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, 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. 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, One Earth editorial team 2020).

How to define extreme events is challenging, since 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 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 extremes such as fires and floods, which may have catastrophic effects on the affected species and ecosystems despite being relatively frequent in certain habitats. 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. However, despite the increased research and management focus on extremes, developing and testing general theories and hypotheses on the effects of extreme events remains more intrinsically challenging than for other aspects of climate and environmental change (van de Pol et al. 2017).

First, since the effects of extreme events are largely context-specific right, developing an overarching causal and predictive framework may 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. In addition, the demographic and genetic effects of climate and point extremes

57 (e.g., population crashes, loss of genetic diversity, inbreeding and maladaptation, changes
58 in population age and size structure, disruption in expression of quantitative traits)
59 (Bryant and Meffert 1995, Kirkpatrick and Jarne 2000) are often the result of chance, and
60 are thus not easily predictable or generalizable across species or habitats. Second, climate
61 and point extremes that result in strong demographic and genetic responses are often rare
62 events, whose occurrence may be also difficult to predict. Thus, when available,
63 pre-disturbance empirical data is likely to have been collected by chance, and the studies
64 on the effects of extreme events prone to be mostly opportunistic and anecdotal instead of
65 planned and comprehensive.

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

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

79 Second, when the change in the environment is abrupt, but not causing mass
80 mortalities, the evolution of fitness-determining traits might occur fast enough to stop
81 population decline and allow population recovery before extinction ("evolutionary
82 rescue", Bell and Gonzalez 2009). However, population bottlenecks such as those caused
83 by extreme events, especially when repeated over time, are predicted to decrease additive
84 genetic variance and allelic diversity in the affected populations (Bouzat 2010). As
85 adaptive potential tends to increase with genetic variability and genetic drift may
86 overwhelm selection in small populations, the effects of extreme events on genetic
87 variability are predicted to increase both short- and long-term risks of population
88 extinction, with smaller chances of evolutionary rescue (Falconer and Mackay 1996,
89 Willi and Hoffmann 2009).
90 Third, species may exhibit various adaptations to extreme events, some more
91 predictable and general than others. For instance, extreme, but predictable variations in
92 the flow regime of streams can select for fish life histories, such as spawning and
93 emergence time, that are synchronized either to avoid or exploit the direct and indirect
94 effects of extreme flows (Lytle and Poff 2004). On the contrary, unpredictable flow
95 events such as flash floods may have low direct selective consequences for the affected
96 populations, even though they might induce massive mortalities (Lytle 2000). In these
97 cases, natural selection after the extreme event is predicted to favor individuals with a
98 high capacity for increase in population size (*r* selection, Reznick et al. 2002). Intuitively,
99 when after an extreme event the population is reduced to a few individuals, faster
100 reproduction may be more critically needed than high fecundity, since the latter depends
101 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 interaction among climate trend (e.g., increase over years of average summer temperatures), climate variability and probability of point extremes (e.g., fires) had a minor effect on risk of extinction, time to extinction, and distribution of a quantitative trait selected for by climate after accounting for their independent effects. 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.

Here, I focus on prediction more than on 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 description and statistical and causal inference. The work is also not purely theoretical in scope, but is motivated 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 a "depressed" population size (e.g., ~ 1/3 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 positive 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 the population

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

150 2 Material and methods

151 The model I use in this work is an extension of the model developed in Vincenzi
152 (2014). The choice of parameter values for the present work was informed by the
153 available literature and by the results of Vincenzi (2014).

154 2.1 Overview of the model

155 I consider a population of monoecious individuals living in a habitat whose population
156 ceiling is K (Mangel and Tier 1993). The population is geographically isolated, with
157 neither immigration nor emigration from or to neighboring populations. A single
158 quantitative trait a corresponding to its breeding value for a phenotypic trait z
159 characterizes the individuals. The population has discrete overlapping generations with
160 $N(t)$ total individuals, where t is time in years. The environment is described by an
161 optimum phenotype $\Theta(t)$ that changes over time as a result from variations in a climate
162 driver such as rainfall or average summer temperature, which selects for the trait z. The
163 distance between the optimum phenotype $\Theta(t)$ and the trait z_i, ($\Theta(t) - z_i$), of the
164 individual i defines the maladaptation of the individual i with respect to the optimum
165 phenotype (or, alternatively, it defines the "extremeness" of the climate event for the
166 individual). Point extreme events such as floods or fires cause non-selective high
167 mortality in the population, i.e. every phenotype has the same chances of surviving the
168 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:

$$\begin{aligned} \mu_\Theta(t) &= \mu_{\Theta,0} + \mathbb{I}(t > t_{ch})\,\beta_{\mu,\Theta} t_{ch} \\ \sigma_\Theta(t) &= \sigma_{\Theta,0} + \mathbb{I}(t_{ch} < t < t_{ch} + t_{inc})\,\beta_{\sigma,\Theta} t_{ch} \end{aligned} \tag{1}$$

where t_{ch} is the time at which there is a change (ch) in the climate, $\mathbb{I}(\bullet)$ is and indicator function equal to 1 when $\bullet$ is true and 0 otherwise. 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 to avoid variability building up to unrealistic values over time. With the model formulation of Eq. (1), both the mean and variance of the distribution of the climate variable change over time so as to make the occurrence of events more likely after climate change (i.e., $t > t_{ch}$) than before, since after climate change, the realized (i.e., random draw from the statistical distribution of climate) climate is increasingly likely to be in the region of extremes (say, in the right 5% or 2.5% of the Gaussian distribution of climate) of the statistical distribution of climate before climate change.

Point extreme events E leading to trait-independent high mortalities occur with annual probability p(E_b) when $t < t_{ch}$ (i.e. b - before climate change) and p(E_a) when $t > t_{ch}$.

