Running title: Contemporary risk of extinction

Contemporary risk of extinction in an extreme environment

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Abstract

The increased frequency and intensity of extreme events are recognized among the most worrisome aspects of climate change. However, despite increased attention from scientists and conservationists, developing and testing general theories and hypotheses on the effects of extreme events on natural populations remains intrinsically challenging.

Using numerical simulations with general—but realistic for moderately fast-leaving species—parameter values, I tested some of the hypotheses on risk of extinction and population and genetic dynamics in an environment in which both climate (e.g., temperature, rainfall) and point (e.g., fires, floods) extremes occur. In the simulations, a quantitative trait is selected for by a climate variable, but point extremes cause trait-independent massive mortalities.

I found additive effects between age at first reproduction and fecundity on risk of extinction. The extent of population bottlenecks (operationally, the number of years in which a population was at low numbers) was a good predictor of allelic richness for the quantitative trait selected for by the climate. Simple models including basic demographic and vital rates information of the species, along with climate/environmental measures, provided excellent predictions of contemporary risk of population extinction. Mean and minimum population size measured in a 10-year "observation window" were largely the most important predictors of risk of population extinction in the following 10-year "prediction window".

Keywords: population dynamics, prediction, adaptation, climate change, genetics

1 Introduction

Extreme events are now recognized among the most worrisome aspects of climate change (IPCC 2007, 2012, Jentsch et al. 2007, The One Earth Editorial Team 2020). They may be defined in terms of extreme values of a continuous climate variable (e.g., daily or mean summer temperature, rainfall) on the basis of the available climate and weather record (Gutschick and BassiriRad 2010), or in the form of a "point" (or discrete) perturbation, such as a hurricane or a storm; the latter category also includes environmental hazards such as fires and floods. Following Vincenzi (2014), throughout this work I will use the term climate extreme for extreme values of a continuous climate or environmental variable and point extremes for discrete extreme perturbations.

The genetic and demographic determinants of both adaptation to a more extreme environment and contemporary risk of extinction are receiving increasing interest from scientists and conservationists. Despite the increased research and management focus on extremes, developing and testing general theories and hypotheses on the effects of extreme events remains more challenging than for other aspects of climate and environmental change (van de Pol et al. 2017). Those challenges are likely to be intrinsic and unavoidable.

First, since the effects of extreme events are largely context-specific, developing an overarching causal and predictive framework might be overly ambitious (Bailey and van de Pol 2016). For instance, the emergence of adaptations may depend on both the life histories of the species and the recurrence interval, intensity, and nature of extreme events. Besides, the demographic and genetic effects of climate and point extremes (e.g., population crashes, loss of genetic diversity, inbreeding and maladaptation, changes in

population age and size structure, disruption in the expression of quantitative traits) (Bryant and Meffert 1995, Kirkpatrick and Jarne 2000) are often the result of chance and are thus not easily predictable or generalizable across species or habitats. Second, climate and point extremes that result in strong demographic and genetic responses are often rare events, whose occurrence may be also difficult to predict. When available, pre-disturbance empirical data is likely to have been collected by chance, and the studies on the effects of extreme events prone to be mostly opportunistic and anecdotal instead of planned and comprehensive.

Despite the intrinsic difficulties of developing and testing general theories on the effects of climate and point extremes on natural populations, there are a few theory-based predictions on the demographic and genetic consequences of extreme events that may be quite general across species and habitats, although with varying degrees of modeling and empirical validation.

The first prediction is that by reducing population size, extreme events directly increase the risk of extinction of the affected populations (Willi et al. 2006, Frankham et al. 2014); mathematical modeling, empirical observations, and common sense all suggest that smaller populations are more likely to go extinct than larger populations. After the occurrence of extreme events, in some cases the extinction of the focal population is inevitable for numerical reasons (no individuals capable of reproducing survived) unless there is immigration from neighboring—either unaffected or less affected—populations (i.e., “demographic rescue”, Brown and Kodric-Brown 1977, Carlson et al. 2014).

Second, when the change in the environment is sudden, but not causing mass mortalities, the evolution of fitness-determining traits might occur fast enough to stop

population decline and allow population recovery before extinction ("evolutionary rescue", Bell and Gonzalez 2009). However, population bottlenecks such as those caused by extreme events, especially when repeated over time, are predicted to decrease additive genetic variance and allelic diversity in the affected populations (Bouzat 2010). As adaptive potential tends to increase with genetic variability and genetic drift may overwhelm selection in small populations, the effects of extreme events on genetic variability are predicted to increase both the short- and long-term risks of population extinction, with smaller chances of evolutionary rescue (Falconer and Mackay 1996, Willi and Hoffmann 2009).

Third, species may exhibit various adaptations to extreme events, some more predictable and general than others. For instance, extreme, but predictable variations in the flow regime of streams can select for fish life histories, such as spawning and emergence time, that are synchronized either to avoid or exploit the direct (e.g., stronger or weaker currents) and indirect (e.g., changes in food webs) effects of extreme flows (Lytle and Poff 2004). On the contrary, unpredictable flow events such as flash floods may have low direct selective consequences for the affected populations, even though they might induce massive mortalities (Lytle 2000). In these cases, natural selection after the extreme event is predicted to favor individuals with a high capacity for increase in population size (*r* selection, Reznick et al. 2002). Intuitively, when after an extreme event the population is reduced to a few individuals, faster reproduction may be more critically needed than high fecundity, since the latter depends on being able to reproduce. However, the interaction effects between age at first reproduction and fecundity on risk of extinction in an extreme environment have been rarely investigated.

In this work, I test using a simulation approach some of the hypotheses on risk of extinction and population and genetic dynamics in an environment in which both climate and point extremes occur. In previous work, Vincenzi (2014) found that the survival chances of a population were found to decrease with increasing strength of selection, as well as with increasing climate trend (e.g., increasing or decreasing *n*-year moving average temperature, rainfall) and variability. They also found that the interactions among climate trend (e.g., increase over years of average summer temperatures), climate variability and probability of point extremes (e.g., fires) had negligible effects on risk of extinction, time to extinction, and distribution of a quantitative trait selected for by climate after accounting for their independent effects.

The present work focuses more on prediction than inference; prediction of future observables has long been included as an aspect of biological and ecological studies, but as a methodological approach it has been much less prominent than either description or statistical and causal inference. The work is also not purely theoretical in scope, but is motivated (and model parameter values inspired) by the study of the population and genetic dynamics, and risk of extinction of marble trout *Salmo marmoratus* living in Slovenian streams (Vincenzi et al. 2016). Marble trout populations are affected by flash floods in autumn and droughts in summer, and the climate threat to the persistence of marble trout is likely to worsen with climate change; for instance, the increase in intra-annual variability in rainfall is predicted to increase the frequency of flash floods (Janža 2013). However, since there is a need for more general investigations of risk of population extinction and population and genetic dynamics in presence of climate and

point extremes, I developed a more widely applicable modeling and conceptual framework.

I modeled an idealized situation of additive genes, a closed population of moderate size with random mating, and variable across simulations—but fixed within simulations—age at first reproduction and expected number of offspring per mating pair, climate trend and variability (i.e., the parameters of the distribution of climate variable that is selecting for a quantitative trait), selection strength, and frequency and severity of point extremes. I assume that point extremes cause massive mortalities, but no trait other than good fortune increases the survival chances of an individual when point extremes occur.

