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, 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

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35   Extreme events are now recognized among the most worrisome aspects of climate

36   change (IPCC 2007, 2012, Jentsch et al. 2007, One Earth editorial team 2020).

37   How to define extreme events is challenging, since they may be defined in terms of

38   extreme values of a continuous climate variable (e.g., daily or mean summer temperature,

39   rainfall) on the basis of the available climate record (Gutschick and BassiriRad 2010), or

40   in the form of a "point" or discrete perturbation, such as a hurricane or a storm. The latter

41   category also includes environmental extremes such as fires and floods, which may have

42   catastrophic effects on the affected species and ecosystems despite being relatively

43   frequent in certain habitats. Following Vincenzi (2014), throughout this work I will use

44   the term climate extreme for extreme values of a continuous climate or environmental

45   variable and point extremes for discrete extreme perturbations.

46   The genetic and demographic determinants of both adaptation to a more extreme

47   environment and contemporary risk of extinction are receiving increasing interest from

48   scientists and conservationists. However, despite the increased research and management

49   focus on extremes, developing and testing general theories and hypotheses on the effects

50   of extreme events remains more intrinsically challenging than for other aspects of climate

51   and environmental change (van de Pol et al. 2017).

52   First, since the effects of extreme events are largely context-specific right, developing

53   an overarching causal and predictive framework may be overly ambitious (Bailey and

54   van de Pol 2016). For instance, the emergence of adaptations may depend on both the life

55   histories of the species and the recurrence interval, intensity, and nature of extreme

56   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

102   reproduction and fecundity on risk of extinction in an extreme environment have been

103   rarely investigated.

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

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

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

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 a minor effect 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. The survival chances of a

111   population were found to decrease with increasing strength of selection, as well as with

112   increasing climate trend (e.g., increasing or decreasing n-year moving average

113   temperature, rainfall) and variability.

114   Here, I focus on prediction more than on inference: prediction of future observables

115   has long been included as an aspect of biological and ecological studies, but as a

116   methodological approach it has been much less prominent than description and statistical

117   and causal inference. The work is also not purely theoretical in scope, but is motivated by

118   the study of the population and genetic dynamics, and risk of extinction of marble trout

119   *Salmo marmoratus* living in Slovenian streams (Vincenzi et al. 2016). Marble trout

120   populations are affected by flash floods in autumn and droughts in summer, and the

121   climate threat to the persistence of marble trout is likely to worsen with climate change;

122   for instance, the increase in intra-annual variability in rainfall is predicted to increase the

123   frequency of flash floods (Janža 2013). However, since there is a need for more general

124   investigations of risk of population extinction and population and genetic dynamics in

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125 presence of climate and point extremes, I developed a more widely applicable modeling

126 and conceptual framework.

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

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

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

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

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

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

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

134 occur.

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

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

137 size (e.g., ~ 1/3 of the habitat carrying capacity), could help predict allelic richness at the

138 end of simulation time for the quantitative trait selected for by the climate variable.

139 Second, I tested whether quantitative trait adaptation was correlated with the increased

140 frequency of theoretically advantageous alleles (i.e., their allelic values are in the same

141 direction of the change in the environment) and whether the genetic dynamics of the

142 populations could be predicted using information on the climate and on the population

143 life histories. Third, I tested for positive interaction effects between age at reproduction

144 and fecundity on risk of population extinction. Finally, I tested whether it is possible to

145 predict the extinction or survival of a population in a 10-year "prediction window" (i.e.,

146 contemporary extinction) when measuring or observing some of the environmental

147 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.

169   **2.2 Optimum phenotype**

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

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

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

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

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

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

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

$$\mu_\Theta(t) = \mu_{\Theta,0} + \mathtt{I}(t > t_{ch})\,\beta_{\mu,\Theta}\,t_{ch}$$

177   (1)

$$\sigma_\Theta(t) = \sigma_{\Theta,0} + \mathtt{I}(t_{ch} < t < t_{ch} + t_{inc})\,\beta_{\sigma,\Theta}\,t_{ch}$$

178   where t_{ch} is the time at which there is a change (ch) in the climate, $\mathtt{I}(\bullet)$ is and

179   indicator function equal to 1 when $\bullet$ is true and 0 otherwise. Eq. (1) indicates that the

