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Evolution in response to extreme events: good or bad?

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Abstract

Climate change is predicted to lead to more severe environmental perturbations, including storms and droughts, which act as strong selective agents. These extreme climatic events often act as pulse disturbances, where the new environment is transitory and populations that have evolved to the new environment may be maladapted to the historic environment when the extreme event ends. Using individual-based models and analytic approximations that fuse quantitative genetics and demography, we explore how heritability and genetic variance affect population size and extinction risk under an extreme event. When an extreme event is sufficiently short in duration, greater heritability results in a stronger evolutionary response and greater maladaptation when the event ends, slowing population recovery and increasing the probability of extinction. Alternatively, when an extreme event is sufficiently long in duration, heritability often helps a population persist, a finding consistent with the classical evolutionary rescue theory. We also find that greater phenotypic variation slows down population recovery when events are mild, but lowers extinction risk when events are severe. Our results highlight the importance of accounting for the length as well as severity of a disturbance when assessing the role of evolution on population recovery.

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Introduction

Globally, humans are causing substantial environmental perturbations, and these perturbations are likely to become more severe in the future. In particular, climate change is projected to lead to more extreme weather events, including droughts and major storms (Ummenhofer and Meehl, 2017). With more severe events comes the potential for dramatic demographic and genetic consequences.

In the process of causing mass mortality, extreme events can act as catalysts of evolutionary change. In fact, there are many examples of rapid evolution in response to extreme events (reviewed in Grant et al., 2017). Famously, Bumpus (1899) documented phenotypic differences in house sparrows that survived a strong winter storm. More recently, Donihue et al. (2018) measured lizards before and after a series of hurricanes and found evidence for selection on body size, relative limb length, and toepad size. Another example is a study of the annual plant *Brassica rapa* in response to summer drought. Post-drought seeds flowered earlier when planted alongside pre-drought seeds (Franks et al., 2007). Finally, Grant and Grant (2014) not only documented shifts in beak depth of Darwin's ground finches in response to drought, but also the reversal of that evolution and population recovery in subsequent years. We have many fewer examples like this latter case, where the recovery from an extreme event is recorded. Hence exploring what factors influence recovery patterns is best done using a modeling approach.

Short-term events such as storms, hurricanes, and droughts are pulse disturbances, defined as a relatively instantaneous alteration in the environment (Bender et al., 1984). Pulse disturbances can be contrasted to press disturbances, defined as a sustained alteration. While, the dichotomy between pulse and press disturbances has received a lot of attention in the ecological literature (Ives and Carpenter, 2007; Kéfi et al., 2019; Yodzis, 1988), evolutionary biologists have been primarily concerned with understanding consequences of a press disturbance. In particular, the evolutionary rescue literature has largely focused on understanding the consequences of phenotypic change in the context of a single, sudden, and non-reversing environmental shift.

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These studies underline the importance of genetic variance and heritability for increasing the probability of rescue (Gomulkiewicz and Holt, 1995, reviewed in Alexander et al., 2014, Bell, 2017). That is, populations that are able to adapt rapidly to the new environment have a higher chance of persisting.

The purpose of this article is to investigate the evolutionary and demographic consequences of a pulse disturbance in the form of an extreme event. Specifically, we explore the impacts of evolution on population size and extinction risk in response to extreme events of varying severity and duration. We use individual-based models that fuse the infinitesimal-model of an evolving quantitative trait with density-dependent demography. To gain insights beyond simulating the model, we derive analytical approximations of the probability of extinction using a mixture of deterministic recursion equations and branching process theory (Harris, 1964). Our key result is that when extreme events have a sufficiently short duration, heritability does not always help a population persist. Because the new environment is transitory, faster evolution results in greater maladaptation when the event ends, thus slowing population recovery and increasing the probability of extinction. However, when extreme events are sufficiently long in duration, heritability often helps a population persist, a finding consistent with the classical evolutionary rescue theory.

Model

We model the evolution of a single quantitative trait in a population experiencing an extreme event. We assume discrete, non-overlapping generations. The life cycle starts with viability selection. In each generation t, we impose stabilizing selection around some optimal trait value θ_t, which is set by the environment in that generation, by making the probability of survival

$$s_t(z) = \exp\left[\frac{-(\theta_t - z)^2}{2\omega^2}\right], \tag{1}$$

a Gaussian function of phenotype, z, with a strength of selection proportional to $1/\omega^2$.

Following viability selection, survivors are randomly drawn with replacement to form mating

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pairs. Each mating pair then produces a Poisson number of offspring with mean λ. The population lives in a habitat that supports at most K individuals. Hence, if more than K offspring are produced, K are randomly chosen without replacement. The genetics of the population follows the infinitesimal model in which breeding values are determined by many loci of small effect (Fisher, 1918; Turelli, 2017). Under this model, an offspring's breeding value is a draw from a normal distribution centered on the mean of its parents' breeding values and with segregation variance V_0 (which we assume is a constant). Its phenotype, z, is this breeding value, g, plus a random environmental component, e, which is a draw from a normal distribution with mean 0 and variance V_e. We ignore dominance and epistasis, thus the phenotypic variance in generation t is the additive genetic variance plus the environmental variance, $V_{p,t} = V_{g,t} + V_e$. At equilibrium, $\widehat{V}_p = \widehat{V}_g + V_e$.

Prior to experiencing an extreme event, the populations in the individual-based simulations start with a 100-generation burn-in from an initial state where all $N = K$ individuals have breeding value $\theta = 0$ and the optimal trait value θ_t equals 0 throughout this period. The 100 generation burn-in is sufficiently long to ensure the model reaches a quasi-stationary state (Supplementary Figure S1). To model the extreme event of length τ after the burn-in period from generation -100 to 0, we increase the optimum trait value, $\theta_t = 0$, by $\Delta\theta$ and revert it back to its original value after τ generations. For example, in a single-generation event, the optimum trait value changes in generation 1 and then reverts back in generation 2 (Figure 1). Unless otherwise stated, we use the parameter values $\omega = 1$, $\lambda = 4$, $K = 500$, $\widehat{V}_p = 1$, and $\Delta\theta = 3$.

