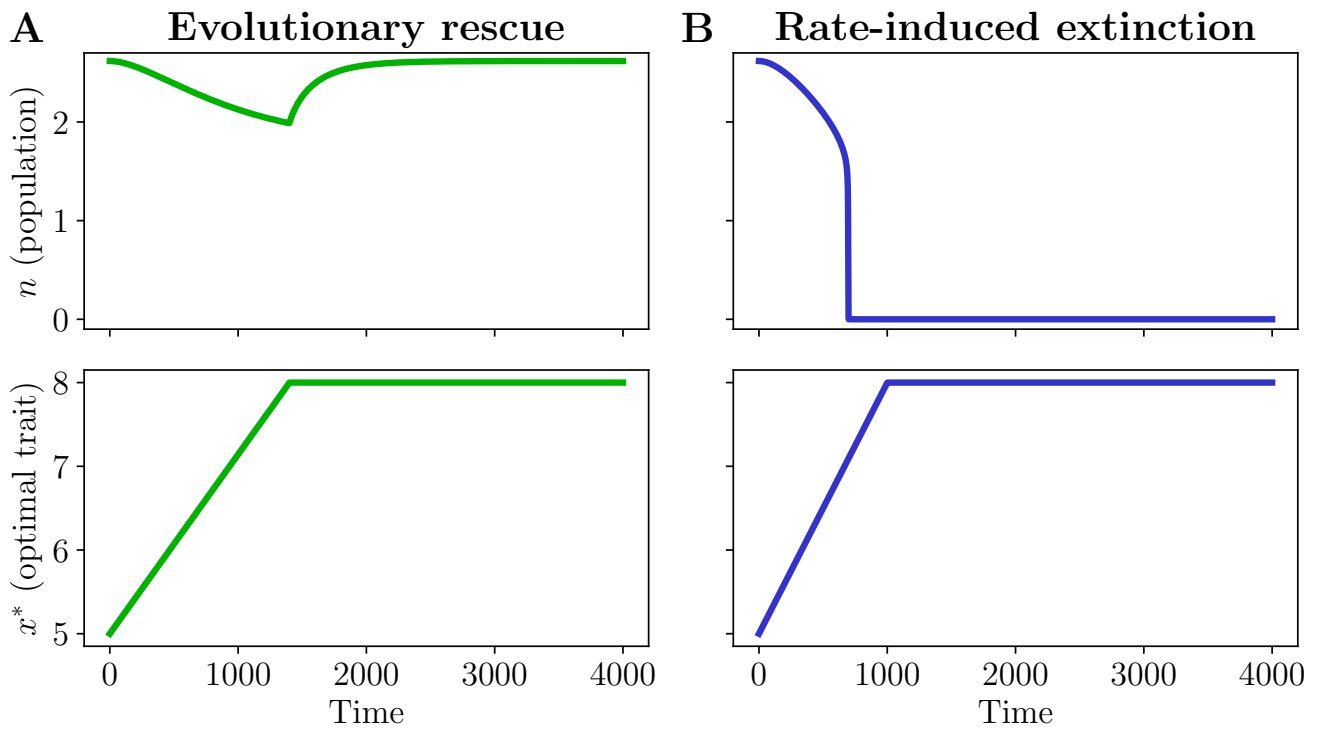
Figure 3: Evolutionary rescue and rate-induced extinction. We change the optimal trait x^* linearly over two slightly different time periods. When we do it more slowly, the system is able to recover (evolutionary rescue, A). When the system is perturbed more quickly, the system collapses (rate-induced extinction, B). We also visualize this in the space of n, x, x^*: here, the extant critical manifold becomes a surface (black line=fixed point), and the distinction between extinction and recovery is given approximately by whether or not the system passes the fold (dashed black line) in the extant critical manifold.

The connection between evolutionary rescue and rate-induced tipping is now clear. Evolutionary rescue and rate-induced tipping towards extinction essentially span the space of possible outcomes when the optimal trait x^* is perturbed (at least in this model). Unsuccessful evolutionary rescue is precisely rate-induced tipping towards extinction, and vice versa. While in special cases rate-induced tipping towards extinction can also be exhibited purely due to ecological dynamics [Vanselow et al., 2019], here we use "rate-induced extinction" to refer specifically to the scenario in which the relevant damping force (i.e. the mechanism combating the deleterious effects of perturbations) is evolutionary adaptation. Since evolutionary adaptation is ubiquituous across real-world systems, it seems that rate-induced extinction should also be common; the rest of the paper is devoted to addressing this.

