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Class Project

The effect of catastrophes on the risk of population extinction

Introduction

In the context of population ecology, catastrophes have usually been defined as "large environmental perturbations that produce sudden major reduction in population size" (Lande 1993, p 912). Catastrophes can be characterized by two parameters: (i) their *frequency* or probability of occurrence in a given time interval; and (ii) their *intensity*, i.e., the magnitude of their impact on the population.

First, a clear distinction must be made between the *frequency* of occurrence and the duration, once it has occurred, of a catastrophe. Catastrophes are events characterized by their low *frequency*, but not necessarily by their short duration in time, once they happen. A rare event that would affect population parameters for a relatively long duration, such that at the end of this period the size of the population has strongly decreased, should still be called a catastrophe. Examples of such *prolonged* catastrophes are prolonged severe cold spells (e.g., Marmontel et al. 1997), prolonged winter flood (e.g., Wilson & Peach 2006) or other persistent modifications of the habitat.

Second, in the literature, catastrophes have almost exclusively been thought and modeled as events inducing (immediate) massive mortality (e.g., Brockwell 1986, Ewens et al. 1987, Lande 1993, Mangel & Tier 1994). Even though this view is relevant for many cases (e.g., Altwegg et al. 2006, Wilson & Peach 2006, Frederiksen et al. 2008), I think that the definition of a catastrophe applies to a broader context and must include cases where other vital rates, not only survival, are affected. Indeed, catastrophes certainly often affect fecundity (i.e., birth rate) as dramatically as survival. Moreover, cases where survival wouldn't be reduced, but fecundity would be dramatically dropped, could still have catastrophic consequences for a population, especially if the birth rate was reduced for a long period. For example, a chemical contamination of a pond that would persist for several years and that would make every living individual sterile could really represent a catastrophe for local fish populations.

Third, the ways how catastrophes are usually defined or modeled in population dynamic studies implicitly assumes that these events affect all age or stage classes of the population similarly. This characteristic, even though rarely discussed in the literature (but see Altwegg et al. 2006), may sometimes be an important feature to distinguish catastrophes from "common" environmental stochasticity. Indeed, while the effects of environmental variability on population persistence may be dampened by the fact that age classes with the higher reproductive values are less susceptible to such variations (a process called demographic buffering; Pfister 1998, Morris & Doak 2004), the effects of a catastrophe will be more drastic, not only because of their higher *intensity*, but also because they reach all age classes with the same strength. However, even if most catastrophic events possess this non-discriminant nature, the definition of a catastrophe should not be restricted to cases where all age classes are impacted. For example, for species in which the juvenile and the mature phases do not occupy the same habitat, a catastrophe occurring in a single of these habitats and thus inducing massive mortalities of only one of the two phases could still compromise the persistence of the population.

Fourth, the consideration of factors that can produce a catastrophe is often limited to extrinsic factors (e.g., extreme weather), whereas the role of factors partially intrinsic to the population (e.g., disease outbreak) is more rarely considered. This bias is reflected by the presence of the term ‘environmental’ in the above definition. A major consequence of ignoring the role of intrinsic factors is that catastrophes have usually been thought as being density-independent events. However, it is relevant to consider that the *intensity* and also the *frequency* of catastrophes can sometimes be density-dependent (e.g., Wilcox & Elderd 2003). For example, some extreme weather events (e.g., hurricanes) that strongly modify the habitat may create situations of starvation in small mammal populations (e.g., Swilling et al. 1998) that are more dramatic when the population density is high. In such a case, the probability of occurrence of the catastrophe is density-independent, while its *intensity* is density-dependent. Examples of catastrophes, whose *frequency* is density-dependent, are provided by disease outbreaks. Indeed, the probability of occurrence of the outbreak is a direct function of the transmission rate of the pathogen, which is favored in high density. The *intensity* of such catastrophes (i.e., induced mortality) can be more (e.g., *Mycoplasma gallisepticum* outbreak in house finches *Carpodacus mexicanus* populations, Hochachka & Dhondt 2000) or less (e.g., crabeater seals *Lobodon carcinophagus* populations, Laws & Taylor 1957, Wilcox & Elderd 2003) density-dependent.

