1   **Running title:** Contemporary risk of extinction

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4   Contemporary risk of extinction in an extreme

5   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

55 population age and size structure, disruption in the expression of quantitative traits)

56 (Bryant and Meffert 1995, Kirkpatrick and Jarne 2000) are often the result of chance and

57 are thus not easily predictable or generalizable across species or habitats. Second, climate

58 and point extremes that result in strong demographic and genetic responses are often rare

59 events, whose occurrence may be also difficult to predict. When available,

60 pre-disturbance empirical data is likely to have been collected by chance, and the studies

61 on the effects of extreme events prone to be mostly opportunistic and anecdotal instead of

62 planned and comprehensive.

63   Despite the intrinsic difficulties of developing and testing general theories on the

64 effects of climate and point extremes on natural populations, there are a few theory-based

65 predictions on the demographic and genetic consequences of extreme events that may be

66 quite general across species and habitats, although with varying degrees of modeling and

67 empirical validation.

68   The first prediction is that by reducing population size, extreme events directly

69 increase the risk of extinction of the affected populations (Willi et al. 2006, Frankham et

70 al. 2014); mathematical modeling, empirical observations, and common sense all suggest

71 that smaller populations are more likely to go extinct than larger populations. After the

72 occurrence of extreme events, in some cases the extinction of the focal population is

73 inevitable for numerical reasons (no individuals capable of reproducing survived) unless

74 there is immigration from neighboring—either unaffected or less affected—populations

75 (i.e., "demographic rescue", Brown and Kodric-Brown 1977, Carlson et al. 2014).

76   Second, when the change in the environment is sudden, but not causing mass

77 mortalities, the evolution of fitness-determining traits might occur fast enough to stop

78   population decline and allow population recovery before extinction ("evolutionary

79   rescue", Bell and Gonzalez 2009). However, population bottlenecks such as those caused

80   by extreme events, especially when repeated over time, are predicted to decrease additive

81   genetic variance and allelic diversity in the affected populations (Bouzat 2010). As

82   adaptive potential tends to increase with genetic variability and genetic drift may

83   overwhelm selection in small populations, the effects of extreme events on genetic

84   variability are predicted to increase both the short- and long-term risks of population

85   extinction, with smaller chances of evolutionary rescue (Falconer and Mackay 1996,

86   Willi and Hoffmann 2009).

87   Third, species may exhibit various adaptations to extreme events, some more

88   predictable and general than others. For instance, extreme, but predictable variations in

89   the flow regime of streams can select for fish life histories, such as spawning and

90   emergence time, that are synchronized either to avoid or exploit the direct (e.g., stronger

91   or weaker currents) and indirect (e.g., changes in food webs) effects of extreme flows

92   (Lytle and Poff 2004). On the contrary, unpredictable flow events such as flash floods

93   may have low direct selective consequences for the affected populations, even though

94   they might induce massive mortalities (Lytle 2000). In these cases, natural selection after

95   the extreme event is predicted to favor individuals with a high capacity for increase in

96   population size (r selection, Reznick et al. 2002). Intuitively, when after an extreme event

97   the population is reduced to a few individuals, faster reproduction may be more critically

98   needed than high fecundity, since the latter depends on being able to reproduce.

99   However, the interaction effects between age at first reproduction and fecundity on risk

100   of extinction in an extreme environment have been rarely investigated.

101   In this work, I test using a simulation approach some of the hypotheses on risk of

102   extinction and population and genetic dynamics in an environment in which both climate

103   and point extremes occur. In previous work, Vincenzi (2014) found that the survival

104   chances of a population were found to decrease with increasing strength of selection, as

105   well as with increasing climate trend (e.g., increasing or decreasing n-year moving

106   average temperature, rainfall) and variability. They also found that the interactions

107   among climate trend (e.g., increase over years of average summer temperatures), climate

108   variability and probability of point extremes (e.g., fires) had negligible effects on risk of

109   extinction, time to extinction, and distribution of a quantitative trait selected for by

110   climate after accounting for their independent effects.