First, I tested whether in an extreme environment the extent of population bottlenecks, which I operationally defined as the total number of years with "depressed" population size (e.g., ~ 1/3 to ~ 1/10 of the habitat carrying capacity), could help predict allelic richness at the end of simulation time for the quantitative trait selected for by the climate variable. Second, I tested whether quantitative trait adaptation was correlated with the increased frequency of theoretically advantageous alleles (i.e., their allelic values are in the same direction of the change in the environment) and whether the genetic dynamics of the populations could be predicted using information on the climate and on the population life histories. Third, I tested for interaction effects between age at reproduction and fecundity on risk of population extinction. Finally, I tested whether it is possible to predict the extinction or survival of a population in a 10-year "prediction window" (i.e., contemporary extinction) when measuring or observing some of the environmental characteristics of the habitat (e.g., occurrence of extreme events) and of

146 the population (e.g., population size, age at reproduction) during a 10-year "observation
147 window" that immediately precedes the "prediction window".

148 2 Material and methods

149 The model I use in this work is an extension of the model developed in Vincenzi
150 (2014). The choice of parameter values for the present work was informed by the
151 available literature on extreme events, population monitoring, and species life histories,
152 and by the results of Vincenzi (2014).

153 2.1 Overview of the model

154 I consider a population of monoecious individuals living in a habitat whose population
155 ceiling is K (Mangel and Tier 1993). The population is geographically isolated, with
156 neither immigration nor emigration from or to other populations. A single quantitative
157 trait a corresponding to its breeding value for a phenotypic trait z characterizes the
158 individuals. The population has discrete overlapping generations with $N(t)$ total
159 individuals, where t is time in years. The environment is described by an optimum
160 phenotype $\Theta(t)$ that changes over time as a result from variations in a climate driver such
161 as rainfall or average summer temperature, which selects for the trait z. The distance
162 between the optimum phenotype $\Theta(t)$ and the trait z_i, $(\Theta(t) - z_i)$ of the individual i defines
163 the maladaptation of the individual i with respect to the optimum phenotype (or,
164 alternatively, it defines the "extremeness" of the climate event for the individual). Point
165 extreme events such as floods or fires cause non-selective high mortality in the
166 population, i.e. every phenotype has the same chances of surviving the event.

2.2 Optimum phenotype

The expected optimum phenotype $\mu_\Theta(t)$ moves at a constant rate $\beta_{\mu,\Theta}$ over time (i.e., trend), fluctuating randomly around its expected value $\mu_\Theta(t)$. The optimum phenotype $\Theta(t)$ is randomly drawn at each time step t from a normal distribution $\Theta(t) \sim N(\mu_\Theta(t), \sigma_\Theta(t))$. It is equivalent to consider $\Theta(t)$ as both the optimum phenotype and the value of a continuous climate variable (e.g., mean summer temperature or yearly rainfall), and I will use the two terms interchangeably throughout this work.

Mean and variance of the climate variable at time t are thus:

$$\begin{cases} \mu_\theta(t) = \mu_{\theta,0} & when\ t < t_{ch} \\ \mu_\theta(t) = \mu_{\theta,0} + \beta_{\mu,\theta}\left(t - t_{ch}\right) & when\ t \geq t_{ch} \end{cases} \tag{1}$$

$$\begin{cases} \sigma_\theta(t) = \sigma_{\theta,0} & when\ t < t_{ch} \\ \sigma_\theta(t) = \sigma_{\theta,0} + \beta_{\sigma,\theta}\left(t - t_{ch}\right) & when\ t_{ch} \leq t \leq \left(t_{ch} + t_{inc}\right) \\ \sigma_\theta(t) = \sigma_{\theta,0} + \beta_{\sigma,\theta}\, t_{inc} & when\ t > \left(t_{ch} + t_{inc}\right) \end{cases}$$

where t_{ch} is the time at which there is a change (*ch*) in the climate. Eq. (1) indicates that the directional climate trend steadily increases through time after t_{ch} years and that the increase in variability starts after t_{ch} years, but stops after $t_{ch}+t_{inc}$ years. An alternative formulation to Eq. (1) would allow variability to more slowly build up over time; however, in the case of variability slowly increasing over longer times, the effects of higher climate variability would affect the individuals only towards the end of simulation time. As informed by the goals of this work, I preferred to let individuals

190 trying to survive a higher climate variability (which is among the least investigated
191 aspects of climate and environmental change) for a longer time period.
192 With the model formulation of Eq. (1), both the mean and variance of the distribution
193 of the climate variable change over time so as to make the occurrence of events more
194 likely after climate change (i.e., $t > t_{ch}$) than before, since after climate change, the
195 realized (i.e., random draw from the statistical distribution of climate) climate is
196 increasingly likely to be in the region of extremes (say, in the right 5% or 2.5% of the
197 Gaussian distribution of climate) of the statistical distribution of climate before climate
198 change.
199 Point extreme events E leading to trait-independent high mortalities occur with annual
200 probability p(E_b) when $t < t_{ch}$ (i.e. b - before climate change) and p(E_a) when $t > t_{ch}$.

201 **2.3 Quantitative trait and survival**

202 I model the phenotype z of an individual i, z_i, as the sum of its genotypic value a_i and a
203 statistically-independent random environmental effect e_i drawn from $N(\mu_E, \sigma_E^2)$:

204 $$z_i = a_i + e_i \quad (2)$$

205 The narrow sense heritability $h^2 = \sigma_G^2 / \sigma_z^2$ is the proportion of the phenotypic variance
206 σ_z^2 present in the population that is explained by the additive genetic variance σ_G^2 (i.e.
207 the variance of $\boldsymbol{a}$ in the population).
208 For an individual i, the genetic value a_i is determined by n_l freely recombining diploid
209 loci, with additive allelic effects within- and among-loci, that is $a_i = \sum_{j=1}^{l} n_{i,j}$, where $n_{i,j}$
210 is the sum of the allelic values at locus j. For computational reasons, I chose $n_l = 10$.
211 Allelic values are randomly drawn from a Gaussian distribution with mean of 0 and

212 variance equal to σ^2_a. For simplicity, I did not model either dominance or epistatic
213 variation or other complicating factors such as genotype-environment interaction and
214 linkages. Likewise, I did not model mutation, since previous work has shown that
215 mutation does not appear to have any effect short-term on extinction risk and the
216 evolution of traits on contemporary temporal scales (Vincenzi 2014).

217 Stabilizing selection is modeled with a Gaussian function (Bürger and Lynch 1995,
218 Zhang 2012), with fitness W (Endler 1986) for an individual with phenotypic trait z_i equal
219 to:

220 $$W(t,z_i) = W(t)_i = exp\left[-\frac{\left(z_i - \Theta(t)\right)^2}{2\omega^2}\right] \quad (3)$$

221 and equivalent in this model to the annual survival probability of individual i. The
222 curvature of the fitness function near its optimum increases with decreasing ω^2; it follows
223 that that the smaller ω^2, the stronger is selection. Stabilizing selection is usually measured
224 by the standardized quadratic selection gradient γ, which is defined as the regression of
225 fitness W on the squared deviation of trait value from the mean (Lynch and Walsh 1998).
226 An optimum phenotype in the tails of the distribution is likely to cause a large drop in
227 population size and can be considered an extreme climate event (Fig. 1).

228 The median γ = -0.1 for stabilizing selection found by Kingsolver et al. (2001)
229 corresponds to a value of $\omega^2/\sigma_E^2 = 5/[1-h^2]$, where σ_E^2 is the variance of the
230 environmental component of the phenotype defined in Eq. (2), when stabilizing selection
231 is modeled using a Gaussian fitness function.

232 Eq. (3) can be written:

$$W_i = exp\left[-s \cdot \left(z_i - \Theta(t)\right)^2\right] \quad (4)$$

where $s = \frac{1}{2\omega^2}$. With γ = -0.1, σ_E^2 = 1, and h^2 = 0.2, the strength of selection s is about 0.08.

I assumed that both strength of selection s and environmental variance σ_E^2 remain constant through time. When a point extreme occurs, the probability of yearly survival of individuals i is $W_i(1 - m_{E_I})$, where m_{E_I} is mortality caused by the point extreme event.