In the existing literature (especially the theoretical literature), catastrophes have usually been defined and modeled with the following characteristics:

- low *frequency*
- high *intensity*
- short duration (immediate effect)
- massive mortality consequences
- non-discriminant nature (all individual are affected)
- density-independent nature

However, I argue that only the two first characteristics (low *frequency* and high *intensity*) are necessary conditions to define an event as being a catastrophe. I would thus propose to broadly define a ‘catastrophe’ as: “**Any *rare* event that has some *unusually strong* negative effects on any component of a population**”. The four other characteristics may however serve as criteria to define sub-categories of catastrophes. For example, catastrophes *may*:

- induce immediate effects or effects that last a relatively long time
- affect survival only, birth rate only, or both parameters
- affect all individuals or only certain age classes
- occur independently or as a function of population density
- induce effects that are density-independent or density-dependent

Existing studies have mainly focused on the impact of catastrophes on population persistence through the effects of their *frequency* and *intensity*. However, virtually nothing has been reported about the effects of the other characteristics. Some questions of interest are: what is the relative importance of these various other characteristics? How do they affect population viability? What are the consequences of ignoring them when modeling the impact of catastrophes on population persistence? Can it be misleading?

Concerning the potential density-dependence nature of catastrophes, some of these aspects have been investigated by Wilcox et al. (2003). Previously, it was generally admitted that ignoring density-dependence of catastrophe *frequency* and *intensity* was a conservative approach. However, Wilcox et al. (2003) demonstrated that including density-dependence caused a relative increase of persistence at intermediate population size, while it decreased persistence at large sizes, leading to the conclusion that intermediary population sizes might, in certain cases, be more persistent than larger populations. Therefore, they proved that ignoring such aspects of catastrophes could really lead to erroneous conclusions and maybe to non-optimal decisions for conservation actions. Here, I propose to investigate the properties of other catastrophe characteristics. I simulated population trajectories with occurrence of different types of catastrophe and recorded how extinction probability was affected in the different cases.

Another relevant question that arises when defining catastrophes is: are catastrophes just extreme realizations of environmental stochasticity or are they something really different? So, should we model catastrophes from the same or from a different distribution as environmental stochasticity? This question is not an easy one to answer and the response probably lies between these two extremes. By adopting the perspective of the mechanisms that may be responsible for catastrophes, we should conclude that some catastrophes arise as extreme realizations of a common process (e.g., extreme weather events) and some others are due to completely different mechanisms (e.g., volcanic eruption, earthquake). Also, we might consider the fact that the effect of common environmental factors may be linear inside a certain range of variation, but may become non-linear outside this range of values. In other words, extreme realizations of such 'common' factors may induce effects that are amplified (i.e., non-linear effects; e.g., Nevoux et al. 2008).

To determine if a different distribution is required to model the effect of catastrophes on population dynamics, we should ask ourselves the two following questions: (1) does the distribution used to represent environmental stochasticity include rare events due to unusual mechanisms? (2) Do extreme realizations of a common mechanism induce effects that are simply a linear extension of commonly induced effects? If the answer is "no" to any of these two questions, then a different distribution should be envisaged. In this study, catastrophes were modeled as events that are different and independent from common environmental variation, as it is usually done in the literature, in order to: (1) represent events from different mechanisms (e.g., volcanic eruption, exceptional pollution/contamination event) than those governing the base environmental variation; and (2) allow their effects to contrast with those from environmental variation (potential non-linear effects).

In this study, I tried to understand what properties of catastrophes are the more dramatic for population persistence. I thus investigated with simulations the consequences on population viability of various catastrophe scenarios. First, I assessed the effects of increasing *frequency* and *intensity* of catastrophes on the risk of extinction. Second, I investigated the marginal effects of three other catastrophe properties (duration, parameters and age classes affected) on population persistence.