111   The present work focuses more on prediction than inference; prediction of future

112   observables has long been included as an aspect of biological and ecological studies, but

113   as a methodological approach it has been much less prominent than either description or

114   statistical and causal inference. The work is also not purely theoretical in scope, but is

115   motivated (and model parameter values inspired) by the study of the population and

116   genetic dynamics, and risk of extinction of marble trout *Salmo marmoratus* living in

117   Slovenian streams (Vincenzi et al. 2016). Marble trout populations are affected by flash

118   floods in autumn and droughts in summer, and the climate threat to the persistence of

119   marble trout is likely to worsen with climate change; for instance, the increase in intra-

120   annual variability in rainfall is predicted to increase the frequency of flash floods (Janža

121   2013). However, since there is a need for more general investigations of risk of

122   population extinction and population and genetic dynamics in presence of climate and

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

124   framework.

125   I modeled an idealized situation of additive genes, a closed population of moderate

126   size with random mating, and variable across simulations—but fixed within

127   simulations—age at first reproduction and expected number of offspring per mating pair,

128   climate trend and variability (i.e., the parameters of the distribution of climate variable

129   that is selecting for a quantitative trait), selection strength, and frequency and severity of

130   point extremes. I assume that point extremes cause massive mortalities, but no trait other

131   than good fortune increases the survival chances of an individual when point extremes

132   occur.

133   First, I tested whether in an extreme environment the extent of population bottlenecks,

134   which I operationally defined as the total number of years with "depressed" population

135   size (e.g., ~ 1/3 to ~ 1/10 of the habitat carrying capacity), could help predict allelic

136   richness at the end of simulation time for the quantitative trait selected for by the climate

137   variable. Second, I tested whether quantitative trait adaptation was correlated with the

138   increased frequency of theoretically advantageous alleles (i.e., their allelic values are in

139   the same direction of the change in the environment) and whether the genetic dynamics

140   of the populations could be predicted using information on the climate and on the

141   population life histories. Third, I tested for interaction effects between age at

142   reproduction and fecundity on risk of population extinction. Finally, I tested whether it is

143   possible to predict the extinction or survival of a population in a 10-year "prediction

144   window" (i.e., contemporary extinction) when measuring or observing some of the

145   environmental characteristics of the habitat (e.g., occurrence of extreme events) and of

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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.

167   **2.2 Optimum phenotype**

168   The expected optimum phenotype $\mu_\Theta(t)$ moves at a constant rate $\beta_{\mu,\Theta}$ over time (i.e.,

169   trend), fluctuating randomly around its expected value $\mu_\Theta(t)$. The optimum phenotype

170    $\Theta(t)$ is randomly drawn at each time step t from a normal distribution $\Theta(t) \sim N$

171    $(\mu_\Theta(t), \sigma_\Theta(t))$. It is equivalent to consider $\Theta(t)$ as both the optimum phenotype and the

172   value of a continuous climate variable (e.g., mean summer temperature or yearly rainfall),

173   and I will use the two terms interchangeably throughout this work.

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

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

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$$
\begin{cases}
\sigma_\theta(t) = \sigma_{\theta,0} & \text{when } t < t_{ch} \\
\sigma_\theta(t) = \sigma_{\theta,0} + \beta_{\sigma,\theta}\left(t - t_{ch}\right) & \text{when } t_{ch} \leq t \leq \left(t_{ch} + t_{inc}\right) \\
\sigma_\theta(t) = \sigma_{\theta,0} + \beta_{\sigma,\theta}\, t_{inc} & \text{when } t > \left(t_{ch} + t_{inc}\right)
\end{cases}
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183   where t_{ch} is the time at which there is a change (*ch*) in the climate. Eq. (1)

184   indicates that the directional climate trend steadily increases through time after t_{ch} years

185   and that the increase in variability starts after t_{ch} years, but stops after $t_{ch}+t_{inc}$ years. An

186   alternative formulation to Eq. (1) would allow variability to more slowly build up over

187   time; however, in the case of variability slowly increasing over longer times, the effects

188   of higher climate variability would affect the individuals only towards the end of

189   simulation time. As informed by the goals of this work, I preferred to let individuals

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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             $z_i = a_i + e_i$ (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:

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

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 $\gamma = -0.1$ for stabilizing selection found by Kingsolver et al. (2001)

229   corresponds to a value of $\omega^2/\sigma^2_E = 5/[1-h^2]$, where σ^2_E 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:

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

234   where $s = \dfrac{1}{2\omega^2}$. With $\gamma = -0.1$, $\sigma_E^2 = 1$, and $h^2 = 0.2$, the strength of selection s is

235   about 0.08.