Approximations

Approximating the evolutionary and population size dynamics

In Appendix A (see the supplementary Mathematica file for more details), we derive deterministic approximations for the dynamics of the mean breeding value, genetic variance, and population size. Briefly, if we assume the distribution of breeding values remains normal distributed,

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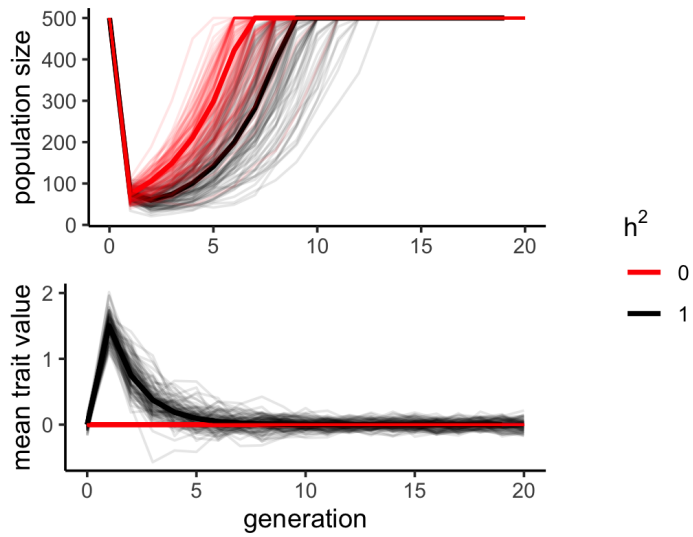

Figure 1: Population size over time for populations with $h^2 = 0$ (red) and $h^2 = 1$ (black) after a single-generation extreme event of size $\Delta\theta = 3$. Phenotypic variance is the same for both populations. Faded lines are 100 simulations and solid lines are the model predictions using Equations (2) and (4).

then we know the whole phenotypic distribution by tracking the mean and variance in the breeding values. Given the mean and variance in a given generation, we can then calculate the mean and variance in the next generation

$$\bar{g}_{t+1} = \bar{g}_t \left(1 - \frac{V_{g,t}}{V_t}\right) + \theta_t \frac{V_{g,t}}{V_t} \tag{2}$$

$$V_{g,t+1} = \frac{V_{g,t} V_s}{V_t} \frac{1}{2} + V_0 \tag{3}$$

as well as the population size in the next generation

$$N_{t+1} = \min\left(N_t \bar{s}_t \lambda / 2, K\right), \tag{4}$$

where $V_t = V_{g,t} + V_s$ and $V_s = \omega^2 + V_e$. The mean survival probability, $\bar{s}_t$, is calculated by integrating Equation (1) over the distribution of phenotypes in the population, giving

$$\bar{s}_t = \sqrt{V_s / V_t} \exp[-(\theta_t - \bar{g}_t)^2 / (2V_t)]. \tag{5}$$

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Therefore, the genetic variance approaches $\widehat{V}_g = \left(2V_0 - V_s + \sqrt{4V_0^2 + 12V_0V_s + V_s^2}\right)/4$, regardless of the trait or environmental dynamics. In a constant environment, $\theta_t = \theta$ for all t, the mean breeding value approaches the optimum, $\widehat{\bar{g}} = \theta$, and, provided $\lambda > 2$, $N_0\bar{s}_0$ is large enough, and $\widehat{V}_p = \widehat{V}_g + V_e$ is small enough, the population size reaches carrying capacity, $\widehat{N} = K$. Starting from this equilibrium, we can then approximate the response of the population to a shift in the optimum using Equations (2)-(4).

Approximating Extinction Risk

We next approximate the probability of extinction using branching processes (Harris, 1964). The probability generating function for the number of offspring produced by an individual with survival probability s is

$$f(x,s) = 1 - s + s\exp\left[-\frac{(1-x)\lambda}{2}\right]. \tag{6}$$

The probability of no offspring is $f(0,s)$. Further, if $s_1, \ldots, s_{N_t}$ are the survival probabilities of the N_t individuals in generation t, then the probability of extinction in generation t is $\prod_{i=1}^{N_t} f(0,s_i)$. Here we approximate this by assuming all individuals in generation t have the average probability of survival, $\bar{s}_t$, which is a reasonable approximation when the strength of selection is weak relative to the phenotypic variance. Defining $f_t(x) = f(x,\bar{s}_t)$, the probability of extinction in generation t is then simply $f_t(0)^{N_t}$. Assuming that the effects of density-dependence are negligible from generation t to generation $T > t$, we can approximate the probability of extinction by the end of generation T as $(f_t \circ f_{t+1} \circ \ldots f_T(0))^{N_t}$, where $\circ$ denotes function composition (Harris, 1964).

We take $t = 1$ to be the first generation of the extreme event and assume the population begins at carrying capacity. For an extreme event of duration τ, we define

$$P_{\text{extinct}}(\tau, T) = (f_1 \circ f_2 \circ \ldots f_T(0))^K \tag{7}$$

as our approximation for the probability of extinction by generation T since an extreme event of length τ began. To calculate the $\bar{s}_t$ in Equation (7) we assume $V_{g,t} = \widehat{V}_g$ and use Equation (2) to

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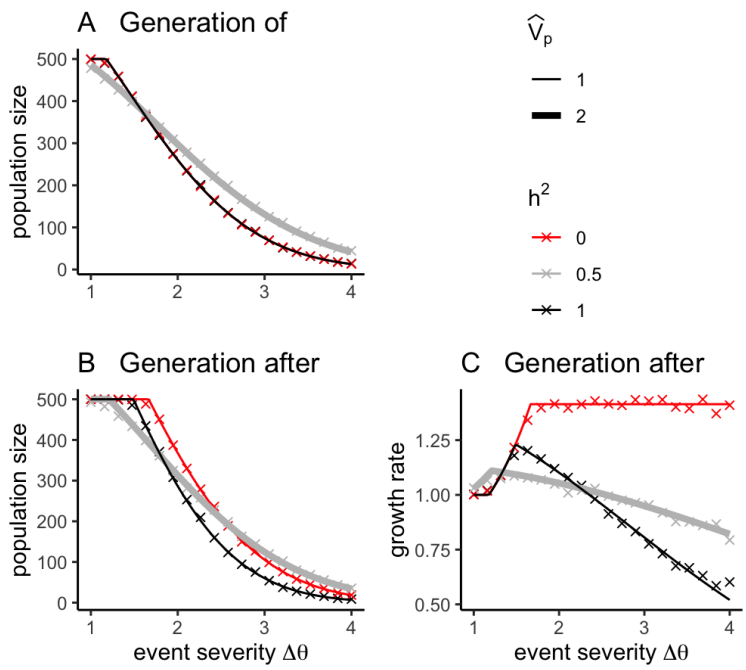

Figure 2: Population size response during the generation of a single-generation extreme event (A), the generation after the event (B), and the population size in the generation after the event divided by the population size in the generation of (C) shown over a range of event severities $\Delta\theta$. Red: $V_0 = 0$, $V_e = 1$. Gray: $V_0 = 1$, $V_e = 1$. Black: $V_0 = 1$, $V_e = 0$. Expectations using Equation (4) as curves and simulation results (mean of 100 replicates) as crosses.

get $\bar{g}_t$, which together give $\bar{s}_t$ (Equation (1)).