Method

a. *Model used to simulate population trajectories*

The relative importance of the various features of catastrophes was evaluated by simulating 500,000 population trajectories for each scenario of catastrophe. Each trajectory was projected over a time horizon of 100 years and the population was considered as being extinct if its size passes below some quasi-extinction threshold (i.e., population size under which the population is assumed not being viable anymore, primarily for genetic and demographic reasons). This threshold was assumed to be 30 individuals. For each particular scenario, the probability of quasi-extinction over the time horizon was thus estimated as the proportion of trajectories that crossed the threshold.

Population trajectories were simulated with a stochastic death-and-birth model with age structure and environmental variation. The model structure and parameter values were set to be representative of the life cycle and the population dynamics of a short-lived vertebrate organism (typically a passerine bird). Specifically, parameters values were picked from estimates of Great tit (*Parus Major*) populations found in the literature (see Sæther & Bakke 2000, Appendix 1; estimates obtained from Kluijver 1951, Clobert et al. 1988). Annual juvenile survival (p_{juv}) was 0.22, annual adult survival (p_{ad}) was 0.48 and per capita annual birth rate (m_{ad}) was 3.9. The model included 5 age classes: the first age class represented the juvenile class with fecundity (i.e., per capita birth rate) equal to zero and a specific juvenile survival probability (p_{juv}), whereas all four other age classes were adult classes with the same per capita fecundity rate (m_{ad}) and the same survival probability (p_{ad}). This age structure is relevant for short-live species like the Great tit in which individuals become mature at young ages and virtually never live over age 5 in nature (with the survival probabilities found in the literature and used here, without considering any senescence, the probability for an individual to live over age 5 is about 0.01).

The model includes demographic stochasticity, which is represented by a Binomial distribution for the annual numbers of survivors and by a Poisson distribution for the annual number of births. Each year, new values of the parameters of these distributions (i.e., survival probabilities and per capita birth rate) were drawn from a multivariate Normal distribution, representing the effect of environmental stochasticity. A multivariate Normal distribution was chosen in order to be able to specify a positive correlation among vital rates, because one expects temporal environmental variation to affect these different rates in the same direction. Annual birth rates were assumed to be log-normally distributed (i.e., only positive values), whereas both juvenile and adult survival probabilities were assumed to have a Normal distribution, restricted between 0 and 1 (See Appendix 1 for details about how survival values were assured to be between 0 and 1). Therefore, parameters of the multivariate Normal distribution (means, variances and covariances) were in the log scale for birth rate and in the original scale for survival probabilities. Means of each of the vital rates were such as to be equal, in the original scale, to the estimated values found in the literature (see above, p_{juv}, p_{ad}, m_{ad}). Standard deviations (expressed in the original scale) were 0.1 for both juvenile and adult survival probabilities and 1.5 for birth rate. The correlation was 0.9 between adult and juvenile survival parameters, 0.8 between adult survival and birth rate and 0.8 between juvenile survival and birth rate.

Also, to avoid unbounded exponential population growth, a ceiling of 1000 individuals for population size was included in the model (i.e., carrying capacity parameter (K)). This ceiling was modeled such that any population surplus was primarily removed from the first age class (e.g., the lack of territory primarily affects juveniles, adults being already established), and the eventual remaining surplus was then removed from other age classes in equal proportions (however, given the high birth rate of this species and thus the predominance of 'newborns', the 'population surplus' happened to never be larger than the first age class size). The initial population size was 20 individuals in each of the five age classes (i.e., 100 individuals total) for all simulations (see Appendix 2 for an example of a population trajectory simulated with this model).

Finally, the model included catastrophes as very rare events that strongly affect vital rates independently of environmental stochasticity. Catastrophe occurrence was modeled as a Bernoulli trial with some low *frequency* parameter. Catastrophe *intensity* was represented as a decrease of vital rates by some multiplicative constant (for example, a 5-fold decrease is represented by a multiplicative constant of 1/5). This *intensity* was allowed to differ among the different parameters, allowing investigating differences among vital rates (survival vs. birth rate) and among age classes (juveniles vs. adults). Also, the duration (in years) of the effects of catastrophes, when they occur, could be set in the model, allowing investigating the effect of this characteristic on population persistence. The "classic" model of catastrophes, as usually found in the literature and corresponding to **immediate** massive **mortality** in **all age classes** of the population, can be specified in this model by setting duration of zero and the same effect for all parameters (see Appendix 3 for proofs).