236   I assumed that both strength of selection s and environmental variance σ_E^2 remain

237   constant through time. When a point extreme occurs, the probability of yearly survival of

238   individuals i is $W_i(1 - m_{E_I})$, where m_{E_I} is mortality caused by the point extreme event.

239   **2.4 Simulations**

240   As this study focuses on the more immediate effects of climate change, the

241   simulations last 250 years. Parents mate at time t-1, offspring are born at time t and

242   become of age 1 at $t+1$. The sequence of operations is mortality of adults, mating and

243   reproduction, mutation, mortality of offspring. At the start of each simulation, for each

244   individual a value of a and e (Eq. 2) is randomly drawn from their initial distribution. A

245   population is considered extinct if at any time during the simulation there are fewer than

246   2 individuals in the population. Parents form mating pairs starting at age a_f and produce a

247   number of offspring randomly drawn from a Poisson distribution with intensity λ_o.

248   Offspring receive for the same locus one allele from each parent.

249   **2.4.1 Parameter values**

250   With numerical simulations, it is inevitable to face a trade-off between specificity and

251   generalizability of the modeled processes and of the simulation results. I reduced

252   parameter space by fixing $K = 500$ individuals, $\mu_{\Theta,1} = 0$, $\sigma_{\Theta,1} = 1$, $\mu_E = 0$, $\sigma_E^2 = 1$, $\sigma_G^2 = 2$

253   10^{-1}, $\sigma_a = 5 \ 10^{-2}$, $p(E_{I,b}) = 0.05$, 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.

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275 For the Poisson distribution of the yearly number of offspring per mating pair, I used

276 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

277 with a step of 1. Parameter values are reported in Table 1.

2.4.2 Initialization

279 To reach mutation-selection-drift balance, I first let the population evolve for t_{ch} years

280 in an environment in which mean and variance of the distribution of the optimal

281 phenotype Θ are constant. In preliminary simulations it was found that after $t_{ch} \sim 100$

282 years both phenotypic mean and variance did not noticeably change. Then, the mean of

283 Θ increases for 150 years and the variance of Θ for 25 years, which was then kept

284 constant up to the end of simulation time.

285 I started every simulation replicate with 500 individuals. I modeled 10 alleles present

286 in the population for each locus, which value was randomly drawn from a normal

287 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

288 was around 0.2 at $t = 1$, close to what commonly observed for life-history traits (Lynch

289 and Walsh 1998) and consistent with the Gaussian allelic approximation including only

290 quasi-neutral and adaptive mutations, for which $\sigma_G^2 = 0.225\sigma_E^2$ (Lande 1995).

2.4.3 Characterization of simulations

292 At the single-replicate level, to characterize the behavior of the simulated populations

293 I tracked or recorded (among other results): (*a*) whether the population was extinct or still

294 persisting at the end of the simulation time (0 for persistence and 1 for extinction, in the

295 latter case I also recorded the year of extinction). At each time t, I then recorded: (*b*) the

296 distribution of the trait z in the population and individual maladaptation; (*c*) population

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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*

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320   using either 150, 100, or 50 individuals as the threshold (results were consistent when

321   using either 150,100, or 50 individuals). For (*ii*), when the climate is changing (i.e., $\beta_{\mu,\Theta}$

322   > 0), alleles with positive allelic values are expected to be more adaptive than those with

323   negative (or positive, but smaller) allelic values. I tested whether a model including

324   climate variables and vital rates trained on data from 80% of the replicates that did not go

325   extinct could predict the difference in mean allelic frequency at year 250 (end of

326   simulation time) of the top and bottom 10% of alleles according to their allelic values in

327   the test data set (20% replicates that did not go extinct). I chose the top and bottom 10%

328   of the alleles (10 alleles in the top and bottom sets), since the fate of single alleles is more

329   likely to be affected by chance than that of a group of advantageous alleles.

330   Then, I investigated whether a combination of demographic and environmental factors

331   measured or estimated in a short time window ("observation window") can predict the

332   risk of extinction of the population in the following years ("prediction window"). First, I

333   set aside a balanced test data set of simulation replicates (50% that went extinct and 50%

334   that survived)—these simulations were not used in any phase of either model

335   development or model training. Second, since the number of simulations that went extinct

336   was approximately one-third of the number of those that survived, I augmented the data

337   set by replicating 3 times the simulations that went extinct and were not included in the

338   test data set.

