



Consequences of extreme events on population persistence and evolution of a quantitative trait

Simone Vincenzi ^{a,b,*}, Giulio A. De Leo ^{c,d}, Michele Bellingeri ^c

^a Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, United States

^b MRAG Americas, POB 1410 Capitola, California 95010, United States

^c Dipartimento di Scienze Ambientali, Università degli Studi di Parma, Viale G. P. Usberti 33/A, I-43100 Parma, Italy

^d Hopkins Marine Station, Stanford University, Pacific Grove, California 93950 United States

ARTICLE INFO

Article history:

Received 5 July 2011

Received in revised form 2 December 2011

Accepted 5 December 2011

Available online 13 December 2011

Keywords:

Extreme climatic event

Population dynamics

Quantitative genetics

Mutational variance

Selection pressure

ABSTRACT

The intensification and increased frequency of weather and climate extremes are emerging as one of the most important aspects of climate change. Using a quantitative genetic model, we explore the effects of increasing environmental stochasticity and its interplay with genetic variation and selection pressure on population dynamics and evolution of a fitness-related trait. We use simulations with variations in trend (i.e., directional change) and stochasticity (i.e., increase in variance) of a climate variable defining a phenotypic optimum, and various hypotheses on mutational variance and strength of selection on a phenotypic trait. We let the population reach mutation–selection balance and then we linearly increase over simulation time both the mean and the variance of the statistical distribution of the climate variable. Higher variance of climate variables increases the probability of extreme climatic events, i.e. events that are both statistically rare and with potentially high ecological impact, that is, causing episodes of massive mortality in the population. Our analysis shows that the population is able to track the directional component of the optimum for low increases of variability, while for high increases the tracking is reduced. Persistence of the population depends quite strongly on the selection pressure and decreases with increasing variance of the climate variable. Higher mutational variance does not substantially decrease the risk of extinction of a population.

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1. Introduction

With climate change, many species will experience selection pressures in new directions and at new intensities, and the degree to which species respond adaptively will have an important influence on their capacity to survive over the coming decades and millennia. Changes in the long-term mean state of climate variables (i.e., climate trends) and their consequences on survival, evolution and adaptation of species have been intensively studied for more than 20 years (Hoffmann and Sgrò, 2011), and a wealth of quantitative genetic studies on the effects of environmental change on population persistence and evolution of traits under selection has been published. Burger and Krall (2004) grouped environmental changes according to their temporal occurrence: stochastic fluctuations of a certain parameter around a constant mean; periodic fluctuations around a constant mean which are at least partially predictable; directional changes, such as global climatic changes, and abrupt change in the environment.

We now describe some of the most relevant results and insights from quantitative genetic studies relevant to environmental and climate change. Lynch and Lande (1993) and Bürger and Lynch (1995, 1997) investigated the extinction dynamics of a population when the optimum moves at a constant rate per generation. They found a critical rate of environmental change beyond which extinction is certain because the lag (difference between the mean trait in the population defining fitness and the optimum for that trait) increases from generation to generation, thus decreasing the mean fitness of the population below a level at which the population starts to decline. With a smaller population size, genetic drift reduces the genetic variance, which leads to an even larger lag, a further decrease of mean fitness, and rapid extinction.

In many systems, changes in environmental factors, and thus selection, are both directional (e.g., higher temperatures, higher rainfall) and fluctuating (e.g., through cycles, stochastically). In addition, climate change models show that the variance of climate variables such as temperature or rainfall may change much more dramatically than their means (e.g., Kharin and Zwiers, 2000) and will thus intensify the stochastic component of selection. Charlesworth (1993) and Lande and Shannon (1996) investigated fluctuating stabilizing selection on a quantitative trait by assuming that the optimum phenotype follows a linear stationary Markov process with autocorrelation

* Corresponding author at: Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, United States.

E-mail address: simon.vincenz@gmail.com (S. Vincenzi).

between -1 and 1 . They showed that genetic variation is only beneficial if the variance of the fluctuations is high or if the process is highly autocorrelated, in which case adaptation, that is tracking the optimum, increases the mean fitness. On the contrary, with uncorrelated environmental noise, an increase in genetic variation always causes a decrease in mean fitness. Bürger (1999) found that when environmental variability is high, a high reproductive rate is much more effective at improving population persistence than a high genetic variance.

Individual-based quantitative genetic models with stochastic dynamics (Gomulkiewicz and Holt, 1995; Holt and Gomulkiewicz, 2004) suggest that evolution may quickly rescue populations after they collapse under abrupt environmental change. Fitness is predicted to initially decline after the abrupt change, but then recover through adaptation (e.g., Burt, 1995). According to such theory, whether populations can be rescued through evolution of fitness-related traits depends upon several crucial variables, including population size, genetic variation within the population, and the degree of maladaptation to the new environment (Bell and Gonzalez, 2009).

Shifts and excursions in climate or environmental variables might cause some populations to perpetually chase alternate optimal phenotypic extremes. Such populations would face a demographic cost if evolution during one environmental phase resulted in maladaptation and reduced favorable genetic variation with respect to the next.

While it is well known that small populations are usually highly vulnerable (i.e., are at high risk of extinction) to even moderate environmental stochasticity, the picture emerging from quantitative genetic studies of population dynamics shows that large populations can also be vulnerable if the environmental variability is sufficiently high.

The intensification of weather (individual events, such as hurricanes) and climate (events over seasons, such as droughts) extremes is emerging as one of the most important aspects of climate change (Jentsch et al., 2007) and the debate is expanding from an analysis of trends to an interest in extreme events. Weather and climate extremes are characterized by intensity, duration, frequency, or spatial extent; they can disrupt ecosystems, communities, or population structure and change resource pools, substrate availability, or physical environment (Jentsch et al., 2007; Wagner, 2003; White et al., 1985). Many adaptations (in life histories, morphological or behavioral traits) are associated with extreme events (Stockwell et al., 2003).