Results

Demographic recovery

We first explore extreme events lasting a single generation. To characterize the impact of phenotypic variance and heritability on population size, we compare the demographic response of populations with low or high phenotypic variance, $\widehat{V}_p$, across a range of heritabilities, $h^2 = \widehat{V}_g / \widehat{V}_p$. During the event, heritability has no effect on population size (compare black and red curves in

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2A). In contrast, we see that phenotypic variation can have a large effect. A population with high phenotypic variance (thick curve) has a smaller population size than one with low phenoytpic variance (thin curves) immediately following a low severity extreme event, but a higher population size following more severe events. We also see this effect in the generation after the event (Figure 2B,C); just given the heritabilities we expect the gray line to fall between the red and black curves, but the larger phenotypic variance causes deviations from this expectation. This pattern stems from the dual role of phenotypic variance, in that it both increases genetic load and contributes individuals with extreme traits who are then able to survive an extreme event. High phenotypic variance therefore reduces both mean fitness within a generation and the variance in fitness across generations–a form of short-term bet-hedging which can increase the geometric mean of fitness in the generations during and after the the disturbance event. The negative impact of load is more apparent in the case of a mild event, when the population remains near the fitness peak and variation means that more individuals are spread farther from the peak. The positive effect of bet hedging is seen when the event is severe and variation means more individuals on the tail of the distribution will survive the event.

While heritability has no effect on survival during the event, it has a strong effect on population recovery in subsequent generations. In particular, heritability dampens the growth rate in subsequent generations (Figure 2C) as evolution in the generation of the event induces future maladaptation. This explains why in the generation after the event increasing segregation variance becomes beneficial to population size (gray crosses red near $\Delta\theta = 3$ in panel B) at a higher severity than the point which increasing environmental variance becomes beneficial (gray crosses black near $\Delta\theta = 2$ in panel B). The maladaptation induced by heritability continues past the generation after the event, generally slowing population recovery (Figure 1). In conclusion, phenotypic variance can be beneficial for population growth under single-generation severe events, but heritability is generally deleterious.

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Extinction Risk

When a single-generation extreme event is severe enough, increasing phenotypic variation lowers extinction risk both during $P_{\text{extinct}}(1,1)$ and after the event $P_{\text{extinct}}(1,T>1)$ (compare thick and thin curves in Figure 3A,C). We expect the gray curve to be between the red and black curves based on heritability alone, but the higher phenotypic variance causes a shift to the right, representing reduced extinction risk. The biological intuition behind this pattern is the same as in Figure 2A, where increased variance means more individuals survive the extreme event. However, at such large population sizes the extinction risk is essentially zero during a mild event. In other words, while having too much variance leads to considerable reduction in population size when events are mild, it is very unlikely to lead to extinction unless there is extremely high phenotypic variance or if carrying capacity is very low. In the former case load will cause extinction in the absence of extreme events (Supplementary Figure S2).

Next, we compare populations with the same phenotypic variance but different heritabilities, to control for the effect of variance (i.e., genetic load and bet hedging) and isolate the effect of evolution (compare black and red in Figure 3). When the extreme event lasts only one generation (Figure 3A,C), heritability, which allows for evolution, increases the probability of extinction in the generations following the extreme event. This is consistent with the population size results above (Figure 2B), where evolution leads to future maladaptation. However, when an extreme event lasts two generations (Figure 3B,D), evolution can be beneficial.

Finally, we explored how extinct risk varies across time for one- to four-generation moderately ($\Delta\theta = 3.5$) extreme events across a range of heritabilities. For single generation events, we find long-term extinction risk (10,000 generations) is an increasing function of heritability (Figure 4A). For two generation events, long-term extinction risk is lowest when heritability is intermediate (Figure 4B). For three and four generation events long-term extinction risk is a decreasing function of heritability (Figure 4C,D). These patterns hold for mild ($\Delta\theta = 2.5$) and severe ($\Delta\theta = 4.5$) extreme events (Supplementary Figures S3-S4).

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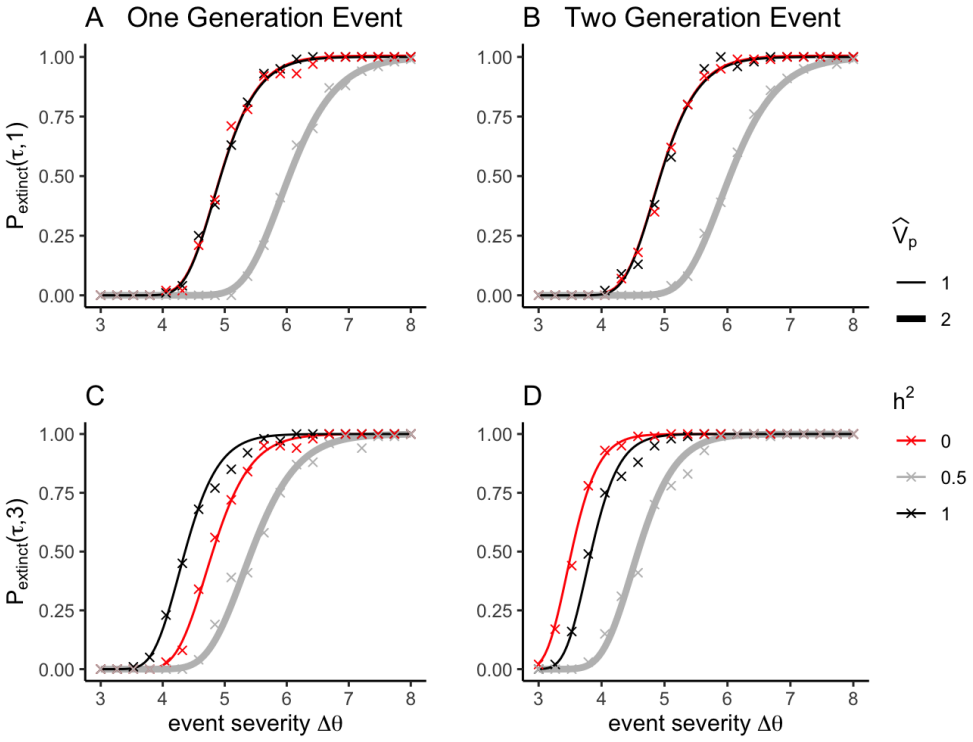

Figure 3: Extinction risk across increasingly severe events in the first generation of an extreme event, (A,B) and two generations later, (C,D). In A and C, the extreme event persists for a single generation, and in B and D, the extreme event persists for two generations. Expectations using Equation (7) as curves and simulation results (mean of 100 replicates) as crosses.