339   Third, I fitted GLMs and GAMs with binomial error distribution (i.e., logistic

340   regression), and classification Random Forests (RFs) with population extinction (1) or

341   persistence (0) between (t_{ext} - *u)* as response variable, where t_{ext} is either (a) the time at

342   extinction for the replicate that went extinct, or (b) a random deviate from a uniform

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343   distribution bounded between 20 and 250 for the replicates that survived; u is a random

344   deviate from a uniform distribution bounded between 1 and 10 years. This way, I am

345   trying to model extinction or persistence not at a specific time, but in a "prediction

346   window" of 10 years, whose beginning lays between year 10 and year 240 of simulation

347   time. I used as candidate predictors, as measured in the 10 years ("observation window")

348   before the "prediction window", minimum and mean population size N, the maximum

349   value of the optimum phenotype, the expected yearly number of offspring per mating

350   pair, age at first reproduction, and maximum and mean distance over the observation

351   window between the mean phenotype and the optimum (i.e., maximum and mean

352   population-level maladaptation, or maximum and mean "extremeness" of the climate).

353   In other words, I wanted to test whether a model including climate and population

354   traits measured over a limited time frame could predict the extinction or persistence of

355   the population in the years immediately following the end of the "observation window".

356   The choice of the length of both the observation and prediction windows was based on

357   what it is considered a "reasonable" length of population monitoring when the goal is to

358   detect changes in population size and estimate the risk of population extinction. White

359   (2019) collected the time series of population size of 822 populations of vertebrate

360   species and found that 72% of time series required at least 10 years of continuous

361   monitoring to achieve a high level of statistical power to detect significant trends in

362   abundance (the code associated with this work allows to use between 5 and 20 years as

363   length of the observation and prediction windows).

364   For the GAMs and GLMs, I estimated the optimal cutoff given equal weight to

365   sensitivity (the probability that the model predicts extinction when the replicate went

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366   extinct) and specificity (the probability that the model predicts persistence when the

367   replicate persisted). Then, I tested the model by predicting population extinction and

368   persistence on the test dataset using the computed optimal cutoff. For the classification

369   RF models, I directly used the binary prediction (population going extinct or surviving)

370   from the models. I used different modeling approaches because I did not explicitly model

371   any mechanism or process that can be hypothesized to lead to extinction (i.e., models are

372   correlative and not mechanistic), and different modeling approaches can give different

373   insights on how contemporary extinctions are predicted (e.g., tree-based models like RFs

374   provide a measure of variable importance for predicting the target variable (Breiman

375   2001a) and GAMs can model non-linear relationships between predictors and target

376   variable using semi-parametric estimation). For the GAMs and GLMs, I centered and

377   scaled the predictors in order to compare their importance (Schielzeth 2010). As I use

378   realistic variable ranges representing the variability that may be observed in nature, some

379   of the estimated parameters can be compared in terms of effects on a standardized scale. I

380   also fitted the same models using non-standardized predictors to test for possible data

381   leakage between training and testing data sets (results were directionally the same). I did

382   not include interactions among predictors in the models in order to improve the

383   interpretability of results. I visually checked residuals for violation of model assumptions.

384   **3   Results**

385   Results are fully reproducible. Data and R code are at

386   https://github.com/simonevincenzi/Contemporary_Extinction.

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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).

410   The average value of population-mean phenotype $\bar{z}$ in the last ten years of simulation

411   time was negatively correlated with the difference in frequency of top and bottom 10% of

412   alleles according to their allelic value at the end of simulation time ($r = 0.71$, $p < 0.01$).

413   The GLM, GAM, and RF models fitted on the training data sets had similar high

414   predictive accuracy and low false positive and negative rates when predicting extinction

415   or survival in the 10-year "prediction window" (Table 3). For more than 98% of

416   replicates included in the test data set, the GLM, GAM, and RF models provided the

417   same prediction of either extinction or persistence (Fig. 5). In the GAM model, only

418   minimum population size in the observation window had a strong non-linear (negative)

419   effect on the log-odds of population extinction. Likewise, minimum population size was

420   the most important predictor in the RF model (Fig. 6a). The models without minimum

421   and mean population size as predictors had fairly low accuracy (Table 3). The RF model

422   without minimum and mean population size as predictors found age at reproduction and

423   expected yearly number of offspring per mating pair as the most important predictors of

424   contemporary extinction (Fig. 6b).