180   directional climate trend steadily increases through time after t_{ch} years and that the

181   increase in variability starts after t_{ch} years, but stops after $t_{ch} + t_{inc}$ years to avoid variability

182   building up to unrealistic values over time. With the model formulation of Eq. (1), both

183   the mean and variance of the distribution of the climate variable change over time so as to

184   make the occurrence of events more likely after climate change (i.e., $t > t_{ch}$) than before,

185   since after climate change, the realized (i.e., random draw from the statistical distribution

186   of climate) climate is increasingly likely to be in the region of extremes (say, in the right

187   5% or 2.5% of the Gaussian distribution of climate) of the statistical distribution of

188   climate before climate change.

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189   Point extreme events E leading to trait-independent high mortalities occur with annual

190   probability p(E_b) when $t < t_{ch}$ (i.e. b - before climate change) and p(E_a) when $t > t_{ch}$.

191   **2.3 Quantitative trait and survival**

192   I model the phenotype z of an individual i, z_i, as the sum of its genotypic value a_i and a

193   statistically-independent random environmental effect e_i drawn from $N(\mu_E,\ \sigma_E^2)$:

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

195   The narrow sense heritability $h^2 = \sigma_G^2/\sigma_z^2$ is the proportion of the phenotypic variance

196   σ_z^2 present in the population that is explained by the additive genetic variance σ_G^2 (i.e.

197   the variance of $\boldsymbol{a}$ in the population).

198   For an individual i, the genetic value a_i is determined by n_l freely recombining diploid

199   loci, with additive allelic effects within- and among-loci, that is $a_i = \sum_{j=1}^{l} n_{i,j}$, where $n_{i,j}$

200   is the sum of the allelic values at locus j. For computational reasons, I chose $n_l = 10$.

201   Allelic values are randomly drawn from a Gaussian distribution with mean of 0 and

202   variance equal to σ_a^2. For simplicity, I did not model either dominance or epistatic

203   variation or other complicating factors such as genotype-environment interaction and

204   linkages. Likewise, I did not model mutation, since previous work has shown that

205   mutation does not appear to have any effect short-term on extinction risk and the

206   evolution of traits on contemporary temporal scales (Vincenzi 2014).

207   Stabilizing selection is modeled with a Gaussian function (Bürger and Lynch 1995,

208   Zhang 2012), with fitness W (Endler 1986) for an individual with phenotypic trait z_i equal

209   to:

210
$$W(t, z_i) = W(t)_i = exp\left[-\frac{(z_i - \Theta(t))^2}{2\omega^2}\right]$$
(3)

211   and equivalent in this model to the annual survival probability of individual i. The

212   curvature of the fitness function near its optimum increases with decreasing ω^2; it follows

213   that that the smaller ω^2, the stronger is selection. Stabilizing selection is usually measured

214   by the standardized quadratic selection gradient γ, which is defined as the regression of

215   fitness W on the squared deviation of trait value from the mean (Lynch and Walsh 1998).

216   An optimum phenotype in the tails of the distribution is likely to cause a large drop in

217   population size and can be considered an extreme climate event (Fig. 1).

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

219   corresponds to a value of $\omega^2/\sigma_E^2 = 5/[1-h^2]$, where σ_E^2 is the variance of the

220   environmental component of the phenotype defined in Eq. (2), when stabilizing selection

221   is modeled using a Gaussian fitness function.

222   Eq. (3) can be written:

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

224   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

225   about 0.08.

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

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

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

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229   **2.4 Simulations**

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

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

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

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

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

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

236   2 individuals in the population. Parents form mating pairs starting at age a_f and produce a

237   number of offspring randomly drawn from a Poisson distribution with intensity λ_o . I did

238   not allow for genetic recombination. Offspring receive for the same locus one allele from

239   each parent.

240   **2.4.1   Parameter values**

241   I reduced parameter space by fixing $K = 500$, $\mu_{\Theta,1} = 0$, $\sigma_{\Theta,1} = 1$, $\mu_E = 0$, $\sigma_E^2 = 1$,

242      $\sigma_G^2 = 2 \times 10^{-1}$, $\sigma_a = 5 \times 10^{-2}$, $p(E_{I,b}) = 0.05$, and $t_{inc} = 25$ years. For the other parameters, I

243   chose range of values that are both realistic for natural populations and instrumental for

244   the main goal of the study, e.g., testing hypotheses on the effects of extreme events on

245   risk of extinction and population and genetic dynamics.