2.3 Quantitative trait and survival

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

$$z_i = a_i + e_i \tag{2}$$

The narrow sense heritability $h^2 = \sigma_G^2 / \sigma_z^2$ is the proportion of the phenotypic variance σ_z^2 present in the population that is explained by the additive genetic variance σ_G^2 (i.e. the variance of $\boldsymbol{a}$ in the population).

For an individual i, the genetic value a_i is determined by n_l freely recombining diploid loci, with additive allelic effects within- and among-loci, that is $a_i = \sum_{j=1}^{l} n_{i,j}$, where $n_{i,j}$ is the sum of the allelic values at locus j. For computational reasons, I chose $n_l = 10$. Allelic values are randomly drawn from a Gaussian distribution with mean of 0 and variance equal to σ^2_a. For simplicity, I did not model either dominance or epistatic variation or other complicating factors such as genotype-environment interaction and linkages. Likewise, I did not model mutation, since previous work has shown that mutation does not appear to have any effect short-term on extinction risk and the evolution of traits on contemporary temporal scales (Vincenzi 2014).

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

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

and equivalent in this model to the annual survival probability of individual *i*. The curvature of the fitness function near its optimum increases with decreasing ω^2; it follows that that the smaller ω^2, the stronger is selection. 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). An optimum phenotype in the tails of the distribution is likely to cause a large drop in population size and can be considered an extreme climate event (Fig. 1).

The median γ = -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 Gaussian fitness function.

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} . I did not allow for genetic recombination. Offspring receive for the same locus one allele from each parent.

2.4.1 Parameter values

I reduced parameter space by fixing K = 500, $\mu_{\Theta,1} = 0$, $\sigma_{\Theta,1} = 1$, $\mu_E = 0$, $\sigma_E^2 = 1$, $\sigma_G^2 = 2\ 10^{-1}$, $\sigma_{\mathrm{a}} = 5\ 10^{-2}$, p($E_{\mathrm{I,b}}$) = 0.05, and t_{inc} = 25 years. For the other parameters, I chose range of values that are both realistic for natural populations and instrumental for the main goal of the study, e.g., testing hypotheses on the effects of extreme events on risk of extinction and population and genetic dynamics.

I performed simulations with selection strength s equal to either 8 (average selection strength) or 1.1 10^{-2} (moderately strong selection). For the rate of increase in the mean of the climate variable, I used $\beta_{\mu,\Theta} = 0$ (base scenario) and 1.5 10^{-2}. I used rates of the increase in the standard deviation of the climate variable $\beta_{\sigma,\Theta}$ from 0 (base scenario) to 1.5 10^{-2}. According to Bürger and Lynch (1995), when the standard deviation of the

distribution of the optimum σ_θ reaches the same order of magnitude as the width ω of the fitness function, the population is at risk of going suddenly extinct, with little role played by genetics. Therefore, I chose values of $\beta_{\sigma,\Theta}$ that strongly increase the probability of climate extremes, but did not inevitably make the population go extinct.

I used frequency of point extreme events p(E_a) of either 5 (no variation before and after climate change, corresponding to a recurrence interval of 20 years), 10 (i.e., recurrence interval is 10 years) or 15 10^{-2} (Table 1). I used moderate mortalities caused by point extremes (simulations with m_E equal to either 0.3, 0.5, 0.7) and moderate p(E_a), since with higher mortality induced by point extremes and higher probability of their occurrence the system will be largely driven by the point extremes, with no or little role 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 remained basically constant. Then, the mean of Θ increases for 150 years and variance of Θ for 25 years. The variance of Θ was then kept constant up to the end of the simulation.

272 I started every simulation replicate with 500 individuals. I modeled 10 alleles present
273 in the population for each locus, which value was randomly drawn from a normal
274 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
275 was around 0.2 at $t = 1$, close to what commonly observed for life-history traits (Lynch
276 and Walsh 1998) and consistent with the Gaussian allelic approximation including only
277 quasi-neutral and adaptive mutations, for which $\sigma_G^2 = 0.225\sigma_E^2$(Lande 1995).

278 **2.4.3 Characterization of simulations**

279 At the level of single replicate, to characterize the behavior of the simulated
280 populations I tracked or recorded (among other results): (*a*) whether the population was
281 extinct or still persisting at the end of the simulation time (0 for persistence and 1 for
282 extinction, in the latter case I also recorded the year of extinction). At each time *t*, I then
283 recorded: (*b*) the distribution of the trait *z* in the population and individual maladaptation;
284 (*c*) population size *N* after mortality of adults; (*d*) total number of alleles and allelic
285 frequencies (the latter every 25 years).
286 For an ensemble of realizations (10 replicates for a fixed set of parameters) I also
287 computed the frequency of population extinction as the number of replicates in which the
288 population went below two individuals during simulation time.

289 **2.5 Statistical analysis**

290 I used simulation results as pseudo-empirical data and analyzed them with standard
291 statistical and machine learning modeling. The main focus of the statistical analyses and
292 modeling was more on prediction than on inference or traditional *p*-value
293 hypothesis-testing.