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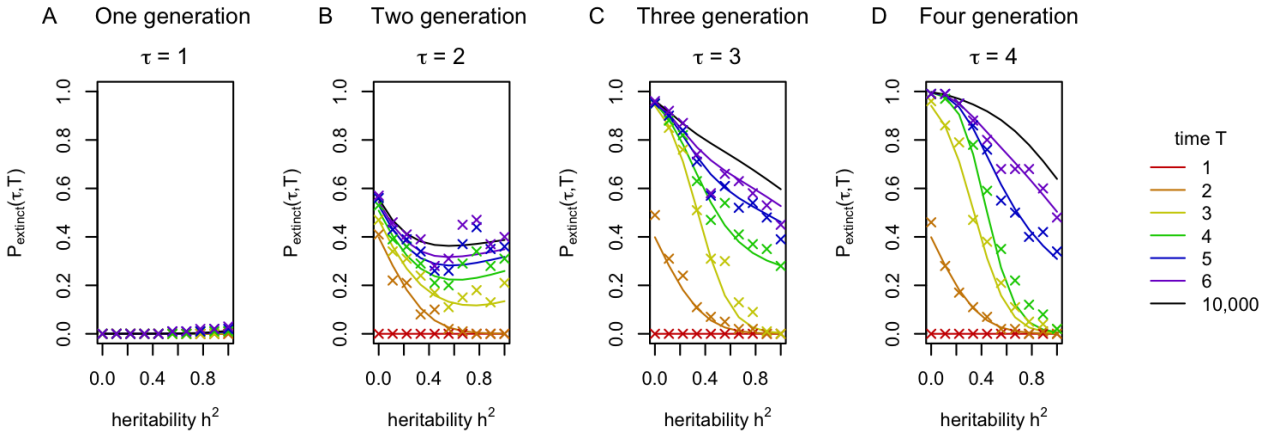

Figure 4: Extinction risk through time T across a range of heritability for extreme events lasting 1, 2, 3, or 4 generations. Time starts the generation the event began. $\widehat{V}_p = 1$, $V_s = 1$, $\Delta\theta = 3.5$. Red: $V_0 = 0$, $V_e = 1$. Gray: $V_0 = 1$, $V_e = 1$. Black: $V_0 = 1$, $V_e = 0$. Expectations using Equation (7) as curves and simulation results (mean of 100 replicates) as crosses.

The approximation (Equation (7)) closely matches extinction risk calculated from the individual-based simulations. While this approach gives exact estimates of extinction risk when computed numerically, the function itself is too complex to give us intuition behind these results. Next, by writing down the geometric mean fitness of a population, we reproduce the general trends in long-term extinction risk, but with added clarity for how maladaptation contributes to these outcomes.

Contribution of Lag Load

To better understand how evolution affects the probability of extinction, we approximate the geometric mean fitness of a population under the assumption that the genetic variance remains at the equilibrium value, $\widehat{V}_g$ as expected based on Equation (3). If the extreme event lasts τ

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generations, then the geometric mean of fitness after $T > \tau$ generations equals:

$$\begin{aligned}\overline{W}(\tau, T) &= \left(\prod_{t=1}^{T} \frac{\lambda}{2}\bar{s}_t\right)^{1/T} \\ &= \frac{\lambda}{2}\sqrt{V_s/\widehat{V}}\exp\left[-\frac{1}{2\widehat{V}T}\sum_{t=1}^{T}(\theta_t - \bar{g}_t)^2\right] \\ &= \frac{\lambda}{2}\sqrt{1-f}\exp\left[-\frac{1-f}{2V_sT}\sum_{t=1}^{T}(\theta_t - \bar{g}_t)^2\right],\end{aligned} \tag{8}$$

where $f = \widehat{V_g}/\widehat{V} = 1 - V_s/\widehat{V}$ is a measure of evolvability (see Equation (2) and, e.g., equation 1 in Charlesworth 1993). From Equation (8), we see that geometric mean fitness depends on the cumulative lag load, $(1-f)\sum_{t=1}^{T}(\theta_t - \bar{g}_t)^2/(2V_s)$. Using induction, we get that the cumulative lag load over $T > \tau$ generations for an event of length τ is

$$\begin{aligned}L(\tau, T) &= \frac{1-f}{2V_s}\sum_{t=1}^{T}(\theta_t - \bar{g}_t)^2 \\ &= \frac{\Delta\theta^2}{2V_s}\frac{(1-f)[1-(1-f)^{\tau}][2-(1-f)^{2(T-\tau)}+(1-f)^{2T-\tau}]}{(2-f)f}.\end{aligned} \tag{9}$$

Taking the limit as time, T, goes to infinity, the cumulative lag load is

$$\begin{aligned}L_{\infty}(\tau) &= \lim_{T\to\infty} L(\tau, T) \\ &= \frac{\Delta\theta^2}{V_s}\frac{(1-f)[1-(1-f)^{\tau}]}{(2-f)f}.\end{aligned} \tag{10}$$

As $f = h^2\widehat{V}_p/(\widehat{V}_p + \omega^2)$, we can use Equation (10) to determine how heritability affects the cumulative lag load (Figure 5), holding $\widehat{V}_p$ and ω^2 (and thus the variance load) constant. When the extreme event only lasts one generation ($\tau = 1$), the cumulative lag load equals $\frac{\Delta\theta^2}{\widehat{V}_p + V_e + 2\omega^2}$. Hence, increasing heritability, by decreasing V_e while holding $\widehat{V}_p$ constant, increases the cumulative lag load (solid purple curve in Figure 5), a trend consistent with the extinction probabilities for $\tau = 1$ (Figure 4A). Alternatively, when the extreme event lasts two generations ($\tau = 2$), the cumulative lag load equals $\frac{\Delta\theta^2}{\widehat{V}_p + \omega^2}$ and is independent of heritability when $\widehat{V}_p$ and ω^2 are held constant (solid pink curve in Figure 5). Finally, when the extreme event lasts for more than two generations, the cumulative lag load is a decreasing function of heritability (yellow and green curves in Figure 5);

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a trend consistent with extinction probabilities decreasing with heritability when $\tau \geq 3$ (Figure 4C,D).