2.4 Simulations

As this study focuses on the more immediate effects of climate change, the simulations last 250 years. Parents mate at time t-1, offspring are born at time t and become of age 1 at t+1. The sequence of operations is mortality of adults, mating and reproduction, mutation, mortality of offspring. At the start of each simulation, for each individual a value of a and e (Eq. 2) is randomly drawn from their initial distribution. A population is considered extinct if at any time during the simulation there are fewer than 2 individuals in the population. Parents form mating pairs starting at age a_f and produce a number of offspring randomly drawn from a Poisson distribution with intensity λ_o. Offspring receive for the same locus one allele from each parent.

2.4.1 Parameter values

With numerical simulations, it is inevitable to face a trade-off between specificity and generalizability of the modeled processes and of the simulation results. I reduced parameter space by fixing K = 500 individuals, $\mu_{\Theta,1}$ = 0, $\sigma_{\Theta,1}$= 1, μ_E= 0, σ_E^2=1, σ_G^2 = 2 10^{-1}, σ_a = 5 10^{-2}, p($E_{I,b}$) = 0.05, and t_{inc} = 25. For the other parameters, I chose range of

254 values that are both realistic for natural populations with moderately fast life histories,
255 like salmonids (e.g., age distribution skewed toward individuals younger than 10 years
256 old, sexual maturity reached when individuals are between 1 and 4 years old), and
257 instrumental for the main goal of the study, e.g., testing hypotheses on the effects of
258 extreme events on population and genetic dynamics and on risk of extinction.

259 I performed simulations with selection strength s equal to either 8 10^{-2} (average
260 selection strength) or 1.1 10^{-2} (moderately strong selection). For the rate of increase in the
261 mean of the climate variable, I used $\beta_{\mu,\Theta}$ = 0 (base scenario) and 1.5 10^{-2}. I used rates of
262 the increase in the standard deviation of the climate variable $\beta_{\sigma,\Theta}$ from 0 (base scenario)
263 to 1.5 10^{-2}. According to Bürger and Lynch (1995), when the standard deviation of the
264 distribution of the optimum σ_θ reaches the same order of magnitude as the width ω of the
265 fitness function, the population is at risk of going suddenly extinct, with little role played
266 by genetics. Therefore, I chose values of $\beta_{\sigma,\Theta}$ that strongly increase the probability of
267 climate extremes, but did not inevitably make the population go extinct.

268 I used frequency of point extreme events p(E_a) of either 5 10^{-2} (no variation before and
269 after climate change, corresponding to a recurrence interval of 20 years), 10 10^{-2} (i.e.,
270 recurrence interval is 10 years) or 15 10^{-2} (Table 1). I used moderate mortalities caused
271 by point extremes (simulations with m_E equal to either 0.3, 0.5, 0.7) and moderate p(E_a),
272 since with higher mortality induced by point extremes and higher probability of their
273 occurrence the system will be largely driven by the point extremes, with no or little role
274 of genetics and demography in determining population dynamics and risk of extinction.

For the Poisson distribution of the yearly number of offspring per mating pair, I used λ_o equal to either 1.0, 1.5, 2.0 or 2.5 and age at first reproduction from 1 to 4 years old with a step of 1. Parameter values are reported in Table 1.

2.4.2 Initialization

To reach mutation-selection-drift balance, I first let the population evolve for t_{ch} years in an environment in which mean and variance of the distribution of the optimal phenotype Θ are constant. In preliminary simulations it was found that after $t_{ch} \sim 100$ years both phenotypic mean and variance did not noticeably change. Then, the mean of Θ increases for 150 years and the variance of Θ for 25 years, which was then kept constant up to the end of simulation time.

I started every simulation replicate with 500 individuals. I modeled 10 alleles present in the population for each locus, which value was randomly drawn from a normal distribution $N(0, \sigma_A^2)$. Since I set $\sigma_E^2 = 1$ and $\sigma_G^2 = 0.2$, the narrow sense heritability h^2 was around 0.2 at $t = 1$, close to 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).

2.4.3 Characterization of simulations

At the single-replicate level, to characterize the behavior of the simulated populations I tracked or recorded (among other results): (*a*) whether the population was extinct or still persisting at the end of the simulation time (0 for persistence and 1 for extinction, in the latter case I also recorded the year of extinction). At each time *t*, I then recorded: (*b*) the distribution of the trait *z* in the population and individual maladaptation; (*c*) population

297 size *N* after mortality of adults*;* (*d*) total number of alleles and allelic frequencies (the
298 latter every 25 years).
299 For an ensemble of realizations (10 replicates for a fixed set of parameters) I also
300 computed the frequency of population extinction as the number of replicates in which the
301 population went below two individuals during simulation time.

302 **2.5 Statistical analysis**

303 I used simulation results as pseudo-empirical data and analyzed them with standard
304 statistical and machine learning models. The main focus of the statistical analyses and
305 modeling was more on prediction than on inference or traditional *p*-value
306 hypothesis-testing.
307 I estimated parameters of Generalized Additive Models (GAMs, Wood 2006),
308 Generalized Linear Models (or Ordinary Least-Square regression models, McCullagh and
309 Nelder 1989), and Random Forests (Breiman 2001a) using as response variable either (*i*)
310 the total number of alleles (overall allelic richness) at the end of simulation time for the
311 populations that persisted, (*ii*) the difference in mean allelic frequency of the top 10% and
312 bottom 10% (according to their allelic value, top 10% were the alleles with the bigger
313 allelic value and *vice versa* for the bottom 10%) of alleles. For (*i*), in particular, I tested
314 whether the number of consecutive years (*n_low,* the only variable in the GAM models
315 for which I hypothesized a non-linear effect on the total number of alleles) under a low
316 population size threshold (*tr_low*) contributed to predicting the number of alleles at the
317 end of simulation time, in addition to climate variables and vital rates such as expected
318 intensity and frequency of extreme events, the variance of the optimum, expected yearly
319 number of offspring per mating pair and age at first reproduction. I calculated *tr_low*

using either 150, 100, or 50 individuals as the threshold (results were consistent when using either 150,100, or 50 individuals). For (*ii*), when the climate is changing (i.e., $\beta_{\mu,\Theta} > 0$), alleles with positive allelic values are expected to be more adaptive than those with negative (or positive, but smaller) allelic values. I tested whether a model including climate variables and vital rates trained on data from 80% of the replicates that did not go extinct could predict the difference in mean allelic frequency at year 250 (end of simulation time) of the top and bottom 10% of alleles according to their allelic values in the test data set (20% replicates that did not go extinct). I chose the top and bottom 10% of the alleles (10 alleles in the top and bottom sets), since the fate of single alleles is more likely to be affected by chance than that of a group of advantageous alleles.

Then, I investigated whether a combination of demographic and environmental factors measured or estimated in a short time window ("observation window") can predict the risk of extinction of the population in the following years ("prediction window"). First, I set aside a balanced test data set of simulation replicates (50% that went extinct and 50% that survived)—these simulations were not used in any phase of either model development or model training. Second, since the number of simulations that went extinct was approximately one-third of the number of those that survived, I augmented the data set by replicating 3 times the simulations that went extinct and were not included in the test data set.

Third, I fitted GLMs and GAMs with binomial error distribution (i.e., logistic regression), and classification Random Forests (RFs) with population extinction (1) or persistence (0) between ($t_{\text{ext}} - u$) as response variable, where t_{ext} is either (a) the time at extinction for the replicate that went extinct, or (b) a random deviate from a uniform

distribution bounded between 20 and 250 for the replicates that survived; u is a random deviate from a uniform distribution bounded between 1 and 10 years. This way, I am trying to model extinction or persistence not at a specific time, but in a "prediction window" of 10 years, whose beginning lays between year 10 and year 240 of simulation time. I used as candidate predictors, as measured in the 10 years ("observation window") before the "prediction window", minimum and mean population size N, the maximum value of the optimum phenotype, the expected yearly number of offspring per mating pair, age at first reproduction, and maximum and mean distance over the observation window between the mean phenotype and the optimum (i.e., maximum and mean population-level maladaptation, or maximum and mean "extremeness" of the climate).