246   I performed simulations with selection strength s equal to either 8 (average selection

247   strength) or 1.1×10^{-2} (moderately strong selection). For the rate of increase in the mean of

248   the climate variable, I used $\beta_{\mu,\Theta} = 0$ (base scenario) and 1.5×10^{-2}. I used rates of the

249   increase in the standard deviation of the climate variable $\beta_{\sigma,\Theta}$ from 0 (base scenario) to

250   1.5×10^{-2}. According to Bürger and Lynch (1995), when the standard deviation of the

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251   distribution of the optimum σ_θ reaches the same order of magnitude as the width ω of the

252   fitness function, the population is at risk of going suddenly extinct, with little role played

253   by genetics. Therefore, I chose values of $\beta_{\sigma,\Theta}$ that strongly increase the probability of

254   climate extremes, but did not inevitably make the population go extinct.

255   I used frequency of point extreme events p(E_a) of either 5 (no variation before and

256   after climate change, corresponding to a recurrence interval of 20 years), 10 (i.e.,

257   recurrence interval is 10 years) or 15 10^{-2} (Table 1). I used moderate mortalities caused

258   by point extremes (simulations with m_E equal to either 0.3, 0.5, 0.7) and moderate p(E_a),

259   since with higher mortality induced by point extremes and higher probability of their

260   occurrence the system will be largely driven by the point extremes, with no or little role

261   of genetics and demography in determining population dynamics and risk of extinction.

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

263   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

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

265   **2.4.2   Initialization**

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

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

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

269   years both phenotypic mean and variance remained basically constant. Then, the mean of

270   Θ increases for 150 years and variance of Θ for 25 years. The variance of Θ was then

271   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.

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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

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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

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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

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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).

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4   Discussion

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

I found additive effects—with largely no interaction effects—between age at first reproduction and fecundity on risk of extinction for the range of values I simulated. In the replicates that survived up to the end of simulation time, the total number of years in which the population was at a small size was a good predictor of allelic richness for the quantitative trait selected for. The population frequency of theoretically advantageous alleles was strongly correlated with the mean value of the phenotype under selection, but was otherwise largely unpredictable. Last, simple models including basic demographic and vital rates information, along with climate/environmental measures, provided excellent predictions of contemporary risk of population extinction.

4.1 Life histories

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

For many animal species that commonly experience the often-catastrophic effects of extreme climate or point events—and have limited movement range for physiological and

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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

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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).

496   Although it may appear from the simulation results that vital rates and environmental

497   conditions play a small role in models that predict contemporary risk of extinction, those

498   rates and conditions heavily contribute to determining population size in the "observation

499   window"; for example, populations with higher fecundity and younger age at first

500   reproduction are less likely to remain at low population sizes than populations with lower

501   fecundity and delayed sexual maturity. Likewise, a more extreme environment (e.g.,

502   greater selection strength and more frequent and/or severe climate and point extremes)

503   tends to decrease average population size, either due to acute events that kill individuals

504   or constant recovery from population crashes.

505   Luck plays also plays a major role in determining whether a population will recover

506   after a population crash. Vincenzi et al. (2017a) found that the almost-complete recovery

507   of a trout populations that was reduced to a handful of individuals after a flash flood was

508   due the large production of offspring by a single mating pair. Considering the high

509   variance in adult reproductive success in trout population—which is at least partially due

510   to differences in individual "quality" (Auld et al. 2019)—had the mating pair been killed

511   or displaced during the flash flood, population recovery would have suddenly become

512   much less likely.

513   **4.3 Modeling considerations**

514   Modeling and simulation approaches can help understand the effects of multiple

515   extreme stressors on the contemporary risk of extinction of species, and can be used to

516   guide or support both the set-up of ecologically relevant experimental designs and the

517   interpretation of biological responses to multiple stressors.