294 I estimated parameters of Generalized Additive Models (GAMs, Wood 2006),
295 Generalized Linear Models (or Ordinary Least-Square regression models, McCullagh and
296 Nelder 1989), and Random Forests (Breiman 2001a) using as response variable either (*i*)
297 the total number of alleles (overall allelic richness) at the end of simulation time for the
298 populations that persisted, (*ii*) the difference in mean allelic frequency of the top 10% and
299 bottom 10% (according to their allelic value, top 10% were the alleles with the bigger
300 allelic value and *vice versa* for the bottom 10%) of alleles. For (*i*), in particular I tested
301 whether the number of consecutive years (*n_low,* the only variable in the GAM models
302 for which I hypothesized a non-linear effect on the total number of alleles) under a low
303 population size threshold (*tr_low*) contributed to predict the number of alleles at the end
304 of simulation time, in addition to climate variables and vital rates such as expected
305 intensity and frequency of extreme events, variance of the optimum, expected yearly
306 number of offspring per mating pair and age at first reproduction. I calculated *tr_low*
307 using either 150 or 100 individuals as threshold (results were very similar when using
308 either 150 or 100 individuals). For (*ii*), when the climate is changing (i.e., $\beta_{\mu,\Theta} > 0$),
309 alleles with positive allelic values are expected to be more adaptive than those with
310 negative (or positive, but smaller) allelic values. I tested whether a model including
311 climate variables and vital rates trained on data from 80% of the replicates that did not go
312 extinct could predict the difference in mean allelic frequency at year 250 (end of
313 simulation time) of the top and bottom 10% of alleles according to their allelic values in
314 the test data set (20% replicates that did not go extinct). I chose the top and bottom 10%
315 of the alleles (10 alleles in the top and bottom sets), since the fate of single alleles is more
316 likely to be affected by chance than that of a group of advantageous alleles.

317 Then, I investigated whether a combination of demographic and environmental factors
318 measured or estimated in a short time window ("observation window") can predict the
319 risk the risk of extinction of the population in the following years ("prediction window").
320 First, I set aside a balanced test data set of simulation replicates (50% that went extinct
321 and 50% that survived)—these simulations were not used in any phase of model
322 development and training. Second, since the number of simulations that went extinct was
323 approximately one third of the number of those that survived, I augmented the data set by
324 replicating 3 times the simulations that went extinct and were not included in the test data
325 set.
326 Third, I fitted GLMs and GAMs with binomial error distribution (i.e., logistic
327 regression), and classification Random Forests (RFs) with population extinction (1) or
328 persistence (0) between (t_{ext} - u) as response variable, where t_{ext} is either (a) the time at
329 extinction for the replicate that went extinct, or (b) a random deviate from a uniform
330 distribution bounded between 20 and 240 for the replicates that survived. u is a random
331 deviate from a uniform distribution bounded between 1 and 10 years. This way, I am
332 trying to model extinction or persistence not at a specific time, but in a "prediction
333 window" of 10 years. I used as candidate predictors, as measured in the 10 years
334 ("observation window") before the "prediction window", minimum and mean population
335 size N, the maximum value of the optimum phenotype, the expected yearly number of
336 offspring per mating pair, age at first reproduction, and maximum and mean distance
337 over the observation window between the mean phenotype and the optimum (i.e.,
338 maximum and mean population-level maladaptation, or maximum and mean
339 "extremeness" of the climate). In other words, I wanted to test whether a model including

340 climate and population traits measured over a limited time frame could predict the
341 extinction or persistence of the population in the years immediately following the end of
342 the "observation window".
343 For the GAMs and GLMs, I estimated the optimal cutoff given equal weight to
344 sensitivity (probability that the model predicts extinction when the replicate went extinct)
345 and specificity (probability that the model predicts persistence when the replicate
346 persisted). Then, I tested the model by predicting population extinction and persistence
347 on the test dataset using the computed optimal cutoff. For the classification RF models, I
348 directly used the binary prediction (population going extinct or surviving) from the
349 models. I used different modeling approaches because I did not explicitly modeled any
350 mechanism or process that can be hypothesized to lead to extinction (i.e., models are
351 correlative and not mechanistic), and different modeling approaches can give different
352 insights on how contemporary extinctions are predicted (e.g., tree-based models like RFs
353 provide a measure of variable importance for predicting the target variable, Breiman
354 2001a, and GAMs can model non-linear relationships between predictors and target
355 variable using semi-parametric estimation). For the GAMs and GLMs, I centered and
356 scaled the predictors in order to compare their importance (Schielzeth 2010). As I use
357 realistic variable ranges representing the variability that may be observed in nature, some
358 of the estimated parameters can be compared in terms of effect on a standardized scale. I
359 also fitted the same models using non-standardized predictors to test for possible data
360 leakage between training and testing data sets (results were directionally the same). As
361 interactions among predictors did not improve model performance, I did not include them

362 in the models in order to improve the interpretability of results. I visually checked
363 residuals for variation to model assumptions.

364 3 Results

365 Results are fully reproducible. Data and R code are at
366 https://github.com/simonevincenzi/Contemporary_Extinction.
367 After year 100, the directional trend, the increase in variability of climate, and the
368 increased occurrence and severity of point extremes led to noticeable fluctuations in
369 population size over time (Fig. 1). Twenty-one per cent of the 34 560 simulation
370 replicates went extinct. As expected, risk of extinction increased with higher frequency
371 and severity of point extreme events, older age at first reproduction, and fewer offspring
372 produced per mating pair (Fig. 2). Given an expected yearly number of offspring per
373 mating pair, the proportion of replicates that went extinct increased approximately
374 linearly with age at first reproduction (Fig. 2a). When considering all replicates or only
375 the most extreme scenario, for a fixed expected number of offspring produced per mating
376 pair, increasing age at first reproduction by one year would increase the probability of
377 going extinct by approximately 10% (Fig. 2a). The combination of relative high
378 frequency and high severity of extreme events led to a noticeably higher proportion of
379 replicates that went extinct (Fig. 2b). Among the replicates that went extinct, 16% (34%)
380 of them were not affected by a point extreme in the 10 years before extinction and 34% in
381 the 5 years preceding extinction.
382 In populations that persisted until the end of simulation time, the GLM and GAM models
383 that included *n_low* provided a good prediction of the total number of alleles at the end of

384 simulation time (Table 2). The total number of years with population size smaller than
385 150 individuals had a strong, negative non-linear effect on the total number of alleles at
386 the end of simulation time (Fig. 3). Models that did not include *n_low* had much lower
387 predictive performance (Table 2).