It is well known that populations can survive a single extreme event, especially if short-lived, and rapidly recover through various compensatory responses (e.g., Spiller et al., 1998; Wingfield et al., 2011). Under scenarios of climate change it is possible that a population may experience a long sequence of particularly extreme climatic events capable of driving the population to extinction (Jentsch et al., 2007). In addition, even when extinction does not immediately follow an extreme event, the loss of genetic variability resulting from the dramatic drop of population size to very low densities can substantially reduce the population's ability to respond to future selective challenges and increases the chances of an extinction vortex (e.g. Caughley, 1994).

There is growing evidence that the frequency and severity of weather and climate extremes and associated ecological responses have already increased in several regions (Karl et al., 2005; Schär et al., 2004). These events may result in rapid mortality of individuals and extinction of populations or species (Bigler et al., 2006, 2007; Gitlin et al., 2006; Miriti et al., 2007; Thibault and Brown, 2008) and changes in community structure and ecosystem function (Ciais et al., 2005; Haddad et al., 2002; Mueller et al., 2005).

Hence, there is the urgent research need to meet the challenges posed by extreme events. However, in the context of quantitative genetic models, the joint effect of a directional change and of a large increase in variance of a climatic variable leading to higher occurrence of extreme events, as expected under scenarios of climate change (IPCC, 2007), has scarcely been investigated.

Here, we use a simple quantitative genetic model to explore the evolution of a fitness-related trait in a population and its effects on population dynamics with a gradual increase in mean and variance of a climate variable determining the optimum for the trait under selection. We perform the analysis with alternative assumptions on strength of the selection pressure, mutation, and on the rate of directional change and increase in climate variability.

2. Model of population dynamics

2.1. General description of the model

We consider a population of hermaphrodite individuals living in a habitat with carrying capacity K , here intended as the maximum number of individuals supported. This allows us not to keep track of males and females and introduces density-dependent population regulation through a ceiling effect, as described below.

The population has discrete generations (i.e., reproduction is discrete in time) and is composed of $N(t)$ individuals. Generations are overlapping, meaning that parents do not die after reproducing. Each individual is characterized by a single quantitative trait a corresponding to its breeding value for a phenotypic trait z . The habitat is characterized by an optimum phenotype θ that changes over time as a result of variations in a climate driver, such as rainfall or temperature, selecting for the phenotypic trait z . The distance between the optimum phenotype $\theta(t)$ and the trait z of the i individual z_i defines the maladaptation of an individual, as described in detail in the following. The time step is one year.

2.2. Temporal change of optimum phenotype

In general, the temporal change of the optimum phenotype θ may be either directional, stochastic or a combination of both. A simple model for this is an optimum phenotype $\theta(t)$ that moves at a constant rate $\beta_{\mu, \theta}$ over time, fluctuating randomly about its expected value $\mu_{\theta}(t)$. We thus introduce a directional and stochastic temporal change of the optimum phenotype (Fig. 1a). $\theta(t)$ is randomly drawn at each time step from a normal distribution $\theta(t) \sim N(\mu_{\theta}(t), \sigma_{\theta}(t))$:

$$\begin{cases} \mu_{\theta} = \mu_{\theta, 0} \\ \sigma_{\theta} = \sigma_{\theta, 0} \end{cases} \quad \text{for } t < t_{ch} \\ \begin{cases} \mu_{\theta}(t) = \mu_{\theta, 0} + \beta_{\mu, \theta} t_{ch} \\ \sigma_{\theta}(t) = \sigma_{\theta, 0} + \beta_{\sigma, \theta} t_{ch} \end{cases} \quad \text{for } t > t_{ch} \end{cases} \quad (1)$$

where t_{ch} is the time since the change in the environment. The definition of extreme events in ecological models is a thorny question. First, while for weather extremes the definition is more straightforward (e.g., a hurricane may always be considered an extreme event), what constitutes a climate extreme strongly depends on the available climate record. In the following, our considerations will be based on climate extremes, e.g., exceptionally high temperatures leading to a drought or rainfall over a season leading to repeated floodings.

A climate extreme for a particular environmental parameter can be readily represented by the distribution of the set of largest values recorded in a time window or, equivalently, by the tails of a probability distribution of a climate variable, whose shape and parameters have been estimated on historical series of observations. Both tails are relevant, since both extremely high and low temperatures or rainfall (potentially causing droughts and floods, respectively) have potentially extreme consequences. Second, a climate extreme is not always driving an extreme ecological response. In fact, depending on the role and abundance of the species impacted, such responses may or may not result in changes that can be distinguished from background variability (Smith, 2011).