Before we move on, it is finally worth assessing how the critical rate of change to induce extinction in the model changes with the timescale, τ; this is shown in Figure 4. We calculate this rate numerically by repeatedly initializing the system at the high-n equilibrium, linearly ramping the optimum trait value x^* to a new value across a time interval τ, and waiting to see whether extinction occurs. The vertical axis (rate of change of forcing) describes how quickly x^* changes; the ecological timescale τ_{ec} and the evolutionary timescale τ_{ev} obtained above are also shown. We find that the critical rate scales approximately as τ^{-1} until τ_{ev} and is constant at longer timescales. This can be understood as follows: only evolutionary adaptation can damp the negative outcomes of changing x^*, and so on timescales too short for it to play a role there is an effective "critical amount" of change to induce extinction. Similar logic has been considered in the context of past mass extinctions [Rothman, 2017, 2019, Arnscheidt and Rothman, 2022]; if indeed valid in this context, one significance of the scaling relationship is that it could allow a rigorous comparison of the fast anthropogenic Earth system perturbation to the slow perturbations of the deep past.
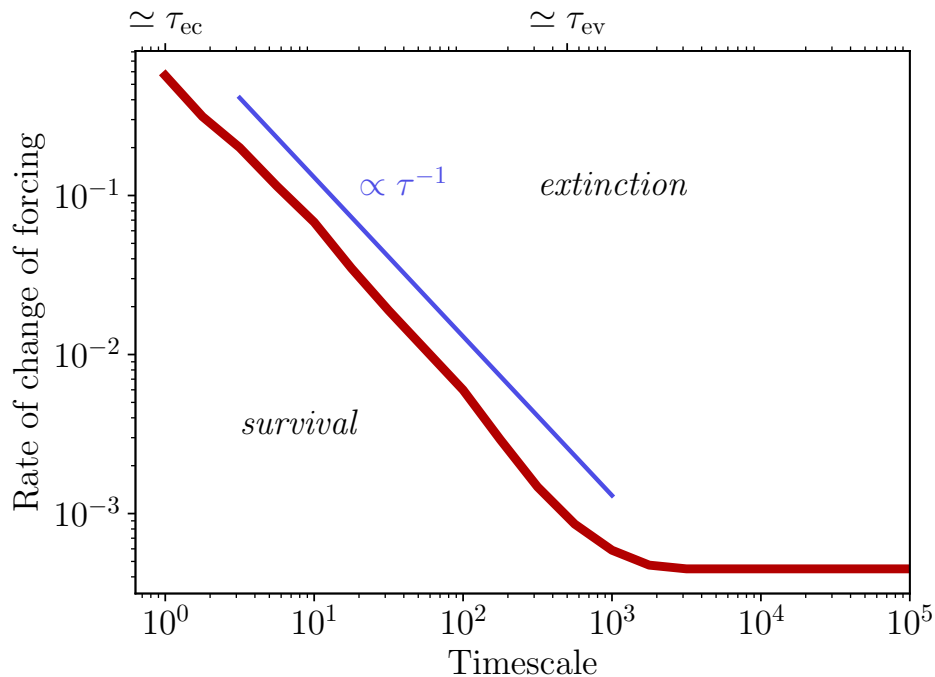
Figure 4: The scaling of the critical rate with time, in the minimal differential-equation model. It scales with τ^{-1} below the evolutionary timescale τ_{ev}, and is constant on longer timescales. Far enough below evolutionary timescales, adaptation is negligible, and so there is an effective critical amount of change in x^* for which extinction occurs.

3   Rate-induced extinction in a model of individual interacting agents

The minimal model is an extremely simplified version of reality, and thus has a number of weaknesses. First, the population dynamics and evolutionary dynamics are described macroscopically by single variables (n and x), making no attempt to represent heterogeneous individual agents. Second, evolutionary hill-climbing is written in explicitly (4), assuming that evolution will always act to increase population mean fitness. This is not necessarily true in nature: the phenomenon of "evolutionary suicide", in which rare mutants drive an entire population to extinction, is an extreme counterexample [Matsuda and Abrams, 1994, Parvinen, 2005]. Third, the model assumes that environmental change is entirely external, while real-world dynamics are coevolutionary: organisms also modify their environment as they evolve (e.g. Dieckmann and Law [1996]). Finally, the model is purely deterministic, while the real world contains unavoidable elements of randomness. It is not obvious that rate-induced extinction, especially with a well-defined threshold as shown above, would still occur when all of these factors are considered; the purpose

of this section is to show that it still can.