425   **4   Discussion**

426   Understanding and predicting the effects of extreme events on risk of extinction and

427   population and genetic dynamics of natural populations is critical for both population

428   forecasting and for managing human intervention in an increasingly more extreme world.

429   The results of the numerical simulations showed additive effects—with largely no

430   interaction effects—between age at first reproduction and fecundity on risk of extinction

431   for the range of values I simulated. In the replicates that survived up to the end of

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432   simulation time, the total number of years in which the population was at a small size was

433   a good predictor of allelic richness for the quantitative trait under selection. The

434   population frequency of theoretically advantageous alleles was strongly correlated with

435   the mean value of the phenotype under selection but was otherwise largely unpredictable.

436   Last, simple models including basic demographic and vital rates information, along with

437   climate and environmental data, provided excellent predictions of contemporary risk of

438   population extinction.

439   **4.1 Life histories**

440   Life-history theory predicts a prevalence of fast life histories in environments in which

441   extreme events occur (Winemiller 2005). Fast life histories—usually defined as including

442   a combination of faster body growth early in life, younger age at maturity, and higher

443   reproductive effort early in the reproductive life of the individual—should allow for

444   faster population growth rate after a drastic reduction in population size, an adaptive life-

445   history strategy when the population is at risk of extinction.

446   For many animal species that frequently experience the often-catastrophic effects of

447   extreme climate or point events—and have limited movement range for physiological and

448   behavioral reasons or for the environment they inhabit (e.g., freshwater fish in mountain

449   streams, insects)—offspring production is typically very high compared to the habitat

450   carrying capacity. Thus, offspring production is not usually what is limiting population

451   recovery, i.e. the re-establishment of the pre-event population size. However, when after

452   a climate or point extreme event the population is reduced to such low numbers that the

453   population is at immediate risk of extinction, younger age at first reproduction for the

454   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

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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.

569   As always, the purpose of a scientific investigation should drive model formulation,

570   the type and amount of data collected, and the acceptable uncertainty of model

571   predictions.

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Ethics

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574   Not applicable

Data accessibility

575

576   Data and relevant code for this research work are stored in GitHub:

577   https://github.com/simonevincenzi/Contemporary_Extinction

Authors' Contributions

578

579   Simone Vincenzi conceived the ideas, designed the methods, run the analyses, and

580   wrote the manuscript.

Competing interests

581

582   The author declares no competing interests

Funding

583

584   Not applicable

Acknowledgements

585

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691   **Tables**

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

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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_A^2	$6.25\ 10^{-3}$	Additive genetic variance per locus at the start of simulation
σ_a^2	$2.5\ 10^3$	Variance of the normal distribution of allelic values
σ_G^2	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 $t_{ch} + t_{inc}$

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697   **Table 2.** Performance of Ordinary Least-Squares regression models (OLS),

698   Generalized Additive Models (GAM) and Random Forest models (RF) when predicting

699   the total number of alleles at the end of simulation time for the replicates that did not go

700   extinct. All populations started with 10 alleles for each of the 10 loci for a total of 100

701   unique alleles. Full models include as predictors n_low, $\beta_{\sigma,\Theta}$, $\beta_{\mu,\Theta}$, $p(E_a)$, m_E, a_f,

702   λ_o, and s. n_low is the number of years the population was below 150 individuals and all

703   other symbols are as in Table 1 (results were similar with $tr\_low = 100$ or 50 and are

704   reported in the computer code associated with this paper). The training data set had

705   21 523 replicates (80% of the replicates that survived up to the end of simulation time)

706   and the test data set had 5 371 replicates. R^2 was calculated with respect to the 1:1

707   predicted-observed line; MAE is the mean absolute error calculated over the whole test

708   data set. Over the entire data set (training and test), the number of alleles at the end of

709   simulation time was [mean ± sd] 79.84 ± 21.11.

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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.