518 However, models of population and genetic dynamics are limited in their scope of

519 prediction by both the understanding of the biology and ecology of the species and the

520 availability of data to parametrize, train, and test models. Although often intuitive, it is

521 nevertheless important to remind ourselves that the simulation results of modeling

522 exercises depend on, first, our biological and ecological understanding, and, second, the

523 simplified modeling of the species and the environment they inhabit. For instance,

524 general trade-offs between allocation of resources to competing physiological functions

525 are not only often intrinsically challenging to model, but they may also vary over time

526 and space for the same species or population. That is, even when there is qualitative

527 understanding of some biological or ecological process, the parameterization and choice

528 of parameter values for the model may be too uncertain too provide actionable

529 predictions.

530 Trade-offs between model accuracy and interpretability also need to be taken into

531 account when developing models of population and genetic dynamics. Accuracy

532 describes the ability of a model to explain observed data and make correct predictions,

533 while interpretability concerns to what degree the model allows for understanding

534 processes. Often, a trade-off exists between accuracy and interpretability: more complex

535 models are usually opaque, while more interpretable models often do not provide the

536 same accuracy or predictive power of more complex models (Breiman 2001b). Then,

537 although intuitively more complex models are expected to provide more accurate

538 predictions of risk of extinction or population and genetic dynamics, this is not always

539 the case. For instance, Ward et al. (2014) tested the predictive performance of short-term

540 forecasting models of population abundance of varying complexity. They found that

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541   more complex models often performed worse than simpler models, which simply treated

542   the most recent observation as the forecast. In their case, the estimation of even a small

543   number of parameters imposed a high cost while providing little benefit for short-term

544   forecasting of species. However, when there was a clear signal of cyclic dynamics, more

545   complex models were able to more accurately predict future population sizes.

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

547   the type and amount of data collected, and the acceptable prediction uncertainty.

548

549 **Ethics**

550 Not applicable

551 **Data accessibility**

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

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

554 **Authors' Contributions**

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

556 wrote the manuscript.

557 **Competing interests**

558   The author declares no competing interests

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563 La Habana, Cuba, and finished writing the manuscript after the 2020 California fires that

564 imperiled the town where he resides (Santa Cruz, CA, US) and the COVID-19 pandemic

565 highlighted the importance of proper simulation modeling for basic science and policy,

566 and the increasing threat of extreme events for people and nature.

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663   **Tables**

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665   **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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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.

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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.