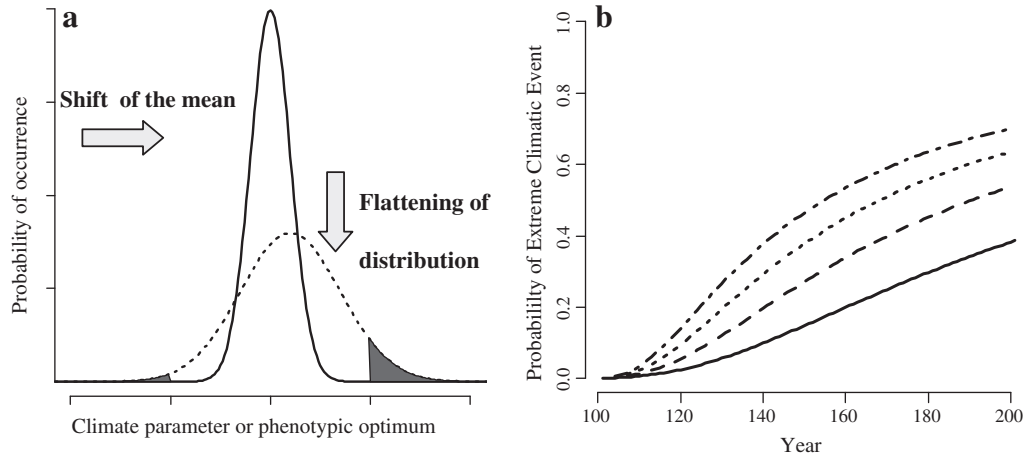


Fig. 1. Weather and climate extremes. (a) Increase in the probability of occurrence of extreme events with climate change (gray areas) for a hypothetical climate variable (e.g., rainfall, temperature), as defined in our model. Solid line represents current scenario, while dotted line represents a hypothetical future scenario at the end of simulation time. Jentsch et al. (2007) and Smith (2011) provided similar representations. (b) Expected probability of optimum phenotype $\theta(t)$ outside the tails of $\theta(t=0)$ defining an extreme climatic event, for $\beta_{\mu, \theta} = 0.02$ and different increases in variance of Θ after the first 100 years simulation time. We here report: solid line – $\beta_{\sigma, \theta} = 1 \cdot 10^{-2}$; short-dashed line – $\beta_{\sigma, \theta} = 1.5 \cdot 10^{-2}$; long-dashed line – $\beta_{\sigma, \theta} = 2 \cdot 10^{-2}$; dashed-dotted line – $\beta_{\sigma, \theta} = 2.5 \cdot 10^{-2}$.

Following Smith (2011), an Extreme Climatic Event (ECE) can be synthetically conceptualized to include “extremeness” in both the driver (climate) and the response at different levels of biological organization. As such, ECE causes a substantial deviation of a system behavior from the usual one. Since the threshold for what is classified as an ECE can vary from one analysis to another and may depend also on both species and general habitat features, here we consider values of the optimum phenotype $\theta(t)$ in the tails of its statistical distribution (probability of occurrence $p > 1-10^{-4}$ or $< 10^{-4}$) at time $t=0$ $\theta(0)$ as ECE. Values of the optimum phenotype in the tails of the distribution are far from the mean value of the trait under selection in the population, and thus a ECE is likely to cause a large drop in population abundance.

2.3. Survival

We assumed stabilizing selection on the phenotypic value of a trait, acting only through differential viability. Many phenotypic traits appear to be under stabilizing selection, i.e. selection favoring an intermediate value of the trait (Lynch and Walsh, 1998).

As commonly modeled (Lynch and Walsh, 1998), the phenotype z of an individual i , z_i , is defined as the sum of its genotypic (also called breeding) value a_i (representing additive genetic variance) randomly drawn from a normal distribution $N(\mu_G, \sigma_G^2)$, and a statistically independent random environmental effect from $N(\mu_E, \sigma_E^2)$:

$$z_i = a_i + e_i \quad (2)$$

where the narrow sense heritability $h^2 = \sigma_G^2 / \sigma_z^2$ indicates how much of the phenotypic variance σ_z^2 present in the population is explained by the additive genetic variance σ_G^2 . We did not model dominance and epistatic variation.

Environmental variance includes all variation of non-genetic origin, i.e. variation due to external environmental conditions (e.g., nutrition, climate, disease) and internal conditions such as developmental noise.

A standard model for stabilizing selection in natural populations is to assume normalizing (also called nor-optimal) selection (Bürger and Lynch, 1995; Haldane, 1954), with relative fitness W equals to:

$$W(z_i) = W_i = \exp \left[-\frac{(z_i - \theta(t))^2}{2\omega^2} \right] \quad (3)$$

and equivalent in our model to the relative annual survival probability of individual i . This corresponds to a situation where an environmental variable affects fitness in a straightforward way. The variance of the fitness function ω^2 represents an inverse measure of the strength of selection, the smaller ω^2 the larger selection strength. Stabilizing selection is usually measured by the standardized quadratic selection gradient γ , which is defined as the regression of fitness W on the squared deviation of trait value from the mean (Lynch and Walsh, 1998). Kingsolver et al. (2001) showed that the strength of stabilizing selection is much stronger than assumed in most theoretical analyses (e.g., Lande, 1975; Turelli, 1984). The median $\gamma = -0.1$ for stabilizing selection found by Kingsolver et al. (2001) corresponds to a value of $\omega^2 / \sigma_E^2 = 5 / [1 - h^2]$, where σ_E^2 is the variance of the environmental component of the phenotype defined in Eq. (2), when stabilizing selection is modeled using a nor-optimal fitness function.

Eq. (3) can be written:

$$W_i = \sigma_{\max} \exp \left[-s \cdot (z_i - \theta(t))^2 \right] \quad (4)$$

where $s = 1/2 \omega^2$ and σ_{\max} is the maximum probability of survival when $z_i = \theta(t)$. With $\gamma = -0.1$, $\sigma_E^2 = 1$, $\sigma_{\max} = 1$ and $h^2 = 0.2$, the strength of selection s is about 0.08. For simplicity, in our model we set $\sigma_{\max} = 1$.

In our model, only the optimum phenotype $\theta(t)$ is assumed to change over time, while the width ω^2 of the fitness function, and thus strength of selection s , is constant. We assume that death caused by maladaptation occurs before the effect of senescence, which allows neglecting the reduction of survival probability with age.