388 Models for differences in allelic frequency of more or less theoretically advantageous
389 alleles were able to explain less than 5% of the variance of the target variable (Fig. 4).
390 The average value of population-mean phenotype $\bar{z}$ in the last ten years of simulation
391 time was negatively correlated with the difference in frequency of top and bottom 10% of
392 alleles according to their allelic value at the end of simulation time ($r = 0.71$, $p < 0.01$).

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

405 # 4 Discussion

406 Understanding and predicting the effects of extreme events on risk of extinction and
407 population and genetic dynamics of natural populations is critical for both population
408 forecasting and managing human intervention in an increasingly more extreme world.
409 I found additive effects—with largely no interaction effects—between age at first
410 reproduction and fecundity on risk of extinction for the range of values I simulated. In the
411 replicates that survived up to the end of simulation time, the total number of years in
412 which the population was at a small size was a good predictor of allelic richness for the
413 quantitative trait selected for. The population frequency of theoretically advantageous
414 alleles was strongly correlated with the mean value of the phenotype under selection, but
415 was otherwise largely unpredictable. Last, simple models including basic demographic
416 and vital rates information, along with climate/environmental measures, provided
417 excellent predictions of contemporary risk of population extinction.

418 **4.1 Life histories**

419 Life-history theory predicts a prevalence of fast life histories in environments in which
420 extreme events occur (Winemiller 2005). Fast life histories, which are often defined as
421 including a combination of faster body growth early in life, younger age at maturity, and
422 higher reproductive effort early in the reproductive life of the individual, should allow for
423 faster population growth rate after a drastic reduction in population size, an adaptive life-
424 history strategy when the population is at risk of extinction.
425 For many animal species that commonly experience the often-catastrophic effects of
426 extreme climate or point events—and have limited movement range for physiological and

427 behavioral reasons or for the environment they inhabit (e.g., freshwater fish in mountain
428 streams, insects)—offspring production is typically very high compared to the habitat
429 carrying capacity. Thus, offspring production is not usually what is limiting population
430 recovery, i.e. the re-establishment of the pre-event population size. However, when after
431 a climate or point extreme event the population is reduced to such low numbers that the
432 population is at immediate risk of extinction, younger age at first reproduction for the
433 surviving individuals could be what makes the difference between population persistence
434 or extinction. Vincenzi et al. (2017a) found that fish born after flash floods had younger
435 mean age at reproduction than fish born before flash floods, and hypothesized that
436 younger age at reproduction after flash floods was due to a combination of faster growth
437 due to lower population density and fewer older fish competing for mates. However,
438 younger age at sexual maturity and higher energetic investment in offspring production
439 often comes at the cost of shorter life expectancy (Fay et al. 2016), and life histories that
440 are adaptive after population crashes can show lower fitness in steady-state conditions
441 (Vincenzi et al. 2012, 2014).

442 **4.2 Prediction of genetic dynamics and of population extinction**

443 It is expected that persisting populations experiencing recurrent bottlenecks should
444 have their genetic pool eroded over time. The erosion of the genetic pool should should
445 be noticeable in particular in the loss of allelic richness, even after a single bottleneck
446 event (Allendorf 1986). I found that the extent of population bottlenecks, which I
447 operationalized as the number of years in which population size was relatively small with
448 respect to the habitat carrying capacity and species numerical potential, was a strong
449 predictor of allelic richness for the quantitative trait under selection. These results appear

450 to be at least partially consistent with recent empirical results. Vincenzi et al. (2017a)
451 found an increase in the proportion of fixed alleles in year-classes of two trout
452 populations born after flash floods that caused massive mortalities. Poff et al. (2018)
453 tested predictions about population genomic change in aquatic insects living in Colorado,
454 US, mountain streams after a one in 500-year rainfall event. They found that allelic
455 richness at presumably neutral loci declined after the event only in two out of six species
456 analyzed. Moderate reduction of allelic diversity after strong bottlenecks might be
457 attributable to the particular demographic history of the populations that are investigated;
458 according to Bouzat (2010), one can expect that populations experiencing recurrent
459 bottlenecks might have had their genetic pool already eroded over time, which would
460 decrease the effectiveness of both purifying selection and random allele loss. In addition,
461 the loss of alleles could be greater in species—like salmonids——with high variance in
462 reproductive success among adults (i.e., greater than Poisson variance in reproductive
463 success), although variance in reproductive success has been found to bias (i.e., make
464 false positives more likely) empirical investigations of genetic bottlenecks (Hoban et al.
465 2013). Moreover, in our simulations, we started from 10 unique alleles for each of the 10
466 loci, and the high initial allelic diversity may explain the strong relationship that was
467 found between the temporal extent of bottlenecks and allelic richness.
468 On the other hand, a model including age at first reproduction and fecundity of the
469 species and some traits of the environment was not able to predict the dynamics of the
470 population frequencies of more advantageous alleles for the quantitative trait under
471 selection. However, a strong correlation was found between the frequencies of more or
472 less advantageous alleles at the end of simulation time and the average value of the

473 phenotype under selection. This result seems to at least suggest that, although the fate of
474 alleles is difficult to predict from just the coarse-grain description of the environment and
475 of the species, even in an extreme environment that also causes trait-independent mass
476 mortalities, a shift in the phenotype is likely to be caused by the increased prevalence of
477 the most advantageous alleles.