b. The different scenarios for catastrophes

In a first step, to investigate the effects of catastrophe *frequency* and *intensity* on the probability of extinction, I compared a model without catastrophe to a set of models of increasing *frequency* and *intensity*. This set consisted of models with the *frequency* parameter set respectively to 1/20, 1/50, 1/100 and 1/200, with a constant *intensity* of 1/3 (i.e., vital rates decline to 1/3 their base value) and of models with the *intensity* parameter set to 1/2, 1/3, 1/5 and 1/10, with a constant *frequency* of 1/50. All these latter models correspond to the “classic” view assuming instantaneous (i.e., duration = 1) and non-discriminant (i.e., same effect on all parameters) catastrophes.

In a second step, in order to investigate the relative and marginal effect of other catastrophe characteristics, I proceeded step by step, by progressively adding and increasing the weight of each characteristic. First, I assessed the consequences of increasing the duration of catastrophe effects. In this series of models, the duration parameter was consecutively set to 1 year (i.e., immediate catastrophe; its effect does not last), 2, 4, 8, 12 and 16 years. *Frequency* was 1/50 in all models, while annual *intensity* of each model was calculated such that the theoretical global *intensity* was the same in each model. Specifically, annual *intensity* corresponded to the chosen global *intensity* raised to the n^{th} root, n being the duration. For example, with a duration of 4 years, to have a similar global *intensity* as an immediate catastrophe (i.e., duration of 1 year) with an *intensity* of 1/3, the annual *intensity* was set to $(1/3)^{1/4} = \sqrt[4]{1/3}$. This way, instead of simply looking at the effects of replicating the same immediate catastrophe for several consecutive years, I was able to really investigate the properties of catastrophe immediateness, while controlling for *intensity*. Second, I investigated differences between catastrophes having effects on survival only, fecundity (i.e. birth rate) only, or both kinds of parameters. *Frequency* was 1/50, duration was 1 year and the parameter-specific *intensities* were chosen as to get an overall *intensity* of 1/3. For example, for the model with catastrophe effects on fecundity only, the *intensity* was set to 1/1 (i.e., no effect) for juvenile and adult survival and to $(1/3)^{9/3}$ = 1/27 for birth rate. Following the same logic, for the model with effects on survival only, *intensity* was set to $(1/3)^{4.5/3}$ for juvenile and adult survival and to 1/1 for birth rate. In the model with effects on all vital rates, *intensity* was set to $(1/3)^{3/3}$ for each one of them. Finally, I investigated differences among catastrophes affecting juveniles only, adults only, or both classes. Here again, *frequency* and duration were set to 1/50 and 1 year respectively, and the class-specific *intensities* were chosen as to get an overall *intensity* of 1/3. For example, for the model with catastrophe effects on juveniles only, the *intensity* was set to 1/1 (i.e., no effect) for adult survival and adult fecundity and to $(1/3)^{9/3}$ = 1/27 for juvenile survival. Following the same logic, for the model with effects on adults only, *intensity* was set to $(1/3)^{4.5/3}$ for adult survival and adult fecundity and to 1/1 for juvenile survival. In the model with effects on all age classes, *intensity* was set to $(1/3)^{3/3}$ for each of the three parameters. Table 3 summarizes the parameterization of the different scenarios representing catastrophes having effects on ‘survival vs. fecundity’ and on ‘adults vs. juveniles’.

Results

1. Effects of the *frequency* and the *intensity* of catastrophes on population persistence

Results from the series of simulations with variable *frequency* (Table 1.a, see also Appendix 4 for more detailed results from simulations) show that the probability of extinction of a population is really affected by catastrophes, even when having a very low probability of occurrence. Indeed, even when the *frequency* of catastrophe occurrence is as low as 1/200 (the time horizon being of 100 years, this means that there is about 0.5 chances for any population trajectory to encounter one catastrophe), the probability of extinction (9.3%) is about 35% higher compared to the case without any catastrophe (probability of extinction being of 6.9%). Moreover, it appears that the risk of extinction increases linearly with increasing *frequency* (Figure 1).