2.4. Inheritance of the trait

In the infinitesimal model of quantitative genetics (Lynch and Walsh, 1998), genetic variances either remain constant during selection or any changes in variance can be predicted solely from the base population variance components, since selection is assumed not to alter allele frequencies. With inheritance rules based on the infinitesimal model, each offspring's a value for a trait z under selection (Eq. (2)) is drawn from a normal distribution centered on the arithmetic mean of the two parental values, while the variance of this distribution is equal to half the total additive genetic variance for the trait at the population level (i.e., the within-family additive variance remains constant). With this formulation, the total additive genetic

variance for the trait at the population level remains constant across generations (Bulmer, 1980; Lynch and Walsh, 1998).

However, long-term response can seldom be predicted from knowledge of the base population variance components alone (Lynch and Walsh, 1998). In fact, while populations with the same variance components show essentially the same short-term response, their long-term responses can be very different.

In an idealized population with no input of new variation from mutation or migration, the additive variance generated from the initial variation in the base population eventually declines. Ultimately, a selection limit or plateau is reached, and as the genetic variation in the base population becomes exhausted, the effects of new mutations become increasingly important for continued response (Johnson and Barton, 2005). The variance introduced by mutation per generation σ_m^2 (mutational variance) at the population level is in the order of 10^{-3} to $10^{-2} \sigma_E^2$, as suggested by reviews of empirical data (Johnson and Barton, 2005; Lynch and Walsh, 1998).

We modified the inheritance model of the infinitesimal model of quantitative genetics theory to account for the decline of additive genetic variance and new input of variation from mutation. Offspring born in year t inherit the trait a_{off} from a normal distribution centered on the arithmetic mean of the two parental values a_{p1} and a_{p2} and with the variance $\sigma_{G,off}^2$ of the distribution at time t is equal to half the mean of population additive genetic variance over time $t - 4 \dots t$ ($\bar{\sigma}_G$):

$$\bar{\sigma}_G(t) = \frac{1}{5} \sum_{j=t-4}^t \sigma_G^2(j) \quad (5)$$

plus the mutational variance σ_m^2 multiplied by a factor M defining the amplitude of mutation (from now on we will refer to M as mutation):

$$\sigma_{G,off}^2 = \frac{1}{2} (\bar{\sigma}_G + \sigma_m^2 M) \quad (6)$$

2.5. Simulation analysis

At the start of each simulation, the population has mean a and z (Eq. (2)) equal to the mean of the distribution of the optimum phenotype $\Theta(0)$.

The Monte Carlo simulation at a time t during the simulation proceeds as follows. We:

- 1) Draw the optimum phenotype $\Theta(t)$ from $\Theta(t) \sim N(\mu_\Theta(t), \sigma_\Theta(t))$.
- 2) Compute the annual survival probability of individuals by applying Eq. (2).
- 3) Determine the survival of individuals using Bernoulli trials.
- 4) Compute the total number of individuals alive $N(t)$ and check the distribution of trait z in the population. A population is considered extinct if at any time during the simulation there are 0 individuals in the population.
- 5) Randomly form mating pairs. Parents produce a number of offspring randomly drawn from a Poisson distribution with expected value λ equal to 2 (we chose 2 as the expected number of offspring produced by a pair following a pattern-oriented procedure (Grimm et al., 2005) to allow for a fairly quick rebound of population size after a collapse caused by an extreme event).
- 6) The breeding values of offspring are randomly drawn from a normal distribution with mean centered on the mean of the breeding values of the parents a_{p1} and a_{p2} and variance computed by Eqs. (5) and (6).
- 7) Randomly place offspring in the population. When carrying capacity K is reached, the remaining offspring die. Offspring at year t become adults at year $t+1$ and are able to reproduce. The generation time is thus one year.

Our simulation model has the following parameters: carrying capacity of the environment K , mutational variance σ_m^2 , mutation factor M , strength of selection s , standing genetic variation σ_G^2 at $t=0$, environmental variance σ_E^2 and the parameters driving directional and stochastic variations of the optimum phenotype (Eq. (1)), that is $\mu_{\Theta,0}$, $\beta_{\mu,\Theta}$, $\sigma_{\Theta,0}$, and $\beta_{\sigma,\Theta}$. The parameter space is rich and a full exploration of it is beyond the scope of this work. To simplify the interpretation of results, since we are mainly interested in differences among scenarios of variability of the optimum phenotype, we fixed $K=500$, $\mu_{\Theta,0}=0$, $\sigma_{\Theta,0}=0.5$, $\sigma_E^2=1$, $\sigma_m^2=10^{-3}$, and $\sigma_G^2=0.2$. We performed simulations for combinations of selection strength s from 0.01 (weak selection), to 0.16 (strong selection), mutation M from 1 to 100, rate of increase in the mean of the climate variable $\beta_{\mu,\Theta}=0.02$ and 0.03 and rate of the increase in the variance of the climate variable $\beta_{\sigma,\Theta}=0, 0.5, 1, 1.5, 2, 2.5, 3 \cdot 10^{-2}$ (Fig. 1b). For weak selection strength s (i.e., $s < 0.08$), fitness declines fairly slowly from the optimal value, while for higher values of s fitness declines sharply with increasing distance from the optimum.

To initialize the system and achieve mutation–selection–balance, we first let the population evolve for 100 years in an environment in which mean and variance of the optimal phenotype Θ are constant. Then, to analyze the effect of climate change, we let the mean and variance of Θ increase according to Eq. (1) for other 100 years.

We start every simulation replicate with 500 individuals (population at carrying capacity) with genetic values of individuals a_1, \dots, a_{500} randomly drawn from the normal distribution $N(0, 0.2)$ (Fig. 2). Since we set $\sigma_E^2=1$, the narrow sense heritability h^2 is around 0.17 at $t=0$, in the order of magnitude of what commonly observed for life-history traits (Lynch and Walsh, 1998) and consistent with the Gaussian allelic approximation including only quasi-neutral and adaptive mutations, for which $\sigma_G^2=0.225\sigma_E^2$ (Lande, 1995).