3.1 Model specification

We consider a simple many-agent model of an evolving population based on that of Ferriere and Legendre [2013], which is itself a reduction of the model of Ferriere et al. [2002]. The primary goal here is not realism but rather to obtain a model that is as computationally simple as possible (allowing for many repeated simulations and robust Monte Carlo statistics) while still improving on the minimal model's weaknesses as noted above. Ferriere and Legendre [2013] demonstrate evolutionary rescue in their model by perturbing the system and alternately turning evolution on and off; here, we extend this to rate-induced extinction by explicitly perturbing the system at different rates, and characterizing the threshold at which extinction occurs.

The model consists of N interacting agents, each of which has a trait x_i that reflects its investment in some public good that benefits the whole population. At each discrete timestep, each agent dies with some probability p_death and gives birth with some probability p_birth. The probability of death is

$$p_\text{death} = \beta x_i(x_i + 1) + \gamma N, \tag{10}$$

where β and γ are constants. The first term reflects the cost to each agent of investing in the public goods, and the second term reflects a carrying capacity-type constraint. Here, and similarly for p_birth, the probability is simply set equal to 0 or 1 if the expression returns a value beyond one of those limits.

At each timestep, the ith agent also has a probability of (asexually) reproducing, determined by the expression

$$p_\text{birth} = \frac{\kappa \sum_j x_j}{1 + \sum_k (\alpha(x_i - x_k) + \theta x_k)}. \tag{11}$$

κ and θ are constants, while α is a function that introduces asymmetric competition [Ferriere et al., 2002, Ferriere and Legendre, 2013]: it is defined as

$$\alpha(z) = 2h \left(1 - \frac{1}{1 + e^{-w(z+a)}} \right), \tag{12}$$

where h, w, and a are also constants. The net effect of this function is that agents who invest more in

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the public goods are better able to compete for those goods; this may be necessary for the persistence of mutually beneficial interactions [Ferriere et al., 2002]. It is worth noting that the public goods create an Allee effect [Ferriere and Legendre, 2013], similar to the assumption made in the minimal model.

Finally, whenever a new agent is born, there is a chance p_{mut} that it mutates its type. If a mutation occurs, the new type x_{child} is randomly chosen from the set $\{x_{\text{parent}} + 1, x_{\text{parent}} - 1\}$, with equal probability. We implement the model using the Julia language [Bezanson et al., 2017]. Default parameter values, largely following Ferriere and Legendre [2013], are $\beta = 10^{-5}, \gamma = 5 \times 10^{-5}, \kappa = 0.01, \theta = 0.01, h = 2.05, w = 0.4, a = -9.16, p_{\text{mut}} = 0.001$.