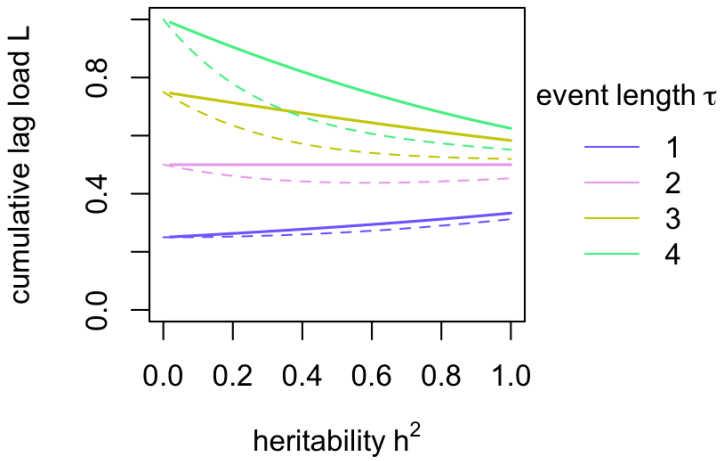

Figure 5: Cumulative lag load as a function of heritability. Dashed curves are Equation (9) with $T = 1$ and solid are Equation (10). Parameters: $\omega = 1$, $\widehat{V}_p = 1$, $\Delta\theta = 1$. Colors correspond to the length of the extreme event.

Discussion

Although it has been long recognized that evolution may affect a population's response to a changing environment, previous studies have primarily focused on understanding this effect in the context of a press disturbance, a single non-reversing environmental shift. Here, we are concerned with a pulse disturbance, a relatively short-term environmental change. By allowing pulses to be of any duration we are able to connect our results to classical approaches in evolutionary rescue. Our results provide two general conclusions about the effect of trait variation

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and its heritability on population growth and extinction risk following a pulse disturbance. First, trait variance is a double-edged sword: adding a genetic load due to stabilizing selection, yet providing individuals with more extreme traits who can survive large shifts in the environment. Second, while variance can be useful in the generation of a severe event, if it is heritable it will slow demographic recovery and increase extinction risk in the generations after the event.

The detrimental impact of phenotypic variance on population growth stems from stabilizing selection around an optimum trait. This genetic load from the phenotypic variance increases with the strength of selection (Lande and Shannon, 1996). On the other hand, greater phenotypic variance ensures that some individuals are adapted for extreme events and, thereby, can buffer the reduction in fitness during an extreme event. Taken together, a net reduction in the mean and variance in fitness during the generations immediately prior, during, and immediately after an extreme event can increase the geometric mean of fitness during this time frame (Figure 2). Consequently, phenotypic variation can serve as a kind of short-term bet-hedging strategy. The beneficial aspect of variance in rescuing a population from an abrupt shift in environment has been previously shown in studies of evolutionary rescue. For example, Barfield and Holt (2016) find populations with more genetic variance at the time of an environmental shift due to a press perturbation have greater persistence.

While there has been limited theoretical exploration of the topic of evolution in response to extreme events (Chevin and Hoffmann, 2017; Haaland and Botero, 2019; Vincenzi, 2014), many other patterns of environmental change have been modeled in the context of evolutionary rescue. Studies of a sudden or gradual directional environmental shift find that high genetic variance along with a large population size promotes rescue (Alexander et al., 2014; Bell and Collins, 2008; Gomulkiewicz and Holt, 1995; Osmond and de Mazancourt, 2013). In these press disturbance scenarios populations with higher heritabilities are more likely to be rescued (Barfield and Holt, 2016; Gomulkiewicz and Holt, 1995). We find the same result when extreme events are sufficiently long.

In contrast, empirical work often considers systems with shorter term perturbations. For

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example, El Niño events last less than a generation for Darwin's finches (Grant et al., 2017) and severe winter storms last less than a generation for sparrows (Bumpus, 1899) and lizards (Campbell-Staton et al., 2017). For these short-term environmental disturbances, we find higher heritability tends to slow population recovery and increase the probability of extinction.

We can gain some intuition for why evolution only reduces extinction if the extreme event lasts at least two generations by considering the limiting cases of traits not evolving versus tracking the optimal trait. When the population is adapted to the original environment, but does not evolve in response to the extreme event, it experiences a reduction in fitness for the duration τ of the extreme event. In contrast, when selection tracks the optimal trait, the population experiences a reduction in fitness only in the first and last generation of the extreme event. These two reductions arise due to maximal evolutionary responses resulting in populations being perfectly adapted to the environmental conditions in the previous generation. Hence, when the extreme event lasts one generation, extinction risk is higher for the evolving populations and when the extreme event lasts more than two generations, extinction risk is higher for the non-evolving populations. When the extreme event lasts exactly two generations, the non-evolving population experiences the reduction in fitness in successive generations while the evolving population experiences this reduction in alternate generations. Hence, the evolving population is less likely to go extinct (see Appendix B).

Future Challenges and Directions

Our results call for the need of more empirical studies assessing trait and fitness changes after an extreme event has ended. The many case studies of evolution in response to extreme events focus on the adaptive nature of species responses in the short-term (e.g. Campbell-Staton et al., 2017). What these studies often fail to mention is that evolution can be maladaptive in the long term. When the environment returns to normal, populations with shifted trait means will be worse off. Empirical studies should be extended to track changes in trait values and population size over several generations following extreme events. For example, lizards can be tracked for several

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generations following a hurricane (Donihue et al., 2018) or a cold snap (Campbell-Staton et al., 2017). We highlight the Darwin's finch example as one such study to do this (Grant and Grant, 2002) where finch traits and selection gradients were found to fluctuate in response to extreme events. Moreover, our findings highlight the data needed for better predictions of a species response to extreme events. Specifically, data on trait heritability and phenotypic variance are important in addition to initial population size and event severity.