Over simulation time h^2 evolved depending on selective pressure, mutation factor and the population dynamics. At the level of single replicates, to characterize the behavior of the simulated populations we:

- a) recorded using a binary variable if the population was extinct or still persisting at the end of the simulation time, (0 for persistence and 1 for extinction);
- b) tracked the distribution of the trait z in the population as a function of time and, in particular, its mean value \bar{z} at the end of simulation time when the population did not go extinct. To avoid transient effects caused by the stochastic series of optimal phenotypes, we averaged \bar{z} in the last 5 years of the simulation.

We do not include in the analysis the number of individuals at the end of simulation time (200 years), since population abundance was largely determined by the succession of optimal phenotypes near the end of simulations (Fig. 2).

For an ensemble of realizations (100 replicates for a fixed set of parameters), we computed:

- a) frequency of population extinction, computed as the number of replicates in which the population went below two individuals during simulation time;
- b) average over the 100 replicates of \bar{z} at the end of simulation time for the replicates in which the populations did not go extinct.

We carried out simulations with alternative models of inheritance in order to understand the sensitivity of model results to the transmission of breeding values from parents to offspring.

3. Results

The model allowed us to compute the probability of ECE as a function of time under alternative assumptions on the rate of increase in variance and of the distribution of the optimum phenotype Θ . Fig. 1b shows that, in the most variable scenario (i.e., $\beta_{\sigma,\Theta}=2.5 \cdot 10^{-2}$) and

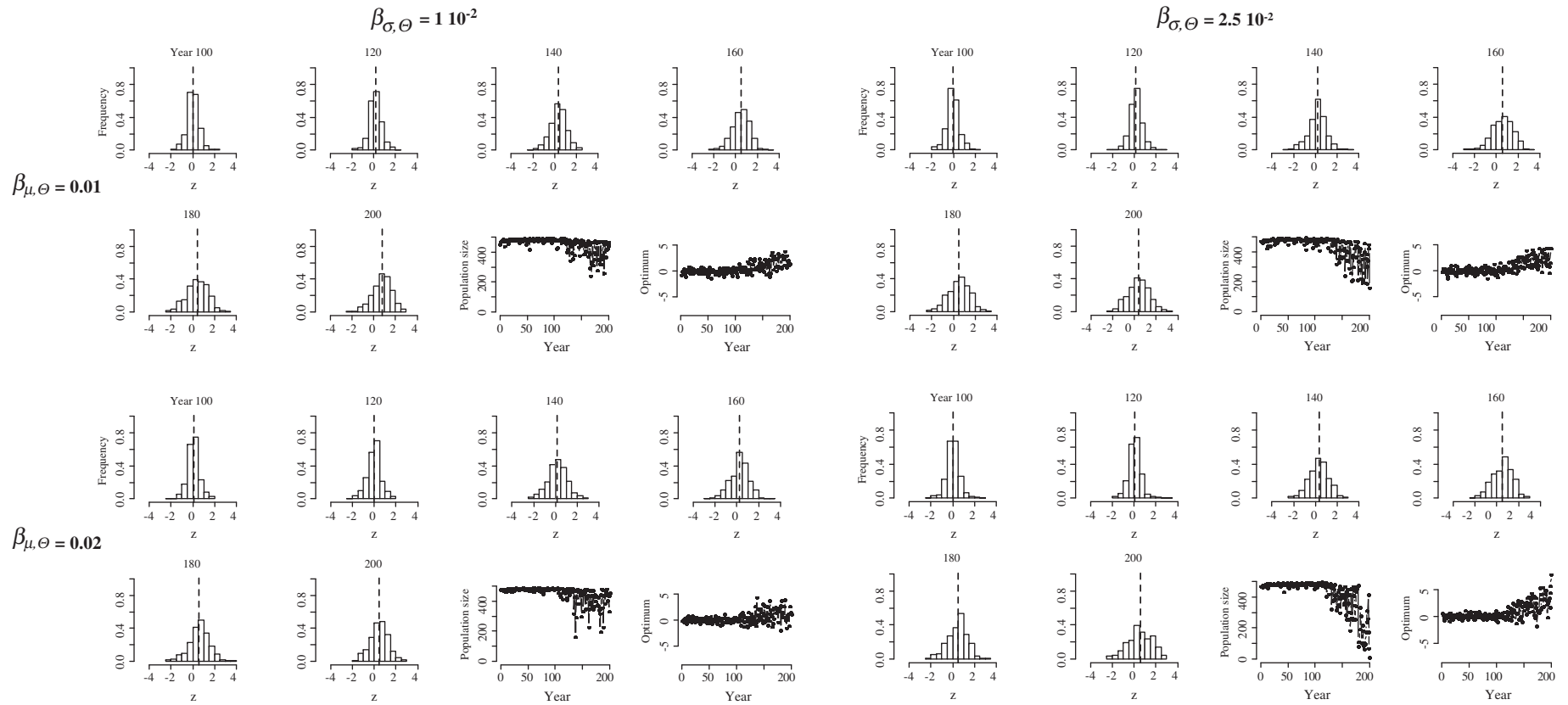


Fig. 2. Examples of simulations. Examples of simulation for two scenarios of rate of increase of variability ($\beta_{\sigma, \theta} = 1 \cdot 10^{-2}$ and $\beta_{\sigma, \theta} = 2.5 \cdot 10^{-2}$) for each scenario of directional increase of the optimum ($\beta_{\mu, \theta} = 0.02$ and $\beta_{\mu, \theta} = 0.03$) with selection pressure $s = 0.08$ (corresponding in our model to the median of the quadratic selection gradient reported by Kingsolver et al., 2001) and mutation factor $M = 20$. The histograms represent the distribution of trait z at $t = 100, 120, 140, 160, 180,$ and 200 . The vertical dashed line is the mean of the trait z , \bar{z} , at that time. The fluctuations in population size tend to increase with increasing $\beta_{\sigma, \theta}$.