3.2 Initial analysis

A simple demonstration of the model, with constant default parameter values, is shown in Figure 5. The model is seeded with 1000 agents at time $t = 0$. All agents have $x_i = 100$. Over evolutionary time intervals (tens of thousands of time steps), we observe evolutionary branching [Geritz et al., 1997], leading to the diversification of the population into different "clusters" in trait space. While we are agnostic as to which degree these different branches could represent different "species", we argue that the branches can be appropriately described as "co-evolving". We eventually reach a point at which the degree of branching does not increase much more, and refer to this as a "quasi-evolutionary stable strategy" (qESS) [Maynard Smith and Price, 1973, Christensen et al., 2002]. Further tests indicate that this qESS survives at least until 5 million timesteps.
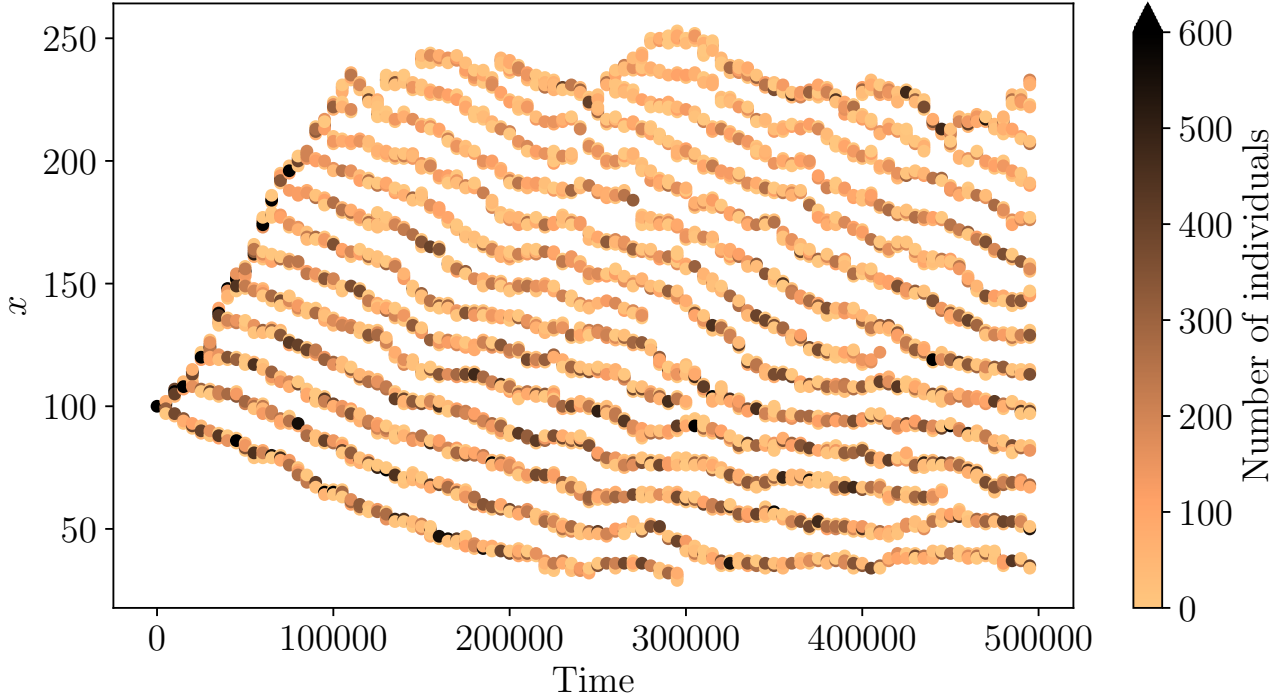
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Figure 5: Demonstration of the basic features of the many-agent model. For every type x that exists at time t, a point is plotted; its color shows how many individuals of that type currently exist. The model is seeded with 1000 agents with $x = 100$ at time $t = 0$, and over evolutionary time intervals (tens of thousands of time steps), evolutionary branching occurs. We eventually reach a quasi-evolutionary stable strategy (qESS).

It is again instructive to estimate the ecological and evolutionary timescales. The ecological timescale τ_{ec} can be straightforwardly estimated using the carrying capacity term in Eq. (10). In the slowest case (with no investment in public goods), and with no births, the number of agents would reduce by a factor of γN each timestep. Using an order-of-magnitude estimate of 1000 agents, and our default parameter settings, we obtain a characteristic timescale of $\tau_{\text{ec}} \simeq 1/\gamma N = 20$.

The evolutionary timescale τ_{ev} can be estimated by asking: how long do we have to wait for N mutations to occur? The expected number of mutations per timestep is $N p_{\text{birth}} p_{\text{mut}}$, hence the time period for N mutations is approximately $(p_{\text{birth}} p_{\text{mut}})^{-1}$. For population numbers to stay approximately constant, $p_{\text{birth}} \simeq p_{\text{death}}$. Then, if we use $p_{\text{birth}} \simeq \gamma N$ as above for our default parameter settings we have $\tau_{\text{ev}} \simeq 20000$. We note that, although these approximations are crude, the goal is only to understand the relationship between the ecological and evolutionary timescales, and for that purpose they are sufficient.