From the series of simulations with variable *intensity*, one concludes that the probability of extinction of a population is also really affected by the *intensity* of catastrophes (Table 1.b, see also Appendix 4). Even when catastrophes (having a *frequency* of 1/50) reduce vital rates by only 50% the probability of extinction (11.8%) is strongly higher (about 71% higher) compared to the case without catastrophe. Moreover, the risk of extinction seems to increase exponentially with increasing *intensity* (Figure 2). Therefore, the effect of catastrophe *intensity* appears to be even more critical than the effect of *frequency*.

2. Relative effect of other catastrophe characteristics on population persistence

Duration

The duration of catastrophe events appears to decrease their impact on population's risk of extinction (Table 2, see also Appendix 4). Therefore, it seems that catastrophes having an immediate effect are more 'efficient' than catastrophes having a spread out effect (remind that annual *intensities* were adjusted in regards of the global *intensity*). Moreover, the risk of extinction appears to decrease with a negative logarithmic trend as duration increases (Figure 3). Immediateness thus seems to be a crucial characteristic of catastrophes.

Effects of catastrophes on survival vs. fecundity

First, results from this set of simulations (Table 3, see also Appendix 4) shows that when catastrophes affect both survival and fecundity their effects on population persistence are stronger than when they affect only one of these parameters (remind that parameter-specific *intensities* were adjusted in regards of the global *intensity*). It means that catastrophes having smaller effects on all these vital rates are more dramatic than catastrophes having larger effects on a subset of these vital rates. Second, it seems that effects on survival are more important than effects on fecundity because the probabilities of quasi-extinction are of 13.7% and 12.6% respectively. However, the difference among these vital rates is not very large.

Effects of catastrophes on adults vs. juveniles

Similarly to the precedent case, it appears that catastrophes having smaller impacts on all age classes induce stronger negative effects on population persistence than catastrophes having larger impacts on a subset of age classes only (Table 3, see also Appendix 4). Moreover, it seems that the effects on adults are more penalizing than effects on juveniles, the probabilities of quasi-extinction being respectively 14.3% and 10.0%. This difference seems to be more significant than in the precedent case (i.e., ‘survival vs. fecundity effects’).

Discussion

1. Effects of the *frequency* and the *intensity* of catastrophes on population persistence

I have shown in this study that catastrophes, even when *infrequent* (e.g., every 200 years in average) or of moderate *intensity* (e.g., 50% of decrease of vital rates), really change the persistence of a population. Moreover, I found that the probability of extinction changed exponentially with *intensity* while it changed linearly with *frequency*. Therefore, the effect of *intensity* seems to be more dramatic than the effect of *frequency*.

Catastrophes represent a threat for population persistence by dropping population size to a level (thereafter, ‘zone of threat’) at which the chances to randomly go to extinction, because of environmental and demographic stochasticity, are larger (as if the population were set to a new, low, initial size). Figure 4 is a display of four ‘hypothetical’ population trajectories in which one catastrophe occurs, and shows how the fate of the population can be affected by the catastrophe. The *intensity* of a catastrophe directly determines the amplitude of the drop that a population will experience when facing such an event. In other words, *intensity* directly determines how close from extinction the population is placed by a catastrophe (see figure 4). This is the reason why increasing this parameter has such dramatic effects on population persistence (figure 2). On the other hand, *frequency* simply determines how often a population will experience such drops. It does not determine how close from extinction the population is placed at each catastrophe occurrence, but just influences how much time (in average) the population has to ‘escape’ the ‘zone of threat’ until the next catastrophe (as *frequency* increases this average time decreases). Therefore, the effect of *frequency* (figure 1) on population persistence is not as dramatic as the effect of *intensity*. To make an explicit comparison, imagine two scenarios: (1) during a 100-year time-frame, one catastrophe of *intensity* 1/9 occurs (figure 4); (2) during the same 100-year time-frame, three catastrophes of *intensity* 1/3 occur (figure 5), i.e., the *frequency* is three times higher than in scenario 1, but the *intensity* is three times lower than in scenario 1. In scenario 2, the population never gets dropped as low as in scenario 1, neither after one single catastrophe because of the lowest *intensity*, nor after the accumulation of the three catastrophes (which cumulated *intensity* equal the one of scenario 1) because population has time to recover after each catastrophe.