with $\beta_{\mu, \theta} = 0.02$, probability of ECE at the end of simulation time is about 0.7. As shown in Fig. 1a, extreme climatic events can occur either when the optimum phenotype $\Theta(t)$ is much smaller than the mean of Θ or much larger. Yet, extreme events in the right tail of the distribution, i.e., in the same direction of change of the mean of the climatic variable, are more likely to occur. In this sense, when the trend is for increasing temperatures, extremely high temperatures are more likely to occur than extremely low temperatures.

The consequences of different rates of increase in variance of Θ , as described by the values of $\beta_{\sigma, \theta}$, emerged clearly 20–30 years after variance of Θ started to increase (Figs. 1b and 2). With higher values of rate of increase in variance of the distribution of Θ ($\beta_{\sigma, \theta}$), the population exhibited repeated collapses. Even though mutation introduces diversity and tends to broaden the distribution of the trait, selection narrows its distribution (Fig. 2).

In Fig. 3, we show lines of equal probability of extinction in the mutation–selection plane under two alternative assumptions on the rate of increase of the mean of the distribution of Θ ($\beta_{\mu, \theta}$) and for only the three highest values of $\beta_{\sigma, \theta}$ since, with lower increases in variance of Θ no extinctions were basically observed for all mutation–selection combinations. The chances of survival of a population decreased substantially with increasing $\beta_{\sigma, \theta}$ for the same selection–mutation combinations (Fig. 4). Increases in mutational variance σ_m^2 did not increase the probability of persistence in either scenario (Fig. 4).

In general, the system was able to track the directional component of the optimum (Fig. 4). For the same mutation–selection combination, the amplitude of the shift of \bar{z} generally decreased with higher rate of increase of variance of Θ . Larger values of \bar{z} were observed in the scenario with higher rate of increase of mean of Θ ($\beta_{\mu, \theta} = 0.03$). The value of \bar{z} at the end of simulation time was larger with increasing strength of selection, but only for moderate or low $\beta_{\sigma, \theta}$ (Fig. 4). With scenarios of high increase of variance of Θ ($\beta_{\sigma, \theta} = 1.5$ and $\beta_{\sigma, \theta} = 2 \cdot 10^{-2}$), we observed the largest shifts of \bar{z} in the case of intermediate strength of selection. Interestingly, in the scenario with the highest rate of increase of variance of Θ ($\beta_{\sigma, \theta} = 2.5 \cdot 10^{-2}$) the amplitude of the shift of \bar{z} decreased with increasing strength of selection. In this last case ($\beta_{\sigma, \theta} = 2.5 \cdot 10^{-2}$), for both scenarios of increase in the mean of

Θ , \bar{z} at the end of simulation time was near 0 for intermediate strength of selection, and basically independent of mutation.

High mutation factors generally increased the shift of the phenotype, but only for intermediate and strong selection. The increased shift driven by high mutation was more noticeable with low rates of increase of the variance of Θ .

4. Discussion

Our analysis showed that an increase in climate variability dramatically reduces the persistence of a population and the tracking of a linearly increasing optimum. In addition, the interplay between mutational variance, strength of selection, and strong increases over time of both mean and variance of the environmental optimum provide a rich and not always intuitive set of possible evolution of a trait under selection.

Extreme events occur in all systems with complex dynamics, but the details of the creation of these large fluctuations are still rarely understood, and therefore the prediction of their occurrence and of their consequences on natural populations remains a challenge. However, since significant impacts of climatic change are likely to occur as a consequence of the shift in the intensity and frequency of extremes (IPCC, 2007), a better understanding of the effects of an increase occurrence of extreme events on population persistence and the evolution of fitness-related traits in natural populations call for wide scientific investigations (Jentsch et al., 2007).

Our results showed that the strength of selection heavily influenced the probability of population extinction across scenarios of climate variation. This may be intuitive, since the strength of selection directly determines the penalty in terms of fitness reduction for values of trait distant from the optimum. It follows that organisms with narrow tolerance (i.e., for which selection is stronger) have a greater risk of extinction than generalist organisms, for which selection is weaker. With lower rates of increase in the variability of the optimum phenotype, extinctions were confined to cases where strength of selection was greater than the corresponding median standardized quadratic selection gradient γ reported by Kingsolver et al. (2001). On the contrary, with a higher rate of increase in the variance of the climate variable, the probability of going extinct was