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3.3 Rate-induced extinction

The model indeed exhibits the possibility of rate-induced extinction; this is shown in Figure 6. We begin at the qESS, and then linearly ramp the parameter β (mortality cost of investing in public goods) across an identical parameter range but at different speeds. When this is done slowly, some branches of the community are able to persist. When it is done more quickly, the entire community goes extinct. This is rate-induced extinction, analogous to Figure 3. When the community persists, it does so due to evolutionary adaptation to the externally imposed changes - i.e. evolutionary rescue.
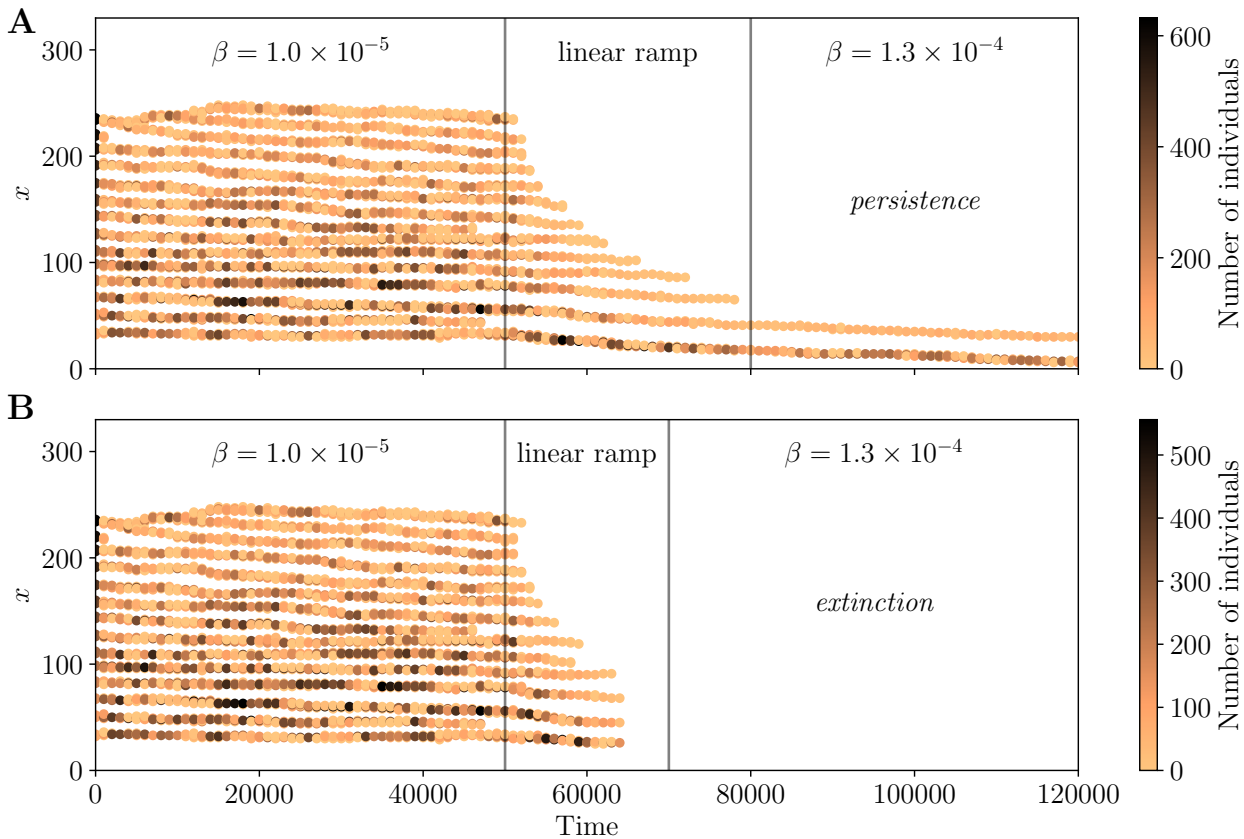

Figure 6: Rate-induced extinction and evolutionary rescue in the many-agent model. In both cases the community is subjected to a linear ramp in the parameter β (mortality cost of investing in public goods). If this is done more slowly (**A**), some branches can persist (evolutionary rescue). If it is done more quickly (**B**), the entire community goes extinct (rate-induced extinction).