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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)
$\mathrm{mean}(\Theta(t) - z(t))$	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.
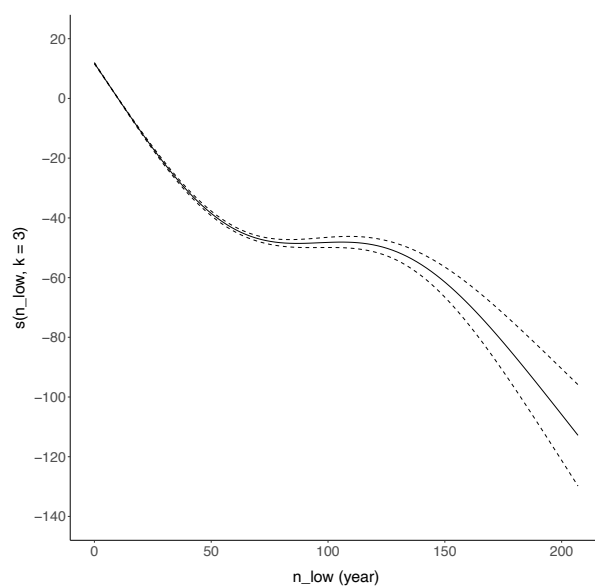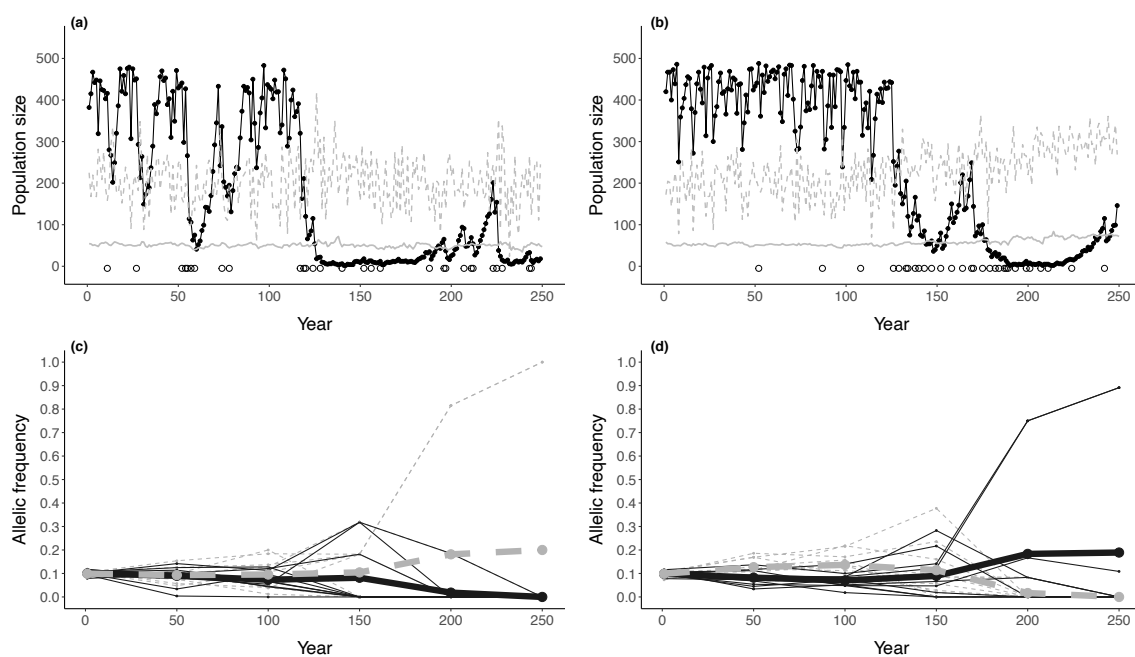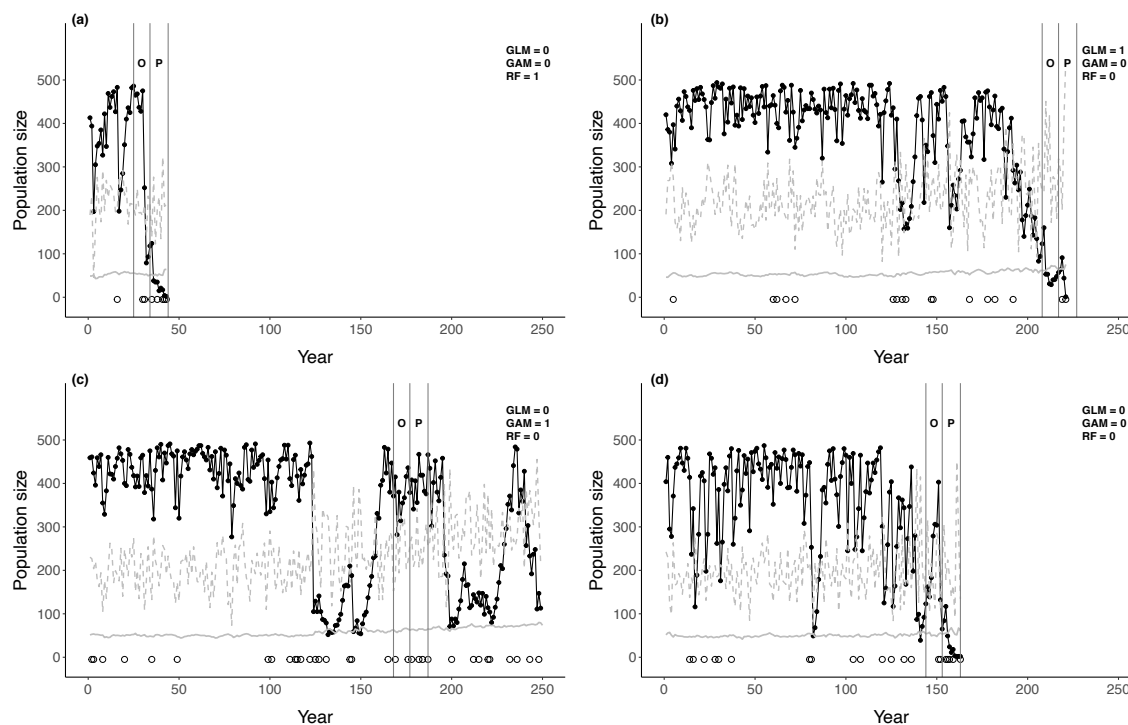