Our models include a number of simplifications to both evolutionary and demographic processes. First, we don't model the erosion of genetic variance with decreasing population size, which is expected due to greater genetic drift in smaller populations (Barfield and Holt, 2016; Lande and Barrowclough, 1987). Furthermore, we have limited our analysis to truly quantitative genetic traits (i.e. infinitely many small-effect alleles) where mutation has a negligible effect on the trait over a short time frame (Barton et al., 2017). Different genetic architectures, such as a few loci mutations of large effect, likely will respond differently. Second, in our model, the phenotypic variation due to environmental variation is random, which ignores the potential for phenotypic plasticity. Phenotypic plasticity has been shown to have variable effects on evolution and extinction risk that depend on the nature of environmental change (Kopp and Matuszewski, 2014). Third, we are only tracking a single trait, whereas extreme events likely select on many correlated traits. As genetic covariance can change the outcome of selection, further work is needed to explore the effects of multiple correlated traits. Fourth, we used the simplest possible model for density-dependence, the ceiling model. This form has been used in previous evolutionary rescue studies (e.g., Bürger and Lynch, 1995). For other models of compensating density-dependence, such as the Beverton-Holt model (Beverton and Holt, 1957), we expect similar results. However, for over-compensatory density-dependence, as seen in the Ricker model (Ricker, 1954), one can have oscillatory population-dynamics for which the timing of the extreme event relative to the oscillations may play a subtle role.

An important next step will be to understand evolution and extinction risk under repeated extreme events. Previous models exploring fluctuating environments are useful comparisons

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(Benaïm and Schreiber, 2019; Chevin, 2013; Lande and Shannon, 1996). Our current results show a single-generation extreme event functions most like a negatively autocorrelated fluctuating or randomly fluctuating environment, in that a strong genetic response to selection in one generation is likely maladaptive in the next generation. However, an extreme event lasting three or more generations acts like a positively autocorrelated environment in that evolvability is favored. Given these parallels, future studies should seek to understand whether heritability rescues populations under different frequencies of extreme events.

Natural populations are facing globally changing environments. One form of environmental change is the increasing frequency and severity of extreme climatic events (Tebaldi and Meehl, 2006), which cause massive mortality and act as strong selective forces on traits. Genetic characteristics underlying these traits are likely to influence how populations respond. Here, we have taken the first step towards understanding which genetic factors increase population size and reduce extinction risk when populations are faced with increasingly severe environmental disturbances. Our results confirm the importance of phenotypic variation and heritability in predicting a population's response to extreme climatic events. We also highlight the importance of the duration of an extreme event in modifying population outcomes.

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Appendix A: Dynamics of the breeding value distribution and population size

Let the trait value of an individual be the sum of a genetic component (breeding value) and an environmental component, $z = g + e$. Assume we start with a population, in generation t, that has a normal distribution of breeding values, $p_g(g,t)$, with mean $\bar{g}_t$ and variance $V_{g,t}$. And assume each environmental component is independently chosen from a normal distribution, $p_e(e)$, with mean 0 and variance V_e. The joint distribution of g and e, $p_{g,e}(g,e,t)$, is then initially multivariate normal with mean $(\bar{g}_t, 0)$, variances $V_{g,t}$ and V_e, and no covariance.

Let the probability of survival for an individual with trait value z in generation t be

$$s(z,t) = \exp\left[-\frac{(\theta_t - z)^2}{2\omega^2}\right], \tag{A1}$$

where θ_t is the optimum trait value in generation t and $1/\omega^2$ is the strength of selection. The joint distribution of g and e following viability selection is

$$p'_{g,e}(g,e,t) = \frac{s(z,t)p_{g,e}(g,e,t)}{\bar{s}_t}, \tag{A2}$$

where

$$\begin{aligned}\bar{s}_t &= \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} s(z,t)p_{g,e}(g,e,t)\mathrm{d}g\mathrm{d}e \\ &= \sqrt{\frac{V_s}{V_t}}\exp\left[-\frac{(\theta_t - \bar{g})^2}{2V_t}\right],\end{aligned} \tag{A3}$$

is the expected fraction of the population that survives in generation t (i.e., the population mean survival probability), with $V_t = V_{g,t} + V_s$ and $V_s = \omega^2 + V_e$ the inverse of the effective strength of selection. Integrating over environmental effects then gives the distribution of breeding values amongst the survivors

$$p'_g(g,t) = \int_{-\infty}^{\infty} p'_{g,e}(g,e,t)\mathrm{d}e, \tag{A4}$$

which is normal with mean $\bar{g}_t(1 - V_{g,t}/V_t) + \theta_t V_{g,t}/V_t$ and variance $V_{g,t}(1 - V_{g,t}/V_t)$. The mean breeding value is thus shifted towards θ_t with a weight of $V_{g,t}/V_t$ and the genetic variance has been reduced by this fraction.

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We next assume that the breeding value is determined by a large number of small effect loci, such that the distribution of breeding values amongst siblings, $p_{g,\text{sibs}}(g|g_{\text{mid}})$, is normal with a mean equal to the midpoint of the parental breeding values, g_{mid}, and a variance, V_0, that does not depend on the parental genotypes or trait values (i.e., the infinitesimal model; Barton et al., 2017; Fisher, 1918). The distribution of breeding values among the offspring is then

$$p_g(g, t+1) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} p'_g(g_m, t)p'_g(g_p, t)p_{g,\text{sibs}}(g|(g_m + g_p)/2)\mathrm{d}g_m\mathrm{d}g_p, \tag{A5}$$

which is normal with mean

$$\bar{g}_{t+1} = \bar{g}_t\left(1 - \frac{V_{g,t}}{V_t}\right) + \theta_t\frac{V_{g,t}}{V_t} \tag{A6}$$

and variance

$$V_{g,t+1} = \frac{V_{g,t}V_s}{V_t}\frac{1}{2} + V_0. \tag{A7}$$

That is, the mean breeding value remains constant through reproduction while the variance before reproduction is first halved (due to essentially "blending inheritance" between the parents) and then increased by segregation, V_0.