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	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)
$\max(\Theta)$	-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)
$\text{mean}(\Theta(t) - z(t))$	0.13(0.04)	0.62(0.03)

742   **Figure captions**

743   **Figure 1.** Examples of simulation replicates. The black solid line and black points

744   represent population size, circles are point extremes, the gray dashed line is the value of

745   the optimum phenotype Θ, and the solid gray line is the mean phenotype $\bar{z}$ in the

746   population. Both Θ and $\bar{z}$ are re-scaled for graphical purposes. Parameters for the

747   simulation in panel (a): $\beta_{\sigma,\Theta} = 0$, $\beta_{\mu,\Theta} = 15 \cdot 10^{-2}$, $p(E_a) = 10 \cdot 10^{-2}$, $m_E = 0.7$, $a_f = 4$, $\lambda_0 = 2$,

748    $s = 11 \cdot 10^{-2}$. (b): $\beta_{\sigma,\Theta} = 15 \cdot 10^{-2}$, $\beta_{\mu,\Theta} = 15 \cdot 10^{-2}$, $p(E_a) = 15 \cdot 10^{-2}$, $m_E = 0.3$, $a_f = 3$, $\lambda_0 = 2$, s

749    $= 8 \cdot 10^{-2}$. (c): $\beta_{\sigma,\Theta} = 15 \cdot 10^{-2}$, $\beta_{\mu,\Theta} = 0$, $p(E_a) = 15 \cdot 10^{-2}$, $m_E = 0.5$, $a_f = 3$, $\lambda_0 = 1$, $s = 8 \cdot 10^{-2}$.

750   In the simulation in panel (c), the population went extinct at year 184. Symbols are as in

751   Table 1.

752   **Figure 2**. Extinction probability (number of populations going extinct divided by the

753   number of replicates run for a given set of parameter values) for scenarios of: (a)

754   different ages at first reproduction and expected yearly number of offspring per mating

755   pair (solid line: all replicates; dashed line = most extreme environment, i.e., $p(E_a) = 15$

756   10^{-2}, $m(E_a) = 0.7$, $\beta_{\mu,\Theta} = 5 \cdot 10^{-2}$, $\beta_{\sigma,\Theta} = 1.5 \cdot 10^{-2}$); (b) different probability of point

757   extremes and probability of dying from point extremes.

758   **Figure 3**. Partial non-linear effect of the total number of years in which the population

759   is below 150 individuals during simulation time (*n_low*) on the total number of alleles at

760   the end of simulation time, as found from the Generalized Additive Model of Table 2.

761   The GAM algorithm found $k = 3$ as the optimal number of degrees of freedom for the

762   spline (i.e., a cubic). Model details and results are in the in the computer code associated