We again characterize the critical rate as a function of timescale. However, since the model is inherently stochastic, we don't search for discrete thresholds such as in Figure 4. Instead, we conduct many simulations where we modify the parameter β at a range of rates across a range of timescales, and obtain

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Monte Carlo estimates of the probability for extinction for each perturbation. The results are shown in Figure 7. A robust quasi-discrete boundary emerges. Below τ_{ev}, we recover the τ^{-1} scaling observed previously. Above τ_{ev} we see a flattening slope indicating a constant critical rate, but there is also no longer such a clear boundary between low and high probabilities of extinction.
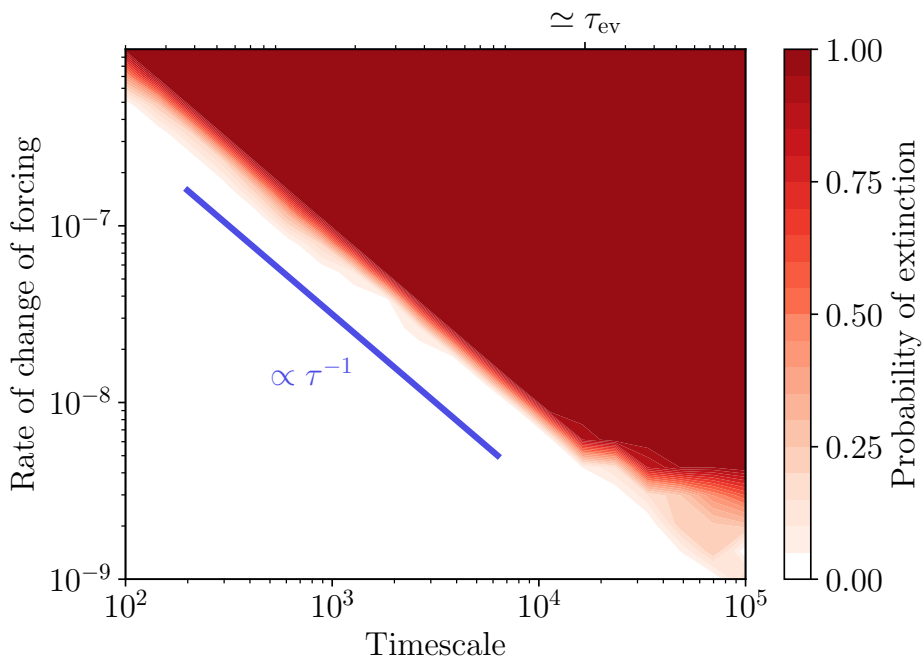

Figure 7: Critical rate of change for extinction for the many-agent model. The probability of extinction is estimated throughout rate-timescale space, using results from around 20000 simulations. Below the evolutionary timescale τ_{ev}, we recover the now familiar τ^{-1} scaling, with a discrete boundary. Above τ_{ev} we see a flattening slope indicating a constant critical rate, but there is also no longer such a clear boundary between low and high probabilities of extinction. Compare to Figure 4.

These results are broadly consistent with those from the minimal model: rate-induced extinction is possible, is indeed a counterpart to evolutionary rescue, and there is a remarkably well-defined (though partially probabilistic) threshold beyond which it is initiated. This shows that the key properties of real-world evolutionary systems listed at the start of this section (heterogeneous individual agents, emergent evolutionary dynamics, coevolution, randomness) do not invalidate the conclusions from the minimal model, at least in principle.

4   Discussion: rate-induced collapse in any evolutionary system?

Our results are likely widely applicable in the context of individual species or simple evolving communities. The minimal model is derived from very general assumptions (e.g. a moving quadratic fitness maximum), and is a plausible approximation for evolutionary-ecological dynamics of single species in a range of contexts. For such systems, there is clearly a class of environmental perturbations where the only two outcomes are evolutionary rescue or rate-induced extinction. Of course this is not all-encompassing: for example, a species can become extinct because its niche disappears and no capacity for rapid evolution could have saved it [Maynard Smith, 1989]. In the language of tipping points, this corresponds to fixed-threshold tipping towards extinction — which is most often due to bifurcations. Nevertheless, as long as evolutionary rescue is possible (and there is mounting evidence that it often is, as discussed in the introduction), rate-induced extinction is its counterpart.

We note that both models considered here contain Allee effects: for populations that are small enough, per-capita growth rate increases with population size. In the minimal model this is written in explicitly, while in the more complex model it emerges from the presence of public goods [Ferriere and Legendre, 2013]. Allee effects are likely ubiquitous in nature, because they are a fundamental consequence of co-operative interactions between organisms [Lidicker, 2010]. Nevertheless, it also seems that rate-induced extinction should still occur in the minimal model if the Allee effect were removed, because one can always force a negative growth rate by moving x^* far enough from x (Eq. 6). The role of Allee effects in rate-induced extinction is worth investigating in future work.