These results allows us to infer that events which *frequency* will stay constant but which *intensity* will increase in future years should have stronger negative impacts on wild populations than events that will increase in *frequency* but not in *intensity*. However, events of the latter case would still negatively affect population persistence as we have shown that even small changes in *frequency* really affected probability of extinction.

2. Relative effect of other catastrophe characteristics on population persistence

Duration

I found that the immediacy of catastrophe effects was a characteristic that strongly affect population persistence. Indeed, a given 'global' *intensity* spread out over several years happened to be less dramatic for population persistence than the same *intensity* acting directly in one year.

This phenomenon seems also to be linked to the fact that the population is more likely to escape the 'zone of threat' when the effect of a catastrophe is spread out over time (see figure 6). Indeed, when *intensity* is spread out over several years it seems that population size never drops as dramatically as in the case of immediate catastrophes, because population dynamics still acts during all the time that it takes to the catastrophe to express its entire *intensity* (population growth rate being greater than 1 in this case study).

Effects of catastrophes on survival vs. fecundity and on adults vs. juveniles

The results from the set of models testing the effects of moving the weights of parameter-specific *intensities* among the different parameters (table 3) are, at a first glance, quite surprising. Indeed, the worst catastrophe scenario (called 'classic' in table 3) is the one inducing a 'weak' *intensity* (1/3) distributed on all parameters. Scenarios where some parameters were not affected (*intensity* 1/1) while others were more intensely affected (*intensity* $(1/3)^{4.5/3}$ or 1/27) all happened to have lower extinction risk than the 'classic' one. This is surprising because one might have expected the worst case being the scenario having an amplified *intensity* on the ‘more crucial parameter(s)’. It means that the dynamic of the population is such that an increased *intensity* on some of these parameters is (more than) compensated by a decreased *intensity* on others.

The way to solve this apparent paradox is to look at the reproductive values and reproductive potentials (thereafter RP; i.e., reproductive value weighted by the size of an age class) of each age class and to assess the impact of each type of catastrophe (“survival only”, “fecundity only”, “adults only” and “juveniles only”) on the size of each age class, and therefore on their respective RP.

Table 4 gives a summary of the general characteristics (mean age distribution, reproductive values and mean RP) of this age-structured population. First, age distribution along trajectories appears to be primarily dominated by juveniles and secondarily by two-year-old individuals (table 4). This is due to the high mean adult fecundity and the low mean survival probabilities of this population. Second, two-year-old individuals have clearly the highest reproductive values (table 4). These two characteristics make that the first (juveniles) and the second age classes have the highest mean RPs (0.72 and 0.84, respectively). Therefore, catastrophes should be even more dramatic as they decrease the size of these two age classes, hence strongly decreasing the RP of the whole population. Table 5 shows the effects (i.e., relative decrease) of catastrophe occurrence on total population size and on different subset of RPs, while table 6 shows the decrease of RP of each age class, for each catastrophe scenario.