763   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.
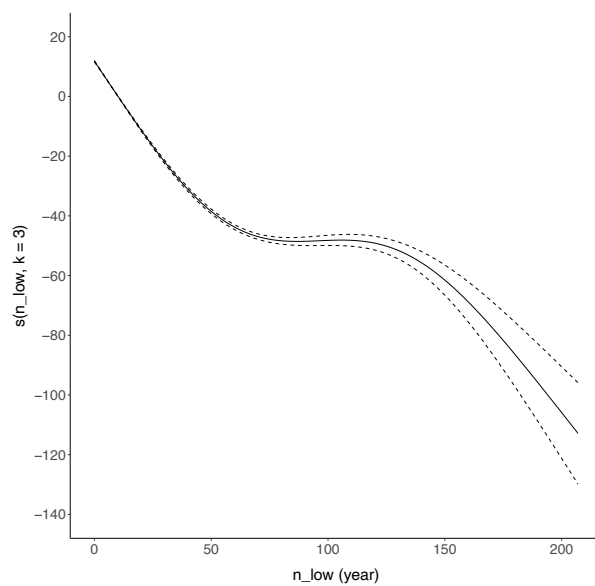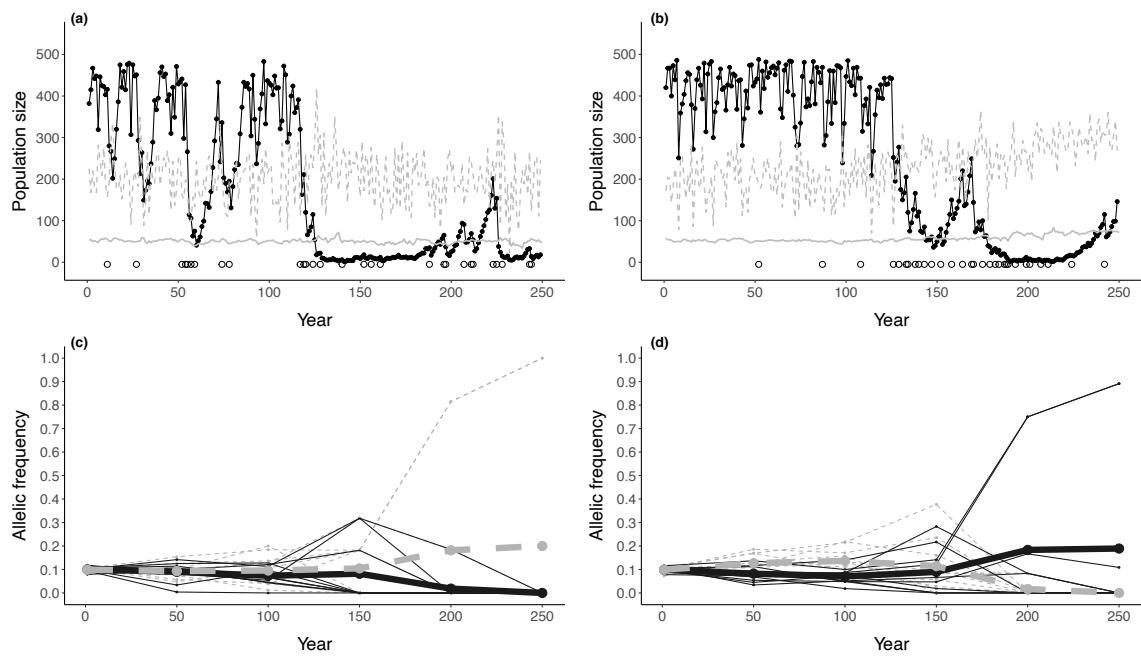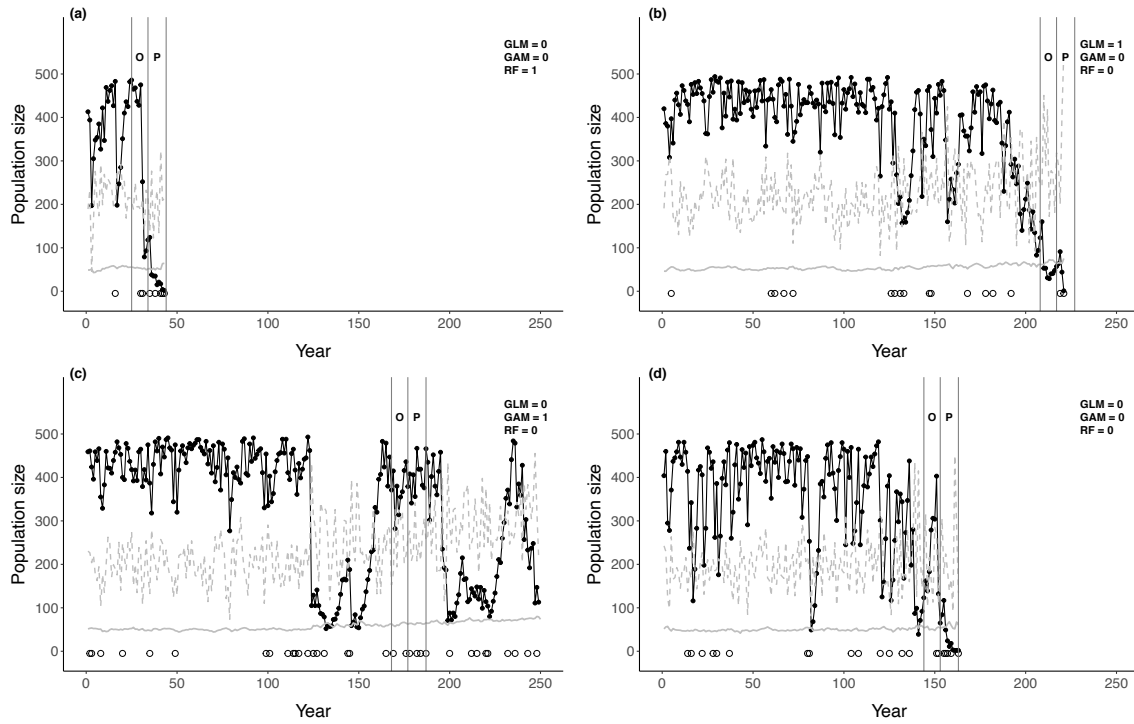