478 One of the foundational tenets of conservation biology is that small, fragmented
479 populations should be considered locally vulnerable to extinction—even more critically
480 so when affected by highly variable climatic conditions and other environmental
481 disturbances. The conditions that led to the extinction of a population or species can
482 almost always be understood retrospectively, but forecasting extinction, especially over
483 contemporary time horizons, is much more challenging. In this work, I found that the
484 most important predictors of contemporary extinctions were mean and minimum
485 population size measured in the few years before the "prediction window". However, it
486 was not uncommon for populations to swiftly rebound after collapses in numbers, and
487 age at reproduction and yearly fecundity were the most important predictors of extinction
488 when measures of population size were not included in the model. This result highlights
489 the importance of age at first reproduction and yearly fecundity for population persistence
490 in highly stochastic environments, as also suggested by theoretical (Bürger and Lynch
491 1995) and experimental (Griffen and Drake 2008) studies. However, other genetic
492 challenges not accounted for in my simulation model are likely to be encountered by
493 populations that decline to very small numbers, such as a reduction of viability and/or
494 fecundity due to either inbreeding or the expression of deleterious alleles (Willi et al.
495 2006).

Although it may appear from the simulation results that vital rates and environmental conditions play a small role in models that predict contemporary risk of extinction, those rates and conditions heavily contribute to determining population size in the "observation window"; for example, populations with higher fecundity and younger age at first reproduction are less likely to remain at low population sizes than populations with lower fecundity and delayed sexual maturity. Likewise, a more extreme environment (e.g., greater selection strength and more frequent and/or severe climate and point extremes) tends to decrease average population size, either due to acute events that kill individuals or constant recovery from population crashes.

Luck plays also plays a major role in determining whether a population will recover after a population crash. Vincenzi et al. (2017a) found that the almost-complete recovery of a trout populations that was reduced to a handful of individuals after a flash flood was due the large production of offspring by a single mating pair. Considering the high variance in adult reproductive success in trout population—which is at least partially due to differences in individual "quality" (Auld et al. 2019)—had the mating pair been killed or displaced during the flash flood, population recovery would have suddenly become much less likely.

4.3 Modeling considerations

Modeling and simulation approaches can help understand the effects of multiple extreme stressors on the contemporary risk of extinction of species, and can be used to guide or support both the set-up of ecologically relevant experimental designs and the interpretation of biological responses to multiple stressors.

However, models of population and genetic dynamics are limited in their scope of prediction by both the understanding of the biology and ecology of the species and the availability of data to parametrize, train, and test models. Although often intuitive, it is nevertheless important to remind ourselves that the simulation results of modeling exercises depend on, first, our biological and ecological understanding, and, second, the simplified modeling of the species and the environment they inhabit. For instance, general trade-offs between allocation of resources to competing physiological functions are not only often intrinsically challenging to model, but they may also vary over time and space for the same species or population. That is, even when there is qualitative understanding of some biological or ecological process, the parameterization and choice of parameter values for the model may be too uncertain too provide actionable predictions.

Trade-offs between model accuracy and interpretability also need to be taken into account when developing models of population and genetic dynamics. Accuracy describes the ability of a model to explain observed data and make correct predictions, while interpretability concerns to what degree the model allows for understanding processes. Often, a trade-off exists between accuracy and interpretability: more complex models are usually opaque, while more interpretable models often do not provide the same accuracy or predictive power of more complex models (Breiman 2001b). Then, although intuitively more complex models are expected to provide more accurate predictions of risk of extinction or population and genetic dynamics, this is not always the case. For instance, Ward et al. (2014) tested the predictive performance of short-term forecasting models of population abundance of varying complexity. They found that

more complex models often performed worse than simpler models, which simply treated the most recent observation as the forecast. In their case, the estimation of even a small number of parameters imposed a high cost while providing little benefit for short-term forecasting of species. However, when there was a clear signal of cyclic dynamics, more complex models were able to more accurately predict future population sizes.

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

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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663 **Tables**

664

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

666

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 $t_{ch} + t_{inc}$

669 **Table 2.** Performance of Ordinary Least-Squares regression models (OLS),
670 generalized additive models (GAM) and Random Forest models (RF) when predicting
671 the total number of alleles at the end of simulation time for the replicates that survived
672 until the end (i.e., year 250). All populations started with 10 alleles for each of the 10 loci
673 for a total of 100 unique alleles. Full models include as predictors *n_low*, $\beta_{\sigma,\Theta}$, $\beta_{\mu,\Theta}$,
674 p(E_a), m_E, a_f, λ_o, and *s*. *n_low* is the number of years the population was below 150
675 individuals and all other symbols are as in Table 1 (results were similar with *tr_low* =
676 100 and reported in the computer code associated with this paper). The training data set
677 had 21 523 replicates (80% of the replicates that survived up to the end of simulation
678 time) and the test data set had 5 371 replicates. R^2 was calculated with respect to the 1:1
679 prediction-observed line; *MAE* is the mean absolute error calculated over the whole test
680 data set. Over the entire data set (training and test), the number of alleles at the end of
681 simulation time was [mean ± sd] 79.84 ± 21.11.
682
683
684
685
686
687

Model	R^2	*MAE*
RF_*full*	0.82	6.64
RF_*red*	0.24	14.97
GAM_*full*	0.78	7.82
OLS_*full*	0.71	8.85
OLS_*red*	0.22	15.23