In other words, I wanted to test whether a model including climate and population traits measured over a limited time frame could predict the extinction or persistence of the population in the years immediately following the end of the "observation window". The choice of the length of both the observation and prediction windows was based on what it is considered a "reasonable" length of population monitoring when the goal is to detect changes in population size and estimate the risk of population extinction. White (2019) collected the time series of population size of 822 populations of vertebrate species and found that 72% of time series required at least 10 years of continuous monitoring to achieve a high level of statistical power to detect significant trends in abundance (the code associated with this work allows to use between 5 and 20 years as length of the observation and prediction windows).

For the GAMs and GLMs, I estimated the optimal cutoff given equal weight to sensitivity (the probability that the model predicts extinction when the replicate went

extinct) and specificity (the probability that the model predicts persistence when the replicate persisted). Then, I tested the model by predicting population extinction and persistence on the test dataset using the computed optimal cutoff. For the classification RF models, I directly used the binary prediction (population going extinct or surviving) from the models. I used different modeling approaches because I did not explicitly model any mechanism or process that can be hypothesized to lead to extinction (i.e., models are correlative and not mechanistic), and different modeling approaches can give different insights on how contemporary extinctions are predicted (e.g., tree-based models like RFs provide a measure of variable importance for predicting the target variable (Breiman 2001a) and GAMs can model non-linear relationships between predictors and target variable using semi-parametric estimation). For the GAMs and GLMs, I centered and scaled the predictors in order to compare their importance (Schielzeth 2010). As I use realistic variable ranges representing the variability that may be observed in nature, some of the estimated parameters can be compared in terms of effects on a standardized scale. I also fitted the same models using non-standardized predictors to test for possible data leakage between training and testing data sets (results were directionally the same). I did not include interactions among predictors in the models in order to improve the interpretability of results. I visually checked residuals for violation of model assumptions.

3 Results

Results are fully reproducible. Data and R code are at https://github.com/simonevincenzi/Contemporary_Extinction.

387 After year 100, the directional trend, the increase in variability of climate, and the
388 increased occurrence and severity of point extremes led to noticeable fluctuations in
389 population size over time (Fig. 1). Twenty-one per cent of the 34 560 simulation
390 replicates went extinct. As expected, risk of extinction increased with higher frequency
391 and severity of point extreme events, older age at first reproduction, and fewer offspring
392 produced per mating pair (Fig. 2). Given an expected yearly number of offspring per
393 mating pair, the proportion of replicates that went extinct increased approximately
394 linearly with age at first reproduction (Fig. 2a). When considering all replicates or only
395 the most extreme scenario, for a fixed expected number of offspring produced per mating
396 pair, increasing age at first reproduction by one year would increase the probability of
397 going extinct by approximately 10% (Fig. 2a). The combination of relative high
398 frequency and high severity of extreme events led to a noticeably higher proportion of
399 replicates that went extinct (Fig. 2b). Among the replicates that went extinct, 16% of
400 them were not affected by a point extreme in the 10 years before extinction and 34% in
401 the 5 years preceding extinction.
402 In populations that persisted until the end of simulation time, the GLM and GAM models
403 that included *n_low* provided a good prediction of the total number of alleles at the end of
404 simulation time (Table 2). The total number of years with population size smaller than
405 150 individuals had a strong, negative non-linear effect on the total number of alleles at
406 the end of simulation time (Fig. 3). Models that did not include *n_low* had much lower
407 predictive performance (Table 2).
408 Models for differences in allelic frequency of more or less theoretically advantageous
409 alleles were able to explain less than 5% of the variance of the target variable (Fig. 4).

The average value of population-mean phenotype $\bar{z}$ in the last ten years of simulation time was negatively correlated with the difference in frequency of top and bottom 10% of alleles according to their allelic value at the end of simulation time ($r = 0.71$, $p < 0.01$).

The GLM, GAM, and RF models fitted on the training data sets had similar high predictive accuracy and low false positive and negative rates when predicting extinction or survival in the 10-year "prediction window" (Table 3). For more than 98% of replicates included in the test data set, the GLM, GAM, and RF models provided the same prediction of either extinction or persistence (Fig. 5). In the GAM model, only minimum population size in the observation window had a strong non-linear (negative) effect on the log-odds of population extinction. Likewise, minimum population size was the most important predictor in the RF model (Fig. 6a). The models without minimum and mean population size as predictors had fairly low accuracy (Table 3). The RF model without minimum and mean population size as predictors found age at reproduction and expected yearly number of offspring per mating pair as the most important predictors of contemporary extinction (Fig. 6b).

4 Discussion

Understanding and predicting the effects of extreme events on risk of extinction and population and genetic dynamics of natural populations is critical for both population forecasting and for managing human intervention in an increasingly more extreme world.

The results of the numerical simulations showed additive effects—with largely no interaction effects—between age at first reproduction and fecundity on risk of extinction for the range of values I simulated. In the replicates that survived up to the end of

simulation time, the total number of years in which the population was at a small size was a good predictor of allelic richness for the quantitative trait under selection. The population frequency of theoretically advantageous alleles was strongly correlated with the mean value of the phenotype under selection but was otherwise largely unpredictable. Last, simple models including basic demographic and vital rates information, along with climate and environmental data, provided excellent predictions of contemporary risk of population extinction.

4.1 Life histories

Life-history theory predicts a prevalence of fast life histories in environments in which extreme events occur (Winemiller 2005). Fast life histories—usually defined as including a combination of faster body growth early in life, younger age at maturity, and higher reproductive effort early in the reproductive life of the individual—should allow for faster population growth rate after a drastic reduction in population size, an adaptive life-history strategy when the population is at risk of extinction.

For many animal species that frequently experience the often-catastrophic effects of extreme climate or point events—and have limited movement range for physiological and behavioral reasons or for the environment they inhabit (e.g., freshwater fish in mountain streams, insects)—offspring production is typically very high compared to the habitat carrying capacity. Thus, offspring production is not usually what is limiting population recovery, i.e. the re-establishment of the pre-event population size. However, when after a climate or point extreme event the population is reduced to such low numbers that the population is at immediate risk of extinction, younger age at first reproduction for the surviving individuals could be the life-history trait that makes the difference between

455 population persistence or extinction. Vincenzi et al. (2017) found that fish born after flash
456 floods had younger mean age at reproduction than fish born before flash floods; they
457 hypothesized that younger age at reproduction after flash floods was due to a
458 combination of faster growth due to lower population density and fewer older fish
459 competing for mates. However, younger age at sexual maturity and higher energetic
460 investment in offspring production often come at the cost of shorter life expectancy (Fay
461 et al. 2016), and life histories that are adaptive after population crashes can show lower
462 fitness in steady-state conditions (Vincenzi et al. 2012, 2014).