First, one can see that only the ‘classic’ scenario induce a reduction of the RP of all age classes. In other scenarios, there is always one of the two high-RP age classes (age 1 or 2) that happen not to be affected (values are highlighted in table 5 and 6). In the ‘survival only’ scenario, the RP of all adults classes is decreased (variation of RP: -63% and -69%, table 5) when a catastrophe occurs, but the RP of the juvenile class is not (it still increases by 44%). This is due to the fact that adult fecundity not being affected, the number of juveniles added to the population at the catastrophe time is not lowered (and thus it keeps increasing as it does in average). On the other hand, because the size of adult classes depends on the survivorship of younger age classes, these classes are strongly affected by the decrease of survival rate. In the ‘fecundity only’ scenario, the situation is inversed: only the juvenile class is reduced. This result is the obvious corollary of the previous statement about the relation between fecundity and the size of the juvenile class, and between survival and the size of adult classes. Therefore, both these scenarios happen not to be as dramatic as the ‘classic’ scenario because there is always one of the two major components of population RP (i.e., one-year or two-year old age class) that is not affected by catastrophes (see table 5 and table 6). In the ‘adults only’ scenario, where adult survival and fecundity are affected by catastrophes, one remarks that it is the two-year-old age class that is not affected, while the RP of juveniles and other adult age classes is. This can be explained by the fact that the size of the two-year-old class depends on the proportion of juvenile survivors from the previous year, hence on juvenile survival, which happens not to be impacted. When a catastrophe occurs, the negative effects on other age classes are thus balanced by the fact that this two-year-old age class keeps its high RP. Conversely, in the ‘juvenile only’ scenario where only juvenile survival is affected, only the RP of the two-year-old class is decreased. In this case, this loss of RP is balanced by the large production of juveniles (due to the still ‘high’ fecundity of adults).

To summarize, the effects of these various scenarios should not be thought in terms of what parameter among the three (i.e., juvenile survival, adult survival, adult fecundity) is the more crucial, but in terms of which age classes have the highest RP and how do the different catastrophes affect these valuable age classes. In this population, the first two age classes have the highest RP, therefore a catastrophe scenario that would put all the *intensity* weight on adult fecundity (affecting the 1-year-old class) and on juvenile survival (affecting the 2-year-old class) should be more dramatic. Indeed, such a model gives a probability of extinction of about 17%, which is in fact higher than in the case of the four last models. However, it is still lower than in the ‘classic’ scenario, what is certainly due to the fact that the two-year-old class from the year just before a catastrophe is not impacted (adult survival staying the same), providing enough three-year-old individuals to reproduce and thus ‘recharge’ the juvenile age class, just after the catastrophe. Therefore, one can predict that the worst scenario would be a catastrophe which *intensity* would be distributed among adult fecundity, juvenile survival and survival of age 2. Indeed, such a model gives a probability of extinction of about 21.5%, which is even higher than in the ‘classic’ scenario.

3. Implications of these results

The immediacy with which the effects of a catastrophe are expressed appears to be an important characteristic of catastrophes. Indeed, the results of this study show that when the *intensity* of a catastrophe is spread out over time it has less chance to lead to extinction because the dynamic of the population dampens the reduction of population size. This understanding might have consequences for the management of endangered population. Indeed, to reduce the risk of population extinction, mitigating perturbations that have brutal effects should overrides the mitigation of perturbations that have temporally spread out and diluted effects.

We also learned here that the (st)age structure of a population should really be taken into account when evaluating the impact of a perturbation on population persistence. Indeed, not all (st)age classes have the same reproductive potential, and the extent of the impact of a catastrophe totally depends on which (st)age classes are affected. Catastrophes are even more dramatic as they affect the fraction of the population having the highest reproductive potential. Previous studies (e.g., Gallucci et al. 2006) already showed that using reproductive potential and reproductive values was the more relevant approach to assess the impact of animal populations' harvesting and exploitation. Therefore, for conservation concerns one should focus on the changes of populations' reproductive potential, rather than on population size changes, when assessing the consequences of any perturbation or even of management actions.

The results of this study also provide some support to the idea that was advanced by Altwegg et al. (2006) that a catastrophe might have very dramatic effects on a population because it usually affects indifferently all age classes. Indeed, while the effects of 'common' environmental stochasticity might be dampened because of demographic buffering, such catastrophes certainly induce far more critical effects because they also strongly affect age classes having high reproductive potentials.

Conclusion

I showed in this study that a characteristic of catastrophes that make them being a really threat for population persistence is the immediateness of their effects. This result is explained by the fact that a population has more chances to go to extinction, because of the influence of demographic and environmental stochasticity, when its size is dropped to a very low level. The amplitude of the drop of population size induced by a catastrophe is dampened by the population dynamics when the effects of the catastrophe are spread out over time. Therefore, when effects are expressed immediately the impact on population size is even more critical.