688 **Table 3.** GLM with logit link function for prediction of extinction (1)/persistence (0)
689 of a population over a 10-year period ("prediction window") with predictors minimum
690 population size min(N), mean population size $\bar{N}$, maximum value of the optimum
691 phenotype max(Θ), maximum and minimum mean population-level maladaptation (or
692 "extremeness" of the climate extreme) max($\Theta(t) - z(t)$) and mean($\Theta(t) - z(t)$), and
693 occurrence of a point extreme E, all measured in the 10 years before the start of the
694 "extinction" window (i.e., in the "observation window"), along with selection strength s,
695 age at first reproduction a_f and expected yearly number of offspring per pair λ_0 (*full*
696 model). In the *reduced* model, I excluded min(N) and $\bar{N}$. All predictors were
697 standardized (s and E are categorical variables with two levels each, so those were not
698 standardized) and I report mean estimate and standard error of the regression coefficients
699 for the GLM models (estimate, standard errors and significance where applicable for the
700 GAM and RF models are in the computer code associated with this paper). The GLM,
701 GAM, and RF models were trained on 39 547 replicates (36% went extinct) and tested on
702 4 600 replicates (50% went extinct). For the full and reduced GLM models, when using
703 the optimal cutoffs (*full* = 0.54, *reduced* = 0.35), accuracy when tested on the validation
704 data set was 97% for the *full* model and 77% for the *reduced* model, false positive rate
705 0.03 and 0.26, false negative rate 0.03 and 0.19. For the GAM models (details in
706 computer code associated with this article), optimal cutoffs were 0.38 for the *full* model
707 and 0.35 for the *reduced* model, accuracy 97% and 77%, false positive rate 0.03 and 0.25,
708 false negative rate 0.03 and 0.20. For the RF models, accuracy when tested on the test
709 data set was 97% for the *full* model and 72% for the *reduced* model, false positive rate
710 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 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 (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.

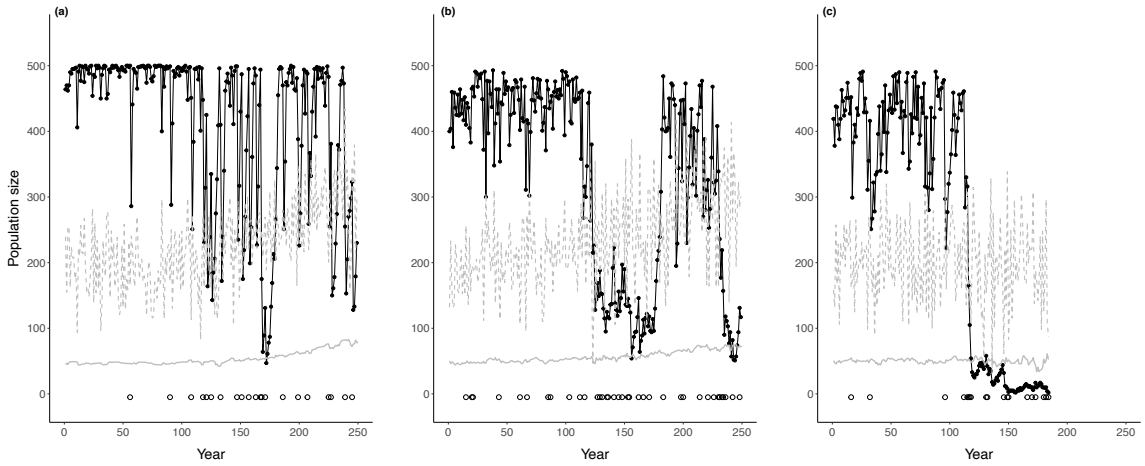
Figure 3. Partial non-linear effect of the total number of years in which the population is below 150 individuals during simulation time (*n_low*) on the total number of alleles at the end of simulation time, as found from the Generalized Additive Model of Table 2. The GAM algorithm found $k = 3$ as 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.

735 **Figure 4**. Panels (a-b): population dynamics of two simulation replicates (details
736 about the replicates are in the computer code associated with this paper). Lines and
737 symbols are as in Figure 1. Panels (c-d) dynamics of allelic frequency for the populations
738 in panels (a-b) (a→c, b→d). Thin dashed gray lines represent the allelic frequencies
739 measured every 50 years for alleles in the bottom 10% of allelic values (for (c): n = 10,
740 allelic value [mean ± sd] = -0.27 ± 0.08; (d) n = 10, allelic value = -0.21 ± 0.04) and thin
741 solid black lines represent the top 10% (for (c): n = 10, allelic value = 0.28 ± 0.08; (d)
742 0.25 ± 0.06). Thick dashed gray lines represent the average frequency in the population
743 of alleles in the bottom 10% of allelic values and thick solid black lines represent the
744 average frequency of the top 10%. In (c), the alleles in the bottom 10% of allelic values
745 were more frequent in the population at the end of simulation time than alleles in the top
746 10%, and *vice versa* in panel (d).
747 **Figure 5.** Examples of Generalized Linear Model (GLM), Generalized Additive
748 Model (GAM), and Random Forest (RF) predictions of extinction in a "prediction
749 window" based on climate and population traits observed in a "observation window".
750 Circles are point extremes, the black solid line and black points represent population size,
751 the gray dashed line is the optimum phenotype re-scaled for graphical purposes. The
752 letter O denotes the "observation window" and P the "prediction window". For each
753 model in the legend, 1 means the model predicted extinction (e.g., RF = 1 means that the
754 RF model predicted extinction) and 0 otherwise; in panel (d), all models predicted
755 extinction, but the replicate did not go extinct. In panel (a) only the RF model predicted
756 extinction and the replicate went extinct, in (b) only the GLM model predicted extinction