How far can we extend the ideas in this paper to more complex evolutionary systems? Throughout this work we have purposely referred to "evolutionary systems" more generally: we consider this category as including all systems with some element of evolution by natural selection. The fundamental mechanism at play in rate-induced extinction and evolutionary rescue is the competition between an external perturbation and the ability for evolutionary adaptation to follow a moving fitness maximum; hence, the question is to which extent evolution can be considered to behave in this way for systems more complex than individual species. This intersects with the complex debate about selection and inheritance on a larger scale than the individual [Damuth and Heisler, 1988, Odling-Smee et al., 1996, Okasha, 2001, Hastings et al., 2007, Danchin et al., 2011, Doolittle and Inkpen, 2018, Lenton et al., 2021], which we will not wade into here.

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One way to sidestep it may simply be to consider emergent large-scale feedbacks in ecosystems and the biosphere within the framework of "complex adaptive systems" [Levin, 1998]; then, when such feedbacks are stabilizing, they may play a role similar to evolutionary adaptation in the models studied in this paper. In any case, the many-agent model serves as an initial demonstration of rate-induced extinction in more complex evolutionary systems, but there is much more work to be done.

There are real-world examples of phenomena analogous to rate-induced extinction and evolutionary rescue in more complex systems. For example, in the evolutionary rescue literature, there is evidence that entire communities of microbes can undergo "community rescue" [Low-Décarie et al., 2015]. On the vastly larger scale of the global biosphere, there is empirical evidence for a critical rate of environmental change to induce mass extinction [Rothman, 2017, 2019, Arnscheidt and Rothman, 2022]. Note that in mass extinctions, unlike the models considered above, a large abrupt nonlinear destructive transition occurs but does not have to lead to the complete destruction of the system — we refer to this more generally as a "collapse".

Finally, one can make an argument for the general existence of rate-induced collapse thresholds in complex evolutionary systems through the following thought experiment. Consider the response of Earth's biosphere to two global warming events of the same magnitude but occurring on very different timescales: a fast one and a slow one. Further assume that the amount of warming is large enough to induce mass extinction on the fast timescale (as suggested for, e.g. the end-Permian extinction, by Joachimski et al. [2012]), but not enough to make the Earth permanently uninhabitable. Now, if we consider the same degree of warming over a slow timescale, it seems intuitive that we can make the timescale slow enough for no such extinction to occur. This does not necessarily mean that there is a sharp threshold for rate-induced collapse as in, e.g., Figure 7, or that every kind of perturbation will eventually lead to rate-induced collapse (as opposed to fixed-threshold collapse) but it does suggest that the general phenomenon is important.

Interestingly, this kind of logic suggests that rate-induced collapse may also be widely relevant for human societies and human civilization as a whole. While there exists debate about the most relevant processes of evolutionary selection and inheritance in human systems [Dawkins, 1976, Ehrlich and Levin, 2005, Danchin et al., 2011, Ellis, 2015], evolution certainly plays a key role. Indeed, human civilization, especially when considered in tandem with its environment, is also a complex adaptive system [Levin et al., 2013]. Paralleling the thought experiment above, one can easily envision a perturbation (such as a

certain degree of global warming) that could lead to civilizational collapse if it occurred across 2 years but not if it occurred gradually across 200. Further research into such collapse thresholds may be of substantial societal importance.

5 Conclusion

In this work, we have attempted to bring together a number of threads from different fields. Evolutionary rescue is a well-recognized phenomenon in which a population can avoid extinction due to evolutionary adaptation. Using a simple model, we have demonstrated the fundamental connection between evolutionary rescue and "rate-induced tipping". The threshold for rate-induced extinction is well-defined, and obeys a scaling law discussed in previous work on the initiation of mass extinctions. The same is true in a more complex many-agent model in which the large-scale dynamics arise from the interactions of heterogeneous individual agents. We suggest that a vast range of evolutionary systems should in principle be susceptible to rate-induced collapse, including ecosystems on all scales as well as human societies, and that this is a fascinating and timely direction for future research.

Author contributions

C.W.A: conceptualization, formal analysis, funding acquisition, investigation, methodology, software, visualization, writing — original draft and writing — review and editing; D.H.R.: conceptualization, funding acquisition, writing — review and editing.

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Data/Code accessibility

This work generated no new data. Code to replicate all of the figures in this paper is available at https://github.com/arnscheidt/rate-induced-collapse-evolution.

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