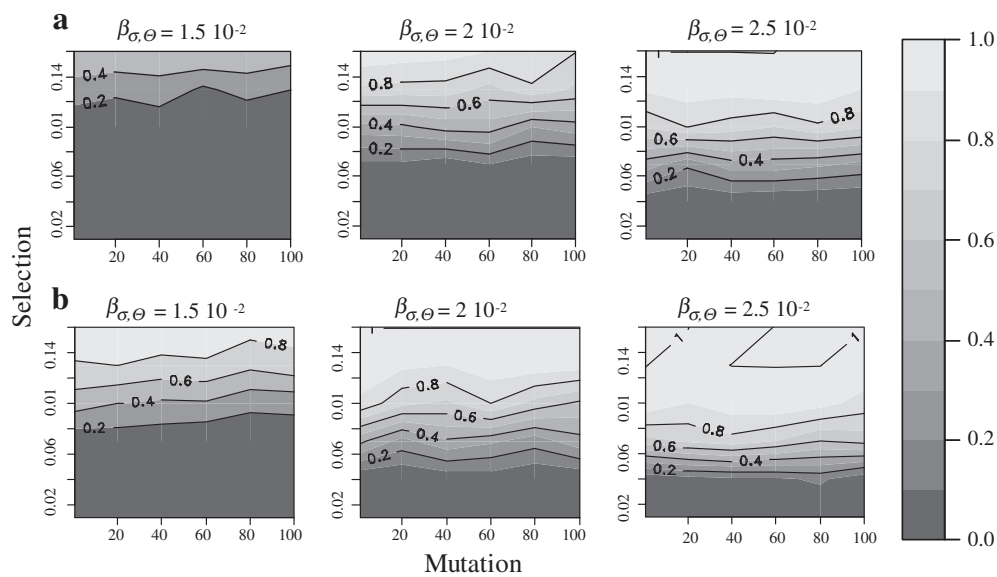


Fig. 3. Iso-probability of extinction. Lines of equal probability of extinction (number of populations going extinct/number of replicates) in the mutation–selection plane for the four scenarios of increasing variance over simulation time of the optimum phenotype Θ ($\beta_{\mu, \theta} = 0, 0.5, 1, 1.5, 2, 2.5 \cdot 10^{-2}$) and two scenarios of increase in trend (panel a: $\beta_{\mu, \theta} = 0.02$; panel b: $\beta_{\mu, \theta} = 0.03$). The frequency of population extinction for combinations of selection pressure s and mutation factor M is computed as the number of replicates in which the population did go below ten individuals during simulation time.

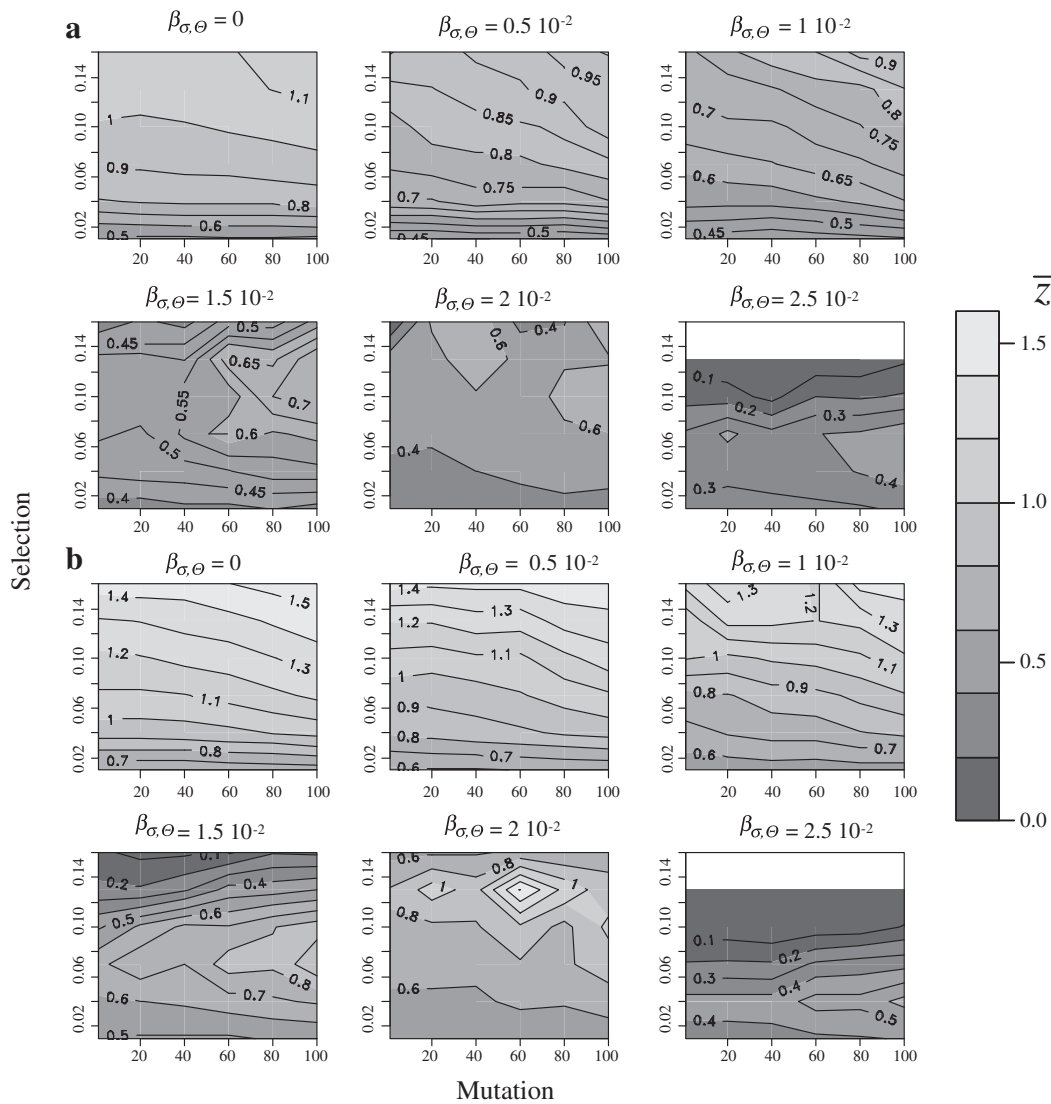


Fig. 4. Mean value of trait under selection. Lines in the mutation–selection plane of equal mean across replicates of \bar{z} at the end of simulation time for the four scenarios of variability of Θ ($\beta_{\sigma, \theta}$ as in Fig. 3) and two scenarios of increase in trend (panel a: $\beta_{\mu, \theta} = 0.02$; panel b: $\beta_{\mu, \theta} = 0.03$). The mean was computed only for the populations which persisted up to the end of simulation time. The white region in the phase diagrams identifies mutation–selection combinations for which populations had no or little chances to persist up to end of simulation time (see Fig. 3).