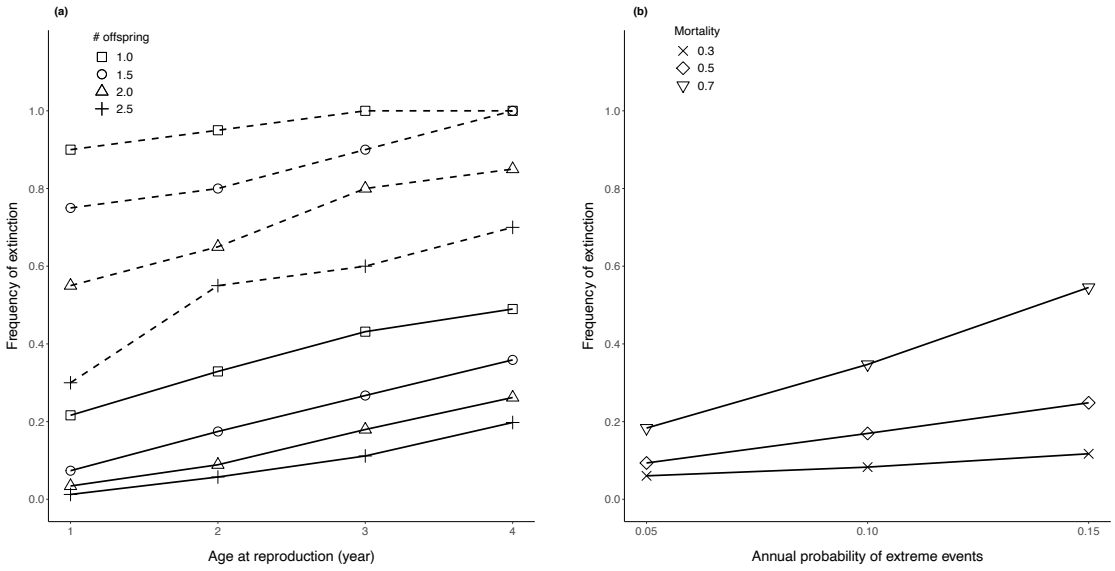
757 and the replicate went extinct, and in (c) only the GAM model predicted extinction and
758 the replicate did not go extinct.

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

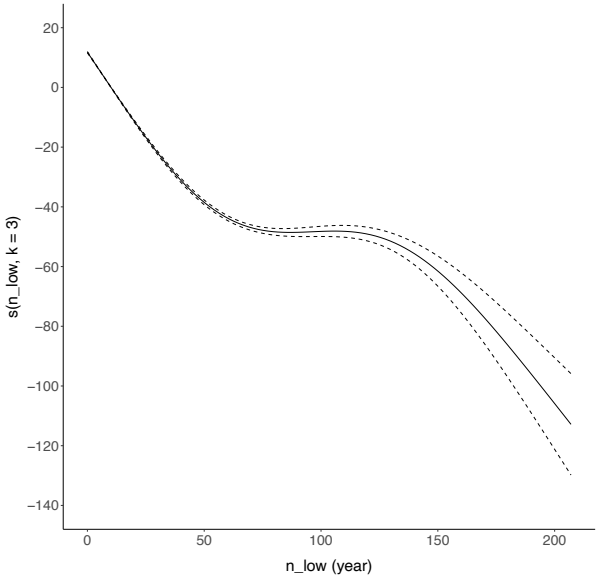
767 **Figure 1**


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

768 **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

769 **Figure 3**



770 **Figure 4**

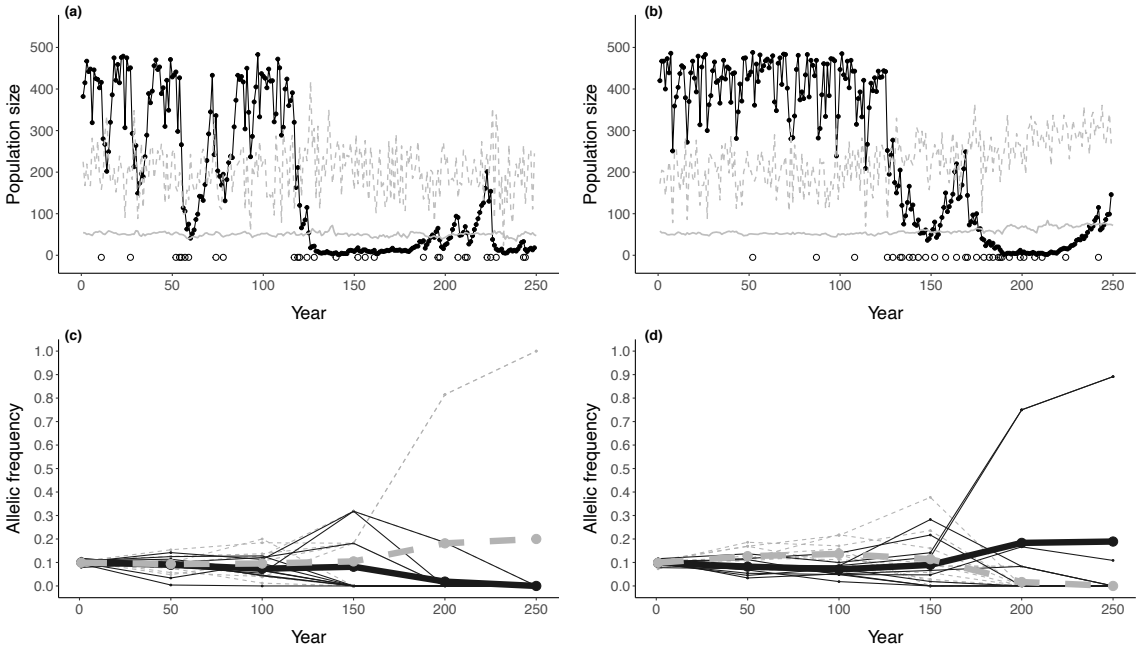

(a)
(b)
(c)
(d)
Population size
Allelic frequency
Year
0
50
100
150
200
250
0
100
200
300
400
500
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0