796   **Figure 1**
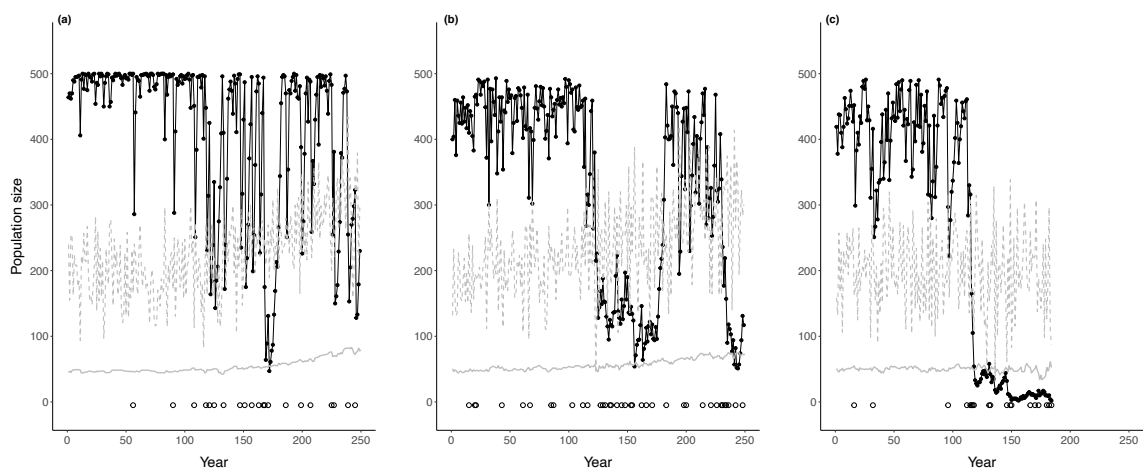
797 **Figure 2**
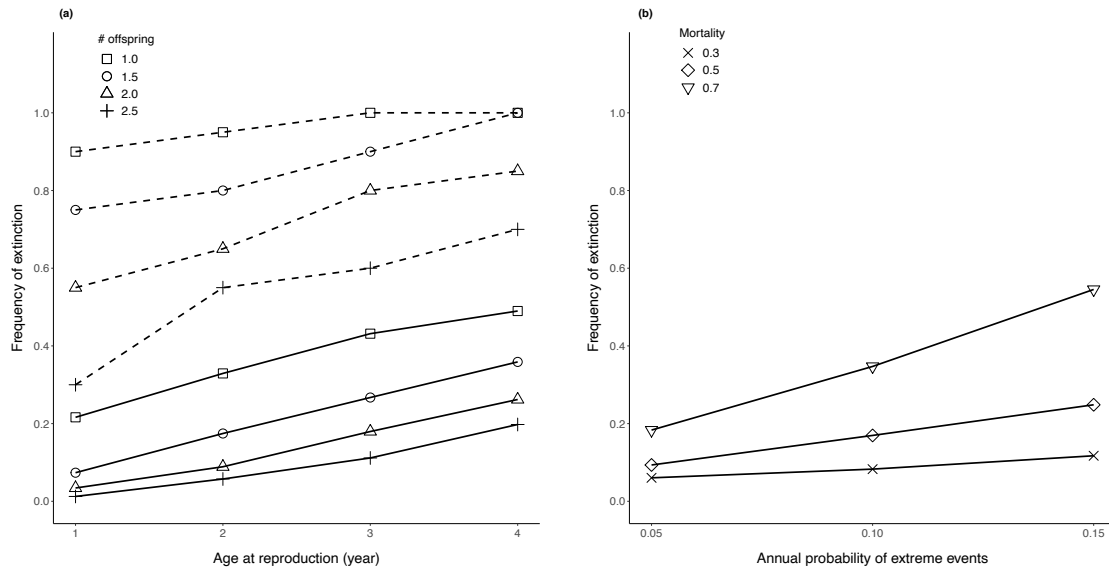
798 **Figure 3**

799 **Figure 4**

800 **Figure 5**

801 **Figure 6**