463 **4.2 Prediction of genetic dynamics and of population extinction**

464 Populations experiencing recurrent bottlenecks are expected to have their genetic pool
465 eroded over time. The erosion of the genetic pool should be noticeable in particular in the
466 loss of allelic richness, even after a single bottleneck event (Allendorf 1986). I found that
467 the extent of population bottlenecks, which I operationalized as the number of years in
468 which population size was relatively small with respect to the habitat carrying capacity
469 and species numerical potential, was a strong predictor of allelic richness for the
470 quantitative trait under selection in the simulations. These results appear to be partially
471 consistent with recent empirical results. Vincenzi et al. (2017) found an increase in the
472 proportion of fixed alleles in year-classes of two trout populations born after flash floods
473 that caused massive mortalities. Poff et al. (2018) tested predictions about population
474 genomic change in aquatic insects living in Colorado, US, mountain streams after a 1-in-
475 500-year rainfall event. They found that allelic richness at presumably neutral loci
476 declined after the event only in two out of six species analyzed. Moderate reduction of
477 allelic diversity after strong bottlenecks might be attributable to the particular

478 demographic history of the populations that are investigated; according to Bouzat
479 (2010), one can expect that populations experiencing recurrent bottlenecks might have
480 had their genetic pool already eroded over time, which would decrease the effectiveness
481 of both purifying selection and random allele loss. In addition, the loss of alleles could be
482 greater in species—like salmonids——with high variance in reproductive success among
483 adults (i.e., greater than Poisson variance in reproductive success), although high
484 variance in reproductive success has been found to bias (i.e., make false positives more
485 likely) empirical investigations of genetic bottlenecks (Hoban et al. 2013). Moreover, in
486 the simulations of population dynamics, we started from 10 unique alleles for each of the
487 10 loci, and the high initial allelic diversity may explain the strong relationship that was
488 found between the temporal extent of bottlenecks and allelic richness.
489 On the other hand, a model including age at first reproduction and fecundity of the
490 species, along with some traits of the environment, was not able to predict the dynamics
491 of the population frequencies of more advantageous alleles for the quantitative trait under
492 selection. However, a strong correlation was found between the frequencies of more or
493 less advantageous alleles at the end of simulation time and the average value of the
494 phenotype under selection. This result seems to at least suggest that, although the fate of
495 alleles is difficult to predict from just the coarse-grain description of the environment and
496 of the species, even in an extreme environment that also causes trait-independent mass
497 mortalities, a shift in the phenotype is likely to be caused by the increased prevalence of
498 the most advantageous alleles.
499 One of the foundational tenets of conservation biology is that small, fragmented
500 populations should be considered locally vulnerable to extinction—even more critically

501 so when affected by highly variable climatic conditions and other environmental
502 disturbances. The conditions that led to the extinction of a population or species can
503 almost always be understood retrospectively, but forecasting extinction, especially over
504 contemporary time horizons, is much more challenging. In this work, I found that the
505 most important predictors of contemporary extinctions were mean and minimum
506 population size measured in the few years before the "prediction window". However, it
507 was not uncommon for the simulated populations to swiftly rebound after collapses in
508 numbers, and age at reproduction and yearly fecundity were the most important
509 predictors of extinction when measures of population size were not included in the model.
510 This result highlights the importance of age at first reproduction and yearly fecundity for
511 population persistence in highly stochastic environments, as also suggested by theoretical
512 (Bürger and Lynch 1995) and experimental (Griffen and Drake 2008) studies. However,
513 other genetic challenges not accounted for in my simulation model are likely to be
514 encountered by populations that decline to very small numbers, such as a reduction of
515 viability and/or fecundity due to either inbreeding or the expression of deleterious alleles
516 (Willi et al. 2006).
517 Although it may appear from the simulation results that vital rates and environmental
518 conditions play a small role in models that predict contemporary risk of extinction, those
519 rates and conditions heavily contribute to determining population size in the "observation
520 window"; for example, populations with higher fecundity and younger age at first
521 reproduction are less likely to remain at low population sizes than populations with lower
522 fecundity and delayed sexual maturity. Likewise, a more extreme environment (e.g.,
523 greater selection strength and more frequent and/or severe climate and point extremes)

524 tends to decrease average population size, either due to acute events that kill individuals
525 or constant recovery from population crashes.
526 Luck also plays a major role in determining whether a population will recover after a
527 population crash. Vincenzi et al. (2017) found that the almost-complete recovery of a
528 trout population that was reduced to a handful of individuals after a flash flood was due
529 to the large production of offspring by a single mating pair. Considering the high
530 variance in adult reproductive success in trout populations—which is at least partially due
531 to differences in individual "quality" (Auld et al. 2019)—had the mating pair been killed
532 or displaced during the flash flood, population recovery would have suddenly become
533 much less likely.

534 **4.3 Modeling considerations**

535 Modeling and simulation approaches can help understand the effects of multiple
536 extreme stressors on the contemporary risk of extinction of species and can be used to
537 guide or support both the set-up of ecologically relevant experimental designs and the
538 interpretation of biological responses to multiple stressors.
539 However, models of population and genetic dynamics are limited in their scope of
540 prediction by both the understanding of the biology and ecology of the species and the
541 availability of data to parametrize, train, and test models, along with modeling choices
542 (e.g., explicit or implicit modeling of alleles, clustered or "well-mixed" individuals or
543 populations). Although often intuitive, it is nevertheless important to remind ourselves
544 that the simulation results of modeling exercises depend on, first, our biological and
545 ecological understanding, and, second, the simplified modeling of the species and the
546 environment they inhabit. For instance, general trade-offs between allocation of resources

547 to competing physiological functions are not only often intrinsically challenging to
548 model, but they may also vary over time and space for the same species or population.
549 That is, even when there is a qualitative understanding of biological or ecological
550 processes, the parameterization and choice of parameter values for the model may be too
551 uncertain to provide actionable predictions.

552 Trade-offs between model accuracy and interpretability also need to be taken into
553 account when developing models of population and genetic dynamics. Accuracy
554 describes the ability of a model to explain observed data and make correct predictions,
555 while interpretability concerns to what degree the model allows for understanding
556 processes. Often, there is a trade-off between accuracy and interpretability: more
557 complex models are usually opaque, while more interpretable models often do not
558 provide the same accuracy or predictive power of more complex models (Breiman
559 2001b). Then, although intuitively more complex models are expected to provide more
560 accurate predictions of risk of extinction or population and genetic dynamics, this is not
561 always the case. For instance, Ward et al. (2014) tested the predictive performance of
562 short-term forecasting models of population abundance of varying complexity. They
563 found that more complex models often performed worse than simpler models, which
564 simply treated the most recent observation as the forecast. In their case, the estimation of
565 even a small number of parameters imposed a high cost while providing little benefit for
566 short-term forecasting of population abundance. However, when there was a clear signal
567 of cyclic dynamics, more complex models were able to more accurately predict future
568 population sizes.

As always, the purpose of a scientific investigation should drive model formulation, the type and amount of data collected, and the acceptable uncertainty of model predictions.

Ethics

Not applicable

Data accessibility

Data and relevant code for this research work are stored in GitHub: https://github.com/simonevincenzi/Contemporary_Extinction

Authors' Contributions

Simone Vincenzi conceived the ideas, designed the methods, run the analyses, and wrote the manuscript.

Competing interests

The author declares no competing interests

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691 **Tables**

692

693 **Table 1.** Values of parameters of the model of population and genetic dynamics.