767   **Figure 1**
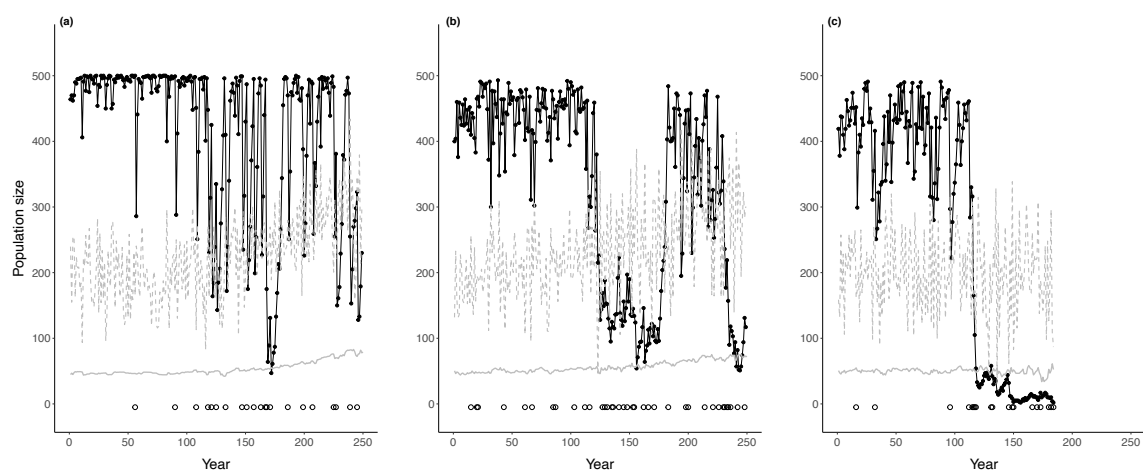
768 **Figure 2**
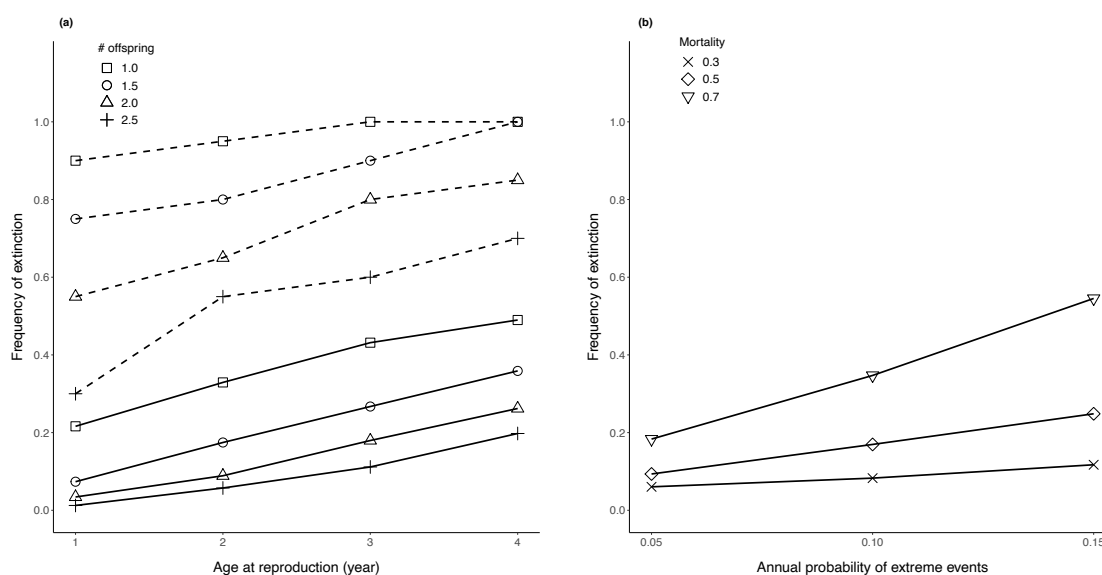
769 **Figure 3**

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770 **Figure 4**

771 **Figure 5**

772 **Figure 6**