So we see that given the initial distribution of breeding values is normal, with Gaussian selection the breeding value distribution remains normal, allowing us to track the entire distribution of breeding values (and therefore phenotypes) across generations by keeping track of only its mean and variance. The variance dynamics are independent of the environment (θ_t) and the breeding values; solving Equation (A7) gives the genetic variance in generation any t. This expression is rather complicated (see Mathematica file), however it reaches an equilibrium

$$\widehat{V_g} = \frac{2V_0 - V_s + \sqrt{4V_0^2 + 12V_0V_s + V_s^2}}{4}. \tag{A8}$$

Holding genetic variance constant at its equilibrium (which is reasonable given the variance is not expected to change with the environment or breeding values), in a constant environment, $\theta_t = \theta$, the mean breeding value in any generation t is found by solving Equation (A6),

$$\bar{g}_t = \theta - (\theta - \bar{g}_0)\left(1 - \frac{\widehat{V_g}}{V_s + \widehat{V_g}}\right)^t, \tag{A9}$$

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implying a geometric approach to $\widehat{\bar{g}} = \theta$ that becomes faster with $\widehat{V_g}/(V_s + \widehat{V_g})$.

We assume each individual that survives viability selection produces $\lambda/2$ offspring (i.e., each mating pair produces λ), and that if more than K offspring are produced then K of these are randomly chosen to start the next generation. If the population size in generation t was N_t then the population size in generation $t+1$ is expected to be

$$N_{t+1} = \min\left(N_t \bar{s}_t \lambda/2, K\right). \tag{A10}$$

Appendix B: Extinction Risk in Single and Two Generation Events

In this Appendix, we examine the effect of long-term extinction risk when populations are either not evolving or are perfectly tracking, with a one-generation lag behind the optimal trait value. Let s_o and s_m be the survivorship of individuals with the optimal trait or the maladaptive trait. The offspring probability generating functions for these individuals are $f_o(x) = f(x, s_o)$ and $f_m(x) = f(x, s_m)$, respectively, where $f(x,s) = 1 - s + s\exp(\lambda(1-x))$. Let x_o^* and x_m^* be the asymptotic extinction probability for the lineage of a single individual if it always exhibits the optimal trait and if it always is maladapted, respectively. Namely, x_o^* and x_m^* are the smallest fixed points of f_o and f_m, respectively, on the interval $0 \le x \le 1$.

If a disturbance event lasts $\tau \ge 1$ generations, then the eventual extinction probability of the lineage of a non-evolving individual equals

$$e_m := \lim_{T\to\infty} f_m^\tau(f_o^{T-\tau}(0)) = f_m^\tau(\lim_{T\to\infty} f_o^{T-\tau}(0)) = f_m^\tau(x_o^*).$$

While the eventual extinction probability of the lineage of an individual with a one-generation lagged tracking of the optimal trait equals

$$e_o := \lim_{T\to\infty} f_m(f_o^{\tau-1}(f_m(f_o^{T-\tau-1}(0)) = f_m(f_o^{\tau-1}(f_m(\lim_{T\to\infty} f_o^{T-\tau-1}(0)) = f_m(f_o^{\tau-1}(f_m(x_o^*))).$$

As $s_o > s_m$, we have $f_o(x) < f_m(x)$ for all $0 \le x < 1$, and $x_o^* < x_m^*$. Furthermore, $f_i(x)$ are strictly increasing functions of x, $f_i(x) > x$ for $x < x_i^*$, and $f_i(x) < x$ for $x > x_i^*$ for $i = o, m$. Now suppose $\tau = 1$. Then $e_m = f_m(x_o^*)$ and $e_o = f_m(f_m(x_o^*))$. As $x_o^* < x_m^*$, $f_m(x_o^*) > x_o^*$. As f_m is an

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increasing function, it follows that $e_o = f_m(f_m(x_o^*)) > f_m(x_o^*) = e_m$. Now suppose $\tau = 2$. Then $e_m = f_m^2(x_o^*)$ and $e_o = f_m(f_o(f_m(x_o^*)))$. As $f_m(x_o*) > x_o^*$, $f_o(f_m(x_o^*)) < f_m(x_0^*)$. As f_m is increasing, it follows that $e_o = f_m(f_o(f_m(x_o^*))) < f_m(f_m(x_o^*)) = e_m$.

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Supplementary Figures

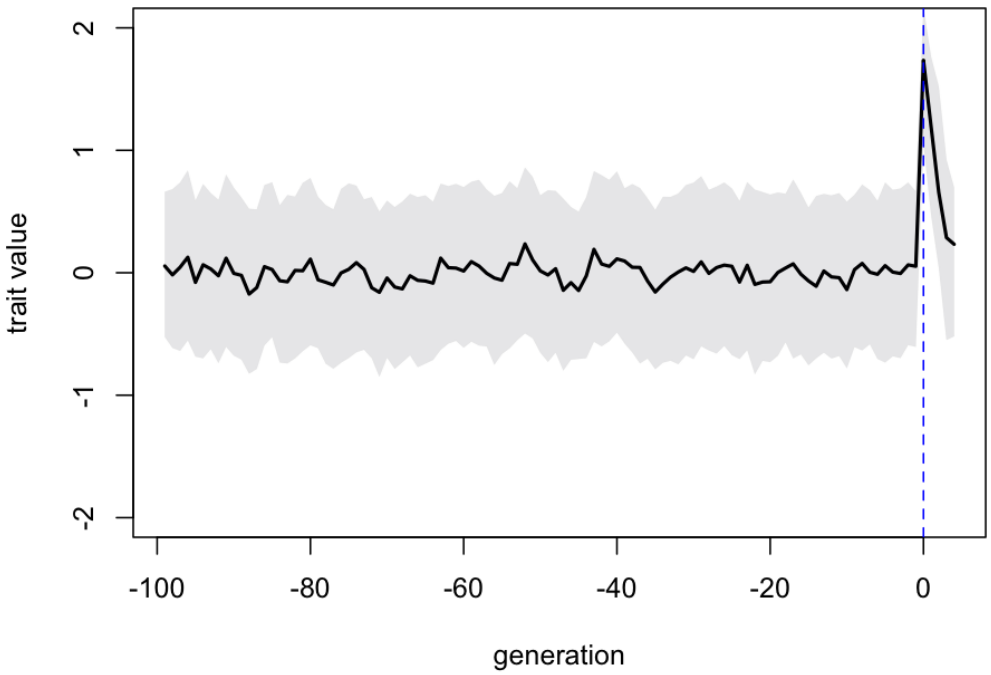

Figure S1: Rapid expansion and stabilization of phenotypic variance during the 100 generation burn-in with $V_e = 0$, $V_0 = 1$. Black line is mean trait value and gray shaded region extends from minimum to maximum trait values. The dashed blue curve indicates a one generation extreme event.