694

Parameters	Values	Description
K	500	Population ceiling
λ_o	1.0, 1.5, 2.0, 2.5	Intensity of the Poisson distribution of yearly number of offspring per mating pair
a_f	1, 2, 3, ,4	Age at first reproduction
t_{ch}	100	Years since the start of the simulation before climate change
t_{inc}	25	Time of increase of variability (variance of the normal distribution of the climate variable) after climate change
n_l	10	Number of diploid loci
σ^2_A	$6.25\ 10^{-3}$	Additive genetic variance per locus at the start of simulation
σ^2_a	$2.5\ 10^3$	Variance of the normal distribution of allelic values
σ^2_G	0.2	Additive genetic variance of the quantitative trait at the start of simulation
μ_E	0	Mean environmental effect

σ_E^2	1	Environmental variance
m_E	0.3, 0.5, 07	Mortality caused by the point extreme event
s	8, 11 10^{-2}	Strength of selection
p(E_b)	5 10^{-2}	Probability of occurrence of point extreme events before climate change
p(E_a)	5, 10,15 10^{-2}	Probability of occurrence of point extreme events after climate change
$\mu_{\Theta,0}$	0	Mean of the normal distribution of the phenotypic optimum from year 1 to t_{ch}
$\sigma_{\Theta,0}$	1	Standard deviation of the normal distribution of the phenotypic optimum from year 1 to t_{ch}
$\beta_{\mu,\Theta}$	0, 1.5 10^{-2}	Annual increase (directional trend) of the mean of the normal distribution of the climate variable from year t_{ch} to the end of simulation
$\beta_{\sigma,\Theta}$	0,1,1.5 10^{-2}	Annual increase of the standard deviation of the normal distribution of the climate variable from year t_{ch} to $t_{ch} + t_{inc}$

Table 2. Performance of Ordinary Least-Squares regression models (OLS), Generalized Additive Models (GAM) and Random Forest models (RF) when predicting the total number of alleles at the end of simulation time for the replicates that did not go extinct. All populations started with 10 alleles for each of the 10 loci for a total of 100 unique alleles. Full models include as predictors *n_low*, $\beta_{\sigma,\Theta}$, $\beta_{\mu,\Theta}$, p(E_a), m_E, a_f, λ_o, and *s*. *n_low* is the number of years the population was below 150 individuals and all other symbols are as in Table 1 (results were similar with *tr_low* = 100 or 50 and are reported in the computer code associated with this paper). The training data set had 21 523 replicates (80% of the replicates that survived up to the end of simulation time) and the test data set had 5 371 replicates. R^2 was calculated with respect to the 1:1 predicted-observed line; *MAE* is the mean absolute error calculated over the whole test data set. Over the entire data set (training and test), the number of alleles at the end of simulation time was [mean ± sd] 79.84 ± 21.11.

Model	R^2	*MAE*
RF_*full*	0.82	6.6
RF_*red*	0.24	15.0
GAM_*full*	0.78	7.8
OLS_*full*	0.71	8.8
OLS_*red*	0.22	15.2

716 **Table 3.** Generalized Linear Model with logit link function for prediction of extinction
717 (1)/persistence (0) of a population over a 10-year period ("prediction window") with
718 predictors minimum population size min(N), mean population size $\bar{N}$, maximum value of
719 the optimum phenotype max(Θ), maximum and minimum mean population-level
720 maladaptation (or "extremeness" of the climate extreme) max($\Theta(t) - z(t)$) and
721 mean($\Theta(t)$-$z(t)$), and occurrence of a point extreme E, all measured in the 10 years before
722 the start of the "prediction window" (i.e., in the "observation window"), along with
723 selection strength s, age at first reproduction a_f and expected yearly number of offspring
724 per pair λ_0 (*full* model). In the *reduced* model, I excluded min(N) and $\bar{N}$. All predictors
725 were standardized (s and E are categorical variables with two levels each and they were
726 not standardized) and I report mean estimate and standard error of the regression
727 coefficients for the GLM models (estimate, standard errors and significance where
728 applicable for the GAM and RF models are in the computer code associated with this
729 paper). The GLM, GAM, and RF models were trained on 39 547 replicates (36% went
730 extinct) and tested on 4 600 replicates (50% went extinct). For the full and reduced GLM
731 models, when using the optimal cutoffs (*full* = 0.54, *reduced* = 0.35), accuracy when
732 tested on the validation data set was 97% for the *full* model and 77% for the *reduced*
733 model, false positive rate 0.03 and 0.26, false negative rate 0.03 and 0.19. For the GAM
734 models (details in computer code associated with this article), optimal cutoffs were 0.38
735 for the *full* model and 0.35 for the *reduced* model, accuracy 97% and 77%, false positive
736 rate 0.03 and 0.25, false negative rate 0.03 and 0.20. For the RF models, accuracy when
737 tested on the test data set was 97% for the *full* model and 72% for the *reduced* model,
738 false positive rate 0.02 and 0.16, false negative rate 0.04 and 0.38.

	full	*reduced*
Intercept	-5.63(0.14)	-2.39(0.03)
min(N)	-5.41(0.20)	-
$\bar{N}$	-1.34(0.10)	-
S	0.62(0.06)	1.02(0.03)
max(Θ)	-0.14(0.04)	-0.11(0.02)
λ_0	-0.42(0.03)	-0.89(0.01)
a_f	0.42(0.03)	0.80(0.01)
E	0.64(0.07)	1.50(0.03)
max($\Theta(t) - z(t)$)	0.06(0.05)	0.28(0.02)
mean($\Theta(t) - z(t)$)	0.13(0.04)	0.62(0.03)

Figure captions

Figure 1. Examples of simulation replicates. The black solid line and black points represent population size, circles are point extremes, the gray dashed line is the value of the optimum phenotype Θ, and the solid gray line is the mean phenotype $\bar{z}$ in the population. Both Θ and $\bar{z}$ are re-scaled for graphical purposes. Parameters for the simulation in panel (a): $\beta_{\sigma,\Theta} = 0$, $\beta_{\mu,\Theta} = 15\ 10^{-2}$, p($E_a$) = 10 10^{-2}, $m_E = 0.7$, $a_f = 4$, $\lambda_0 = 2$, $s = 11\ 10^{-2}$. (b): $\beta_{\sigma,\Theta} = 15\ 10^{-2}$, $\beta_{\mu,\Theta} = 15\ 10^{-2}$, p($E_a$) = 15 10^{-2}, $m_E = 0.3$, $a_f = 3$, $\lambda_0 = 2$, s = 8 10^{-2}. (c): $\beta_{\sigma,\Theta} = 15\ 10^{-2}$, $\beta_{\mu,\Theta} = 0$, p(E_a) = 15 10^{-2}, $m_E = 0.5$, $a_f = 3$, $\lambda_0 = 1$, $s = 8\ 10^{-2}$. In the simulation in panel (c), the population went extinct at year 184. Symbols are as in Table 1.

Figure 2. Extinction probability (number of populations going extinct divided by the number of replicates run for a given set of parameter values) for scenarios of: (a) different ages at first reproduction and expected yearly number of offspring per mating pair (solid line: all replicates; dashed line = most extreme environment, i.e., p(E_a) = 15 10^{-2}, $m(E_a) = 0.7$, $\beta_{\mu,\Theta} = 5\ 10^{-2}$, $\beta_{\sigma,\Theta} = 1.5\ 10^{-2}$); (b) different probability of point extremes and probability of dying from point extremes.

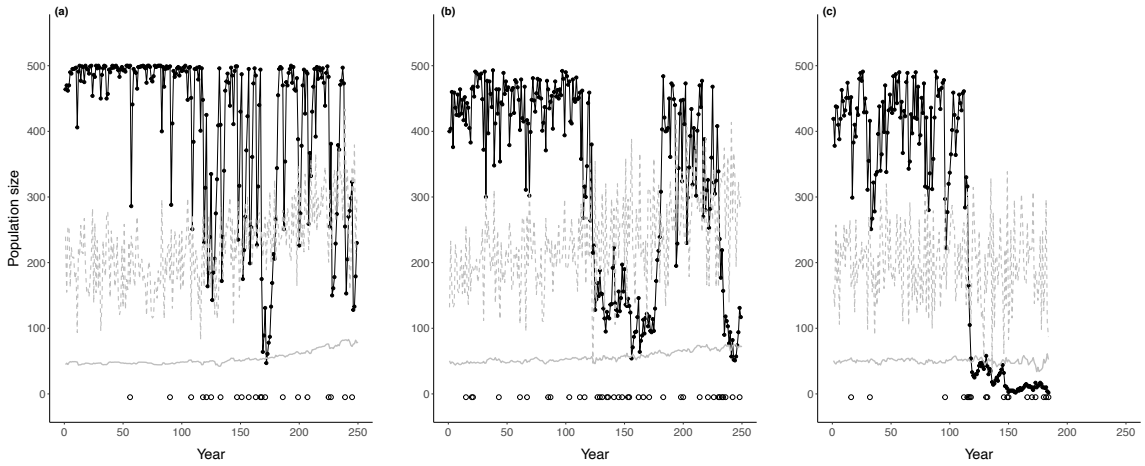
Figure 3. Partial non-linear effect of the total number of years in which the population is below 150 individuals during simulation time (*n_low*) on the total number of alleles at the end of simulation time, as found from the Generalized Additive Model of Table 2. The GAM algorithm found $k = 3$ as the optimal number of degrees of freedom for the spline (i.e., a cubic). Model details and results are in the in the computer code associated with this paper.