Figure 5

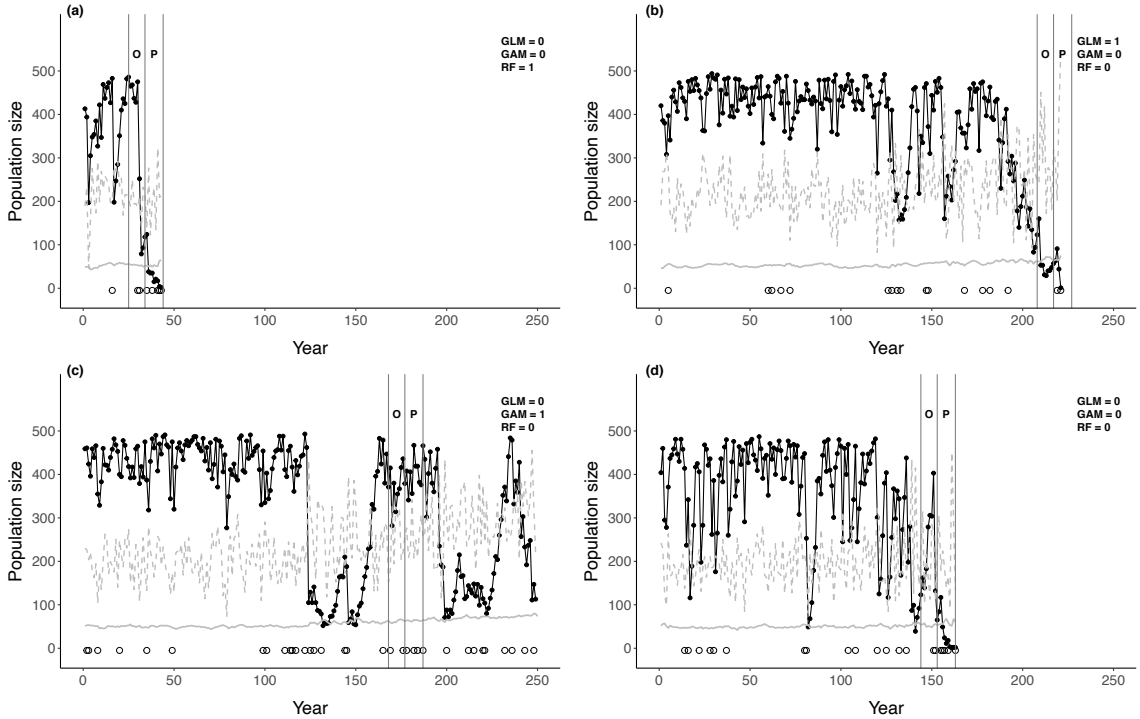
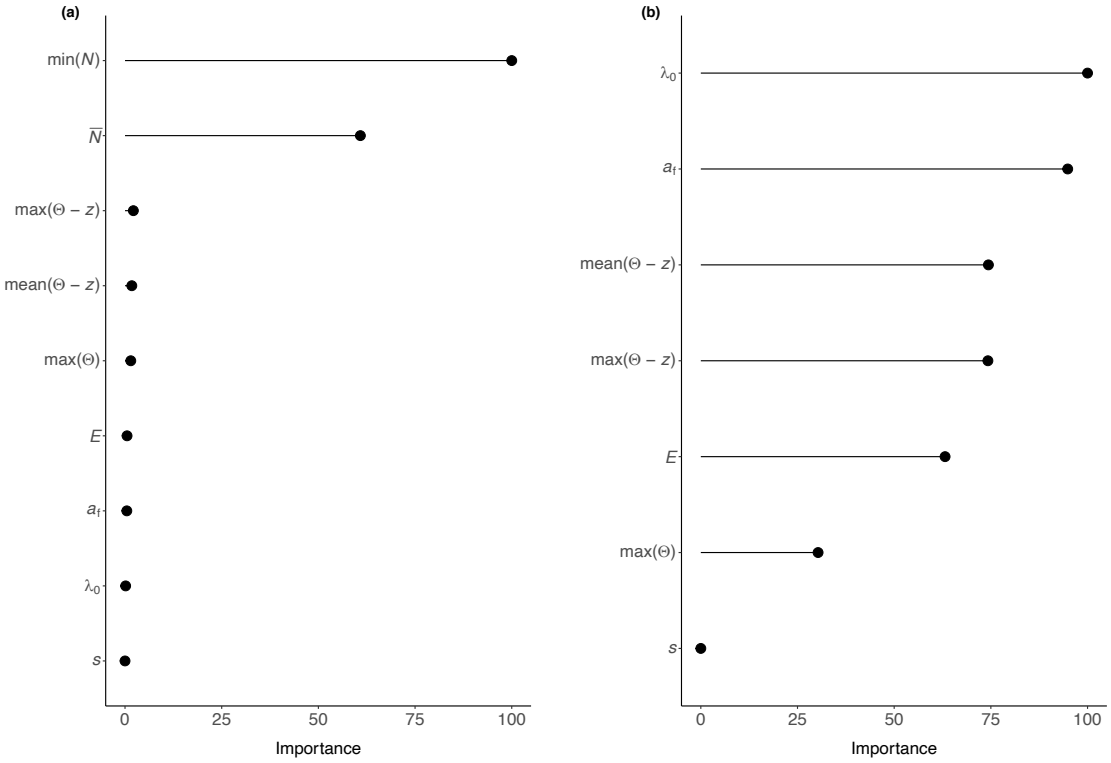

(a)
GLM = 0
GAM = 0
RF = 1
O
P
(b)
GLM = 1
GAM = 0
RF = 0
O
P
(c)
GLM = 0
GAM = 1
RF = 0
O
P
(d)
GLM = 0
GAM = 0
RF = 0
O
P
Population size
Year
0
100
200
300
400
500
0
50
100
150
200
250

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