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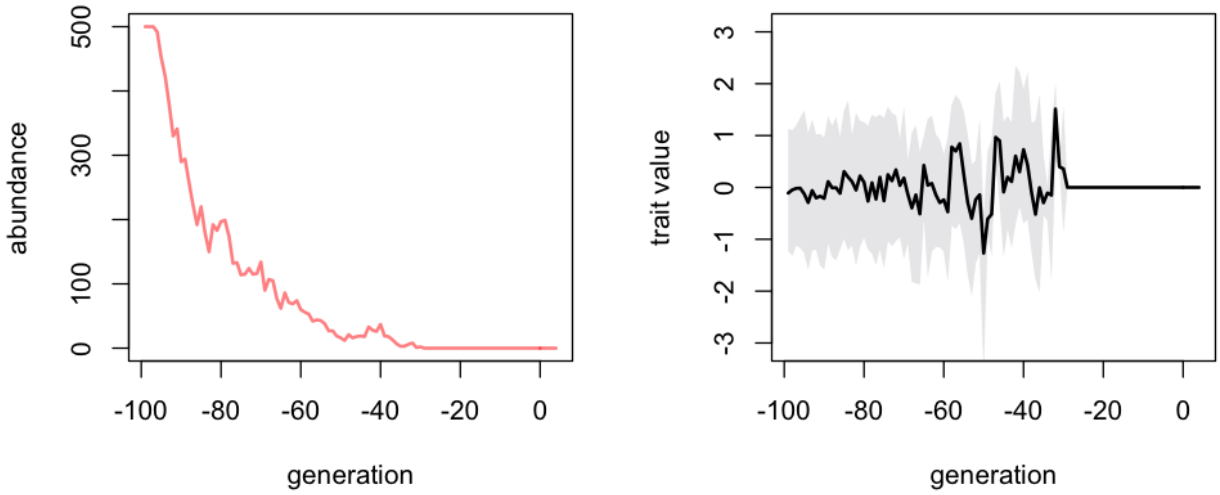

Figure S2: Extinction in a population with high variance load with $V_0 = 3$, $V_e = 0$. Black line is mean trait value, grey shaded region extends from minimum to maximum trait values.

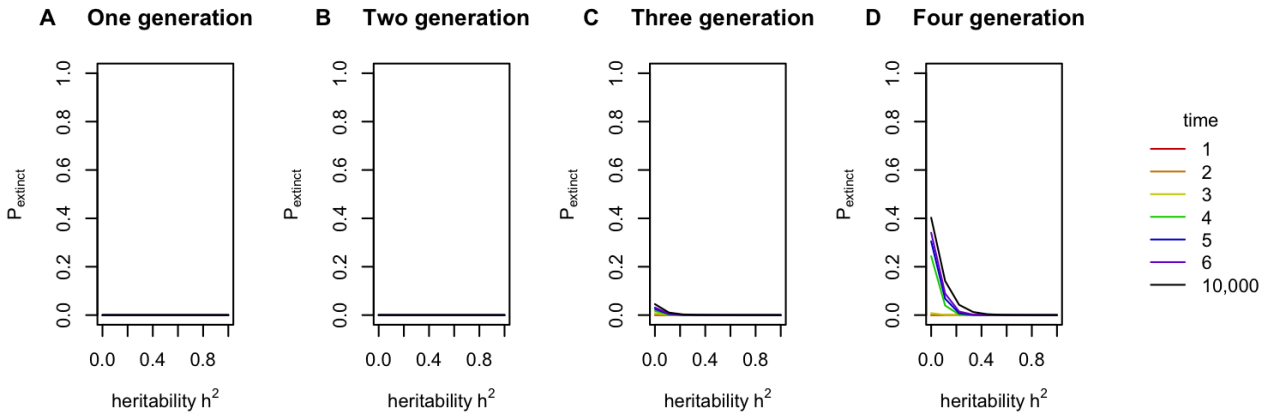

Figure S3: Extinction risk through time across a range of heritability for extreme events lasting 1, 2, 3, or 4 generations. Time starts the generation the event began. $\widehat{V}_p = 1$, $V_s = 1$, $\Delta\theta = 2.5$.

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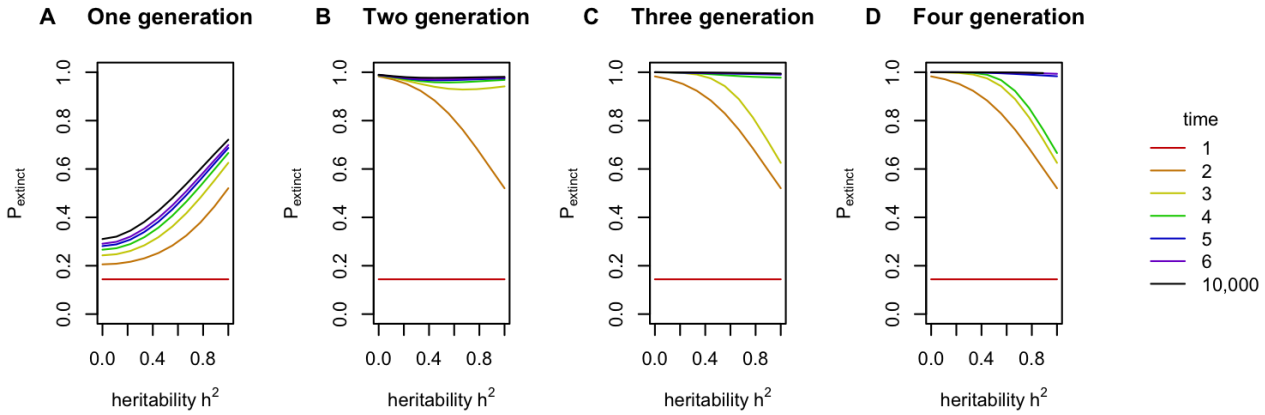

Figure S4: Extinction risk through time across a range of heritability for extreme events lasting 1, 2, 3, or 4 generations. Time starts the generation the event began. $\widehat{V}_p = 1$, $V_s = 1$, $\Delta\theta = 4.5$.