764 **Figure 4**. Panels (a-b): population dynamics of two simulation replicates (details
765 about the replicates are in the computer code associated with this paper). Lines and
766 symbols are as in Figure 1. Panels (c-d) dynamics of allelic frequency for the populations
767 in panels (a-b) (a→c, b→d). Thin dashed gray lines represent the allelic frequencies
768 measured every 50 years for alleles in the bottom 10% of allelic values (for (c): n = 10,
769 allelic value [mean ± sd] = -0.27 ± 0.08; (d) n = 10, allelic value = -0.21 ± 0.04) and thin
770 solid black lines represent the top 10% (for (c): n = 10, allelic value = 0.28 ± 0.08; (d)
771 0.25 ± 0.06). Thick dashed gray lines represent the average frequency in the population
772 of alleles in the bottom 10% of allelic values and thick solid black lines represent the
773 average frequency of the top 10%. In (c), the alleles in the bottom 10% of allelic values
774 were more frequent in the population at the end of simulation time than alleles in the top
775 10%, and *vice versa* in panel (d).
776 **Figure 5.** Examples of Generalized Linear Model (GLM), Generalized Additive
777 Model (GAM), and Random Forest (RF) predictions of extinction in a "prediction
778 window" based on climate and population traits observed in a "observation window".
779 Circles are point extremes, the black solid line and black points represent population size,
780 the gray dashed line is the optimum phenotype re-scaled for graphical purposes. The
781 letter O denotes the "observation window" and P the "prediction window". For each
782 model in the legend, 1 means the model predicted extinction (e.g., RF = 1 means that the
783 RF model predicted extinction) and 0 otherwise; in panel (d), all models predicted
784 extinction, but the replicate did not go extinct. In panel (a) only the RF model predicted
785 extinction and the replicate went extinct, in (b) only the GLM model predicted extinction

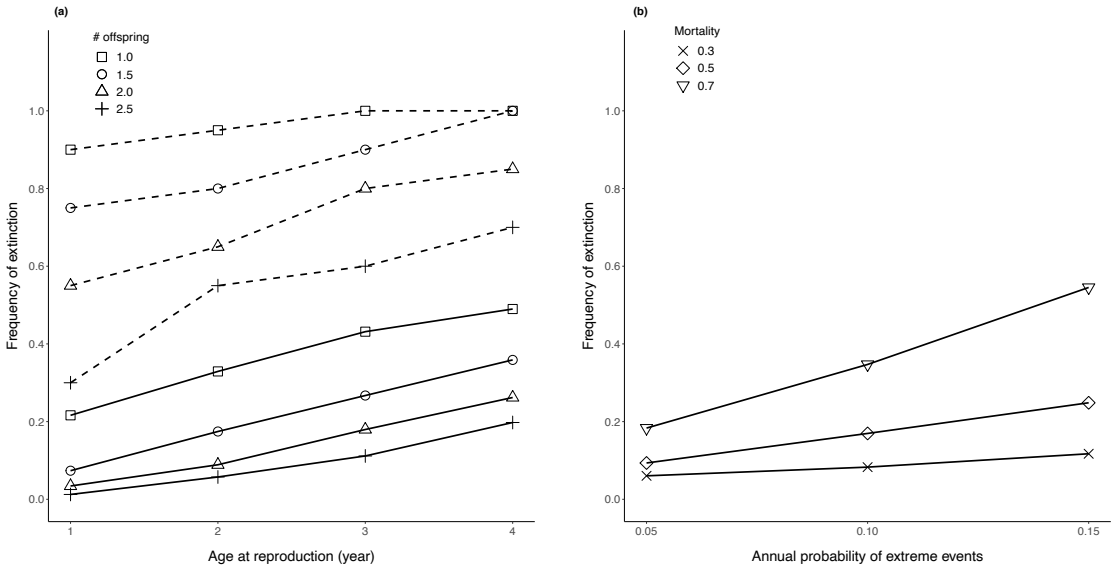
786 and the replicate went extinct, and in (c) only the GAM model predicted extinction and
787 the replicate did not go extinct.

788 **Figure 6.** Variable importance for the full (panel (a)) and reduced (i.e., without
789 min(N) and $\bar{N}$, panel (b)) Random Forest models for prediction of extinction in the 10-
790 year "prediction window" based on climate/environmental and population traits measured
791 in the 10-year "observation window". To compute variable importance, for each tree, the
792 prediction accuracy on the out-of-bag portion of the data is recorded, and the same is
793 done after permuting each predictor. The difference between the two accuracies are then
794 averaged over all trees and normalized by the standard error. The most important
795 predictor is assigned the value of 100 and the other predictors are scaled accordingly.

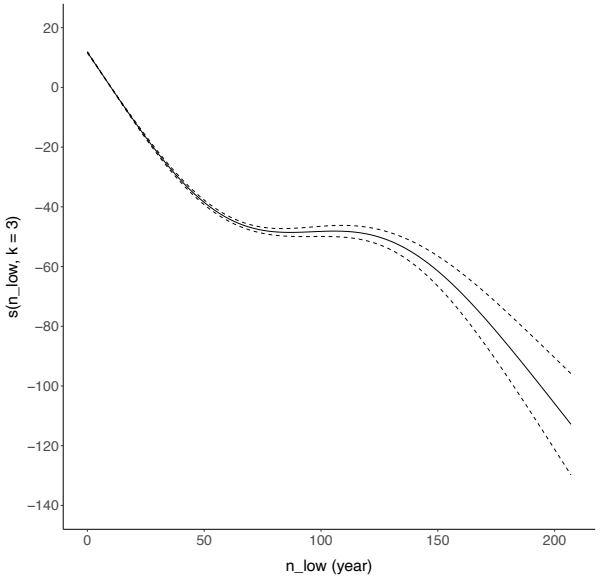
796 **Figure 1**


(a)
(b)
(c)
Population size
Year
Year
Year
0
100
200
300
400
500
0
50
100
150
200
250