fairly high also in case of weak selection. This was true regardless the specific value of the rate of increase in the mean of the distribution of the optimum. Yet, for any given level of selection pressure and for the same scenario of rate of increase of climate variability, the probability of extinction was higher in case of faster directional increase. An increase in extinction risk with increasing strength of selection was found also by Björklund et al. (2009), while Huey and Kingsolver (1993) suggested that there might be an intermediate strength of selection that maximizes the time to extinction, since a reduction in the strength of selection leads to a high lag load (difference between the mean trait in the population defining fitness and the optimum for that trait), whereas an increased strength reduces the lag, but induces a high load. Bürger and Lynch (1995) also found that there is an intermediate strength of selection that maximizes the mean extinction time (i.e., increases persistence) in a changing environment, unless the environment changes too fast. We found that with higher rates of increase of optimum variability, but now with highest increase modeled in this work, intermediate strength of selection combined with high mutation favored the tracking of the directional component of the optimum. However, the risk of extinction was lower with weaker selection.

Mutation did not substantially influence the probability of extinction. Ecological studies with approaches similar to our simulation analysis did not explicitly include mutational variance, since the infinitesimal model, which implicitly includes mutation, is often used. In a physics approach to a similar problem, Bena et al. (2007) found that mutation is unfavorable to the survival of a population in a constant environment, since it increases the probability of a mismatch of offspring phenotype to the environment optimum, even though the parents might be well-adapted. Therefore, any level of mutation results in the production of non-optimal trait in a constant environment, given an adapted population. On the contrary, in our model higher mutation generally increases the probability of tracking a moving optimum. According to our results, the probability of population persistence does not increase with increasing mutation, in particular when variability of the optimum is too high.

As also found by Bürger and Lynch (1995), populations that would be able to evolve and cope with a steadily changing environment may go rapidly extinct if random fluctuations of appreciable size occur. In their analysis, superimposition of low stochasticity reduced the mean time to extinction by one or more orders of magnitude relative to a smoothly moving optimum. In our work, no extinctions were

recorded for low increases of variance, but extinction probability quickly raised with moderate to high increase in variance.

As noted by Siepielski et al. (2009), the “temporal landscape” of selection across taxa shows that the strength and the direction of selection often vary through time, even in absence of climate change. Especially with strong selection pressure and high variability of the optimum alternating selection over time might cancel out periods of directional selection, such that effective selective quasi-neutrality of trait variation is maintained over time. This is what happens in the scenario with the highest rate of increase of the variance of the distribution of the optimum and intermediate strength of selection. With this scenario, extreme events with high probability of occurrence may cause strong selection of individuals in either direction in alternate years (e.g., a drought followed by an extremely intense rainfall season the following year). As a consequence, periods of directional selection towards a higher mean value of the trait are canceled out by a single ECE or a series of ECEs in the opposite direction. With scenarios of low and moderate increase in variability, a higher directional trend is likely to cause only larger shifts of the mean value of the trait under selection at the end of simulation time.

The tracking of the optimum is also influenced by the standing genetic variation before the change in the environment, number of offspring produced by a pair, generation time and whether individuals survive after reproduction. How the dynamics of genetic variation over simulation time are modeled is likely to influence the results, both in term of extinction probability and tracking of the optimum. However, it is particularly difficult to describe the evolution of genetic variation without an explicit genetic model, especially when selection is sufficiently strong and its direction varies through time. Different approximations have been used. For example, Björklund et al. (2009) randomly drew the breeding value of the offspring from a normal distribution centered on the mean of the breeding value of the parents and variance computed on the same breeding values. Then, the environmental component was created by keeping heritability constant. In our case, the environmental component remained constant and the heritability changed, typically becoming smaller over time. This happens as a result of the decrease of additive genetic variance over time, and especially with higher strength of selection and low mutation. However, we performed simulations with the same equation proposed by Björklund et al. (2009) for estimating the variance of the offspring’s breeding value, and results of our simulations did not substantially change. We also carried out other simulations in which the variance of the distribution of offspring breeding value was the half the mean of additive genetic variance over the previous either 10 or 20 years to account for a slower decrease of genetic variance in the population, and also in this case results were consistent with the findings we have reported.

In absence of fluctuations of the optimum, we found in simulations not reported here that an increase in trend between 5% and 10% of the phenotypic standard deviation per generation was sufficient to cause extinction for every mutation–selection combination during simulation time. This result was also found by Bürger and Lynch (1995) and Björklund et al. (2009) and confirms that if the rate of increase in trend is already too high for a population to adapt, small random fluctuations add little to the extinction risk.

In conclusion, the results of our work provide a useful starting point for the investigation of the potential of the populations to adapt to and survive a substantial increase in the variability of environmental conditions. The simulations showed that the probability of survival of populations is dramatically affected by increases of the variance of the distribution of the optimum phenotype. Increasing selection pressure consistently decreases the probability of population persistence. In the scenarios considered, higher mutation does not seem to contribute to population persistence, although it contributes to tracking the optimum.

Acknowledgments

The authors thank Marc Mangel, Luca Bolzoni, Steve Munch, Grant Pogson, and Carlos Garza for discussion and comments which greatly increased the quality of the manuscript. An anonymous referee provided suggestions and comments which greatly improved the quality of our work.

The work was partially supported by the Italian Ministry of Research under PRIN2008.

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