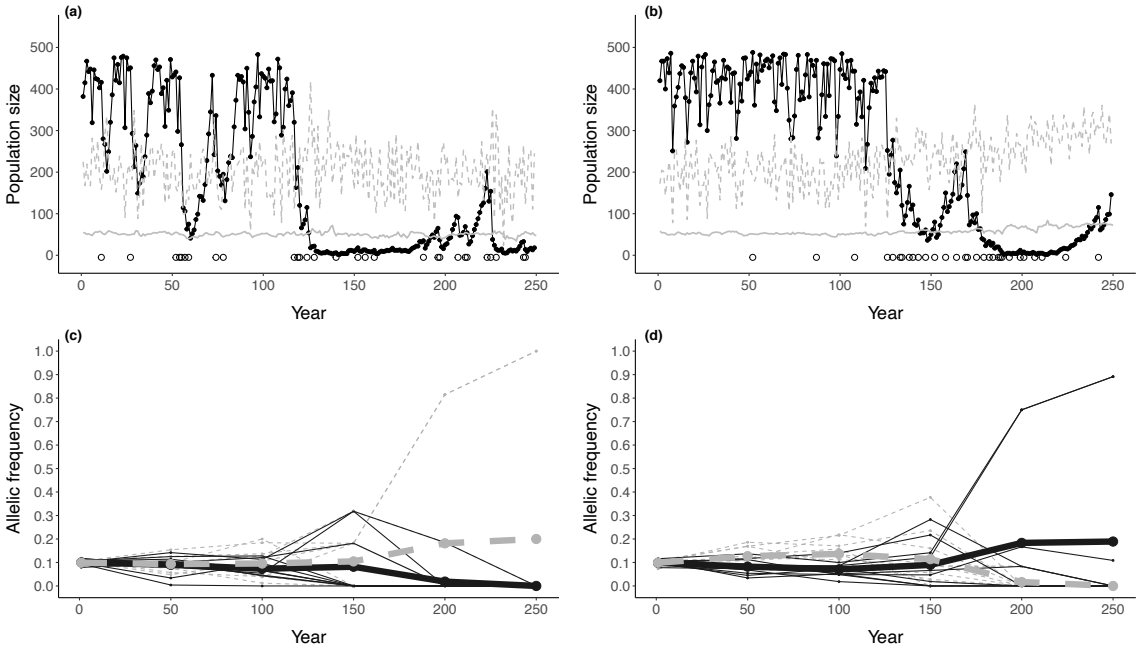
797 **Figure 2**


(a)
offspring
1.0
1.5
2.0
2.5
Frequency of extinction
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
Age at reproduction (year)
(b)
Mortality
0.3
0.5
0.7
Frequency of extinction
0.0
0.2
0.4
0.6
0.8
1.0
0.05
0.10
0.15
Annual probability of extreme events

798 **Figure 3**



799 **Figure 4**


(a)
(b)
(c)
(d)
Population size
Allelic frequency
Year
0
50
100
150
200
250
0
100
200
300
400
500
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

800 **Figure 5**

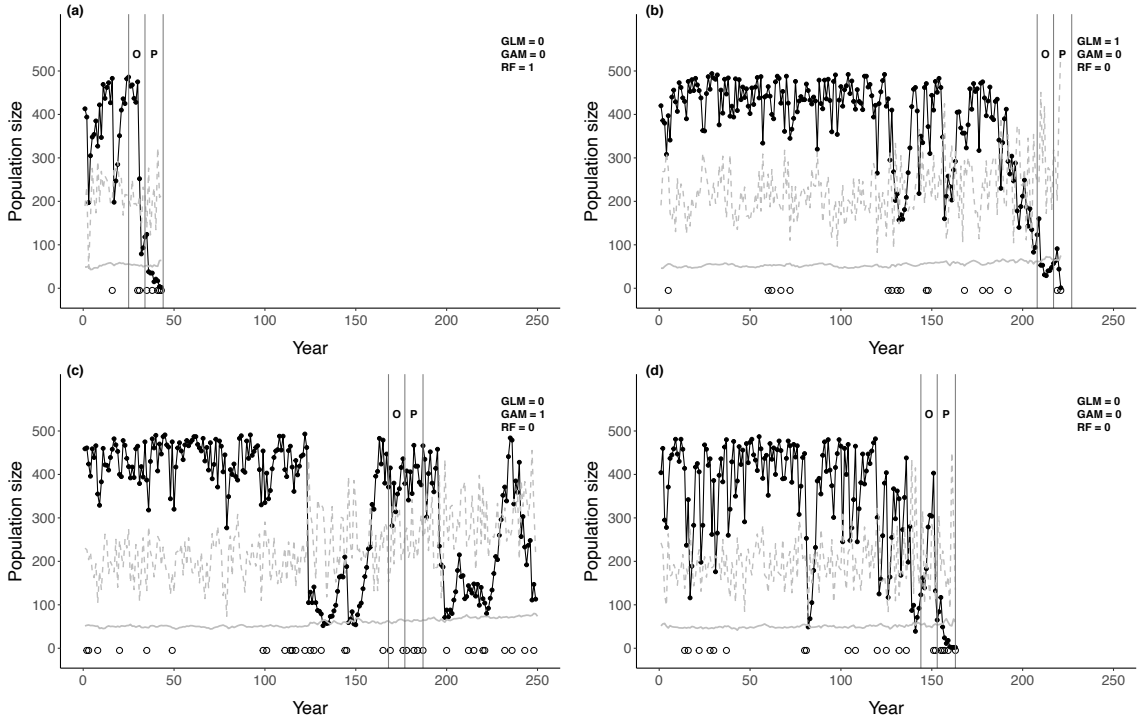
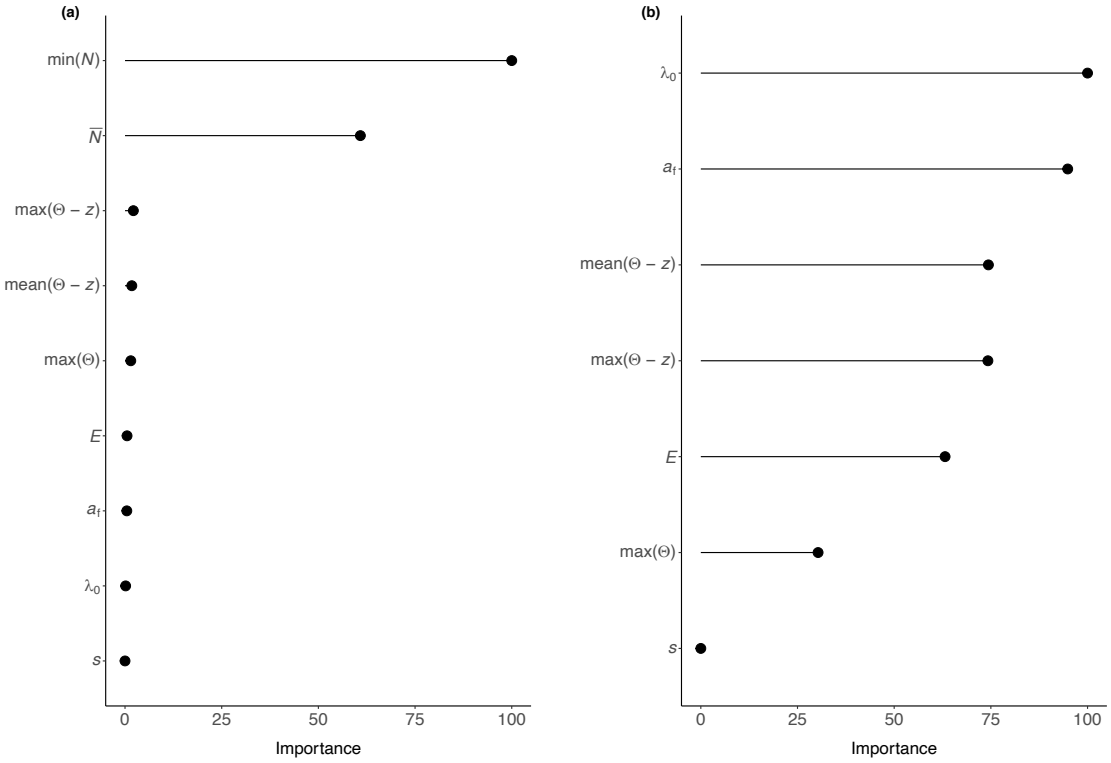

(a)
GLM = 0
GAM = 0
RF = 1
O
P
Population size
Year
(b)
GLM = 1
GAM = 0
RF = 0
O
P
Population size
Year
(c)
GLM = 0
GAM = 1
RF = 0
O
P
Population size
Year
(d)
GLM = 0
GAM = 0
RF = 0
O
P
Population size
Year

Figure 6


(a)
min(N)
N̄
max(Θ − z)
mean(Θ − z)
max(Θ)
E
a_f
λ_0
s
0
25
50
75
100
Importance
(b)
λ_0
a_f
mean(Θ − z)
max(Θ − z)
E
max(Θ)
s
0
25
50
75
100
Importance