I also showed that the impact of catastrophes on population persistence is better captured by the impact on the reproductive potential of the different (st)age-classes. To predict the extent of impacts of any perturbation on population persistence one should thus focus on which vital rates are affected and how this will impact each age classes. This way, we should be better able to evaluate how the reproductive potential of the population is impacted and thus the consequences of the perturbation in terms of extinction risk.

Table 1. Results of the series of simulations with varying *frequency* (a) and varying i*ntensity* (b). Duration was set to 1 year in all these models, *intensity* was set to 1/3 for all parameters in the series of models with varying *frequency* (a) and *frequency* was set to 1/50 in the series of models with varying i*ntensity* (b).

a.

Frequency	0	1/200	1/100	1/50	1/20
Probability of Quasi-Extinction	0.069	0.093	0.121	0.186	0.432

b.

Intensity	1	1/2	1/3	1/5	1/10
Probability of Quasi-Extinction	0.069	0.118	0.186	0.32	0.524

Table 2. Results of the series of simulations with varying duration of catastrophes. *Frequency* was set to 1/50 and *intensity* to 1/3.

Duration (years)	1	2	4	8	12	16
Probability of Quasi-Extinction	0.186	0.174	0.156	0.132	0.119	0.109

Figure 1. Variation of probability of quasi-extinction with increasing *frequency*.

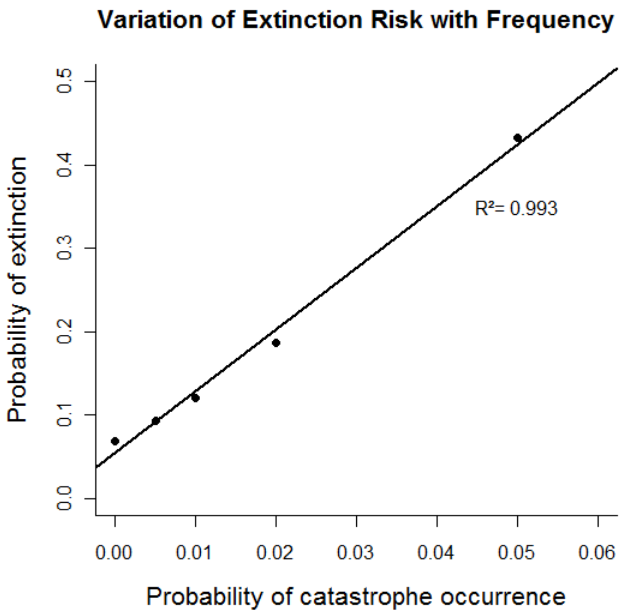

Figure 2. Variation of probability of quasi-extinction with increasing *intensity*. Here, i*ntensity* is represented as the constant by which vital rates are divided when a catastrophe occurs (e.g., *intensity* = 1 means that catastrophe has no effect).

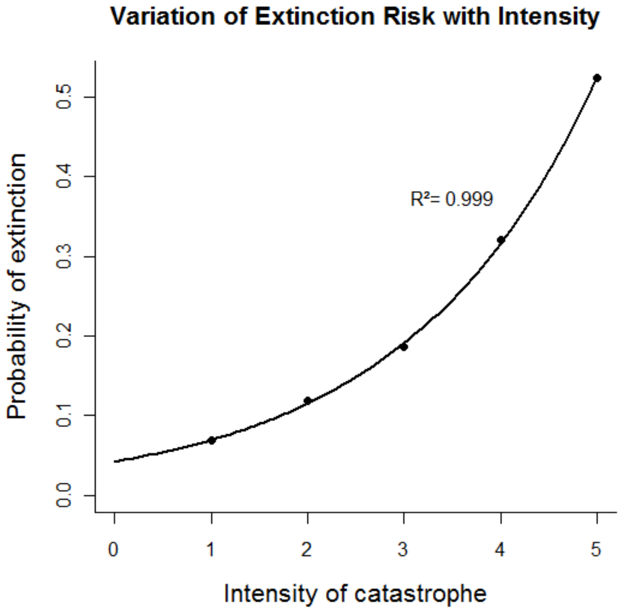

Figure 3. Variation of probability of quasi-extinction with duration of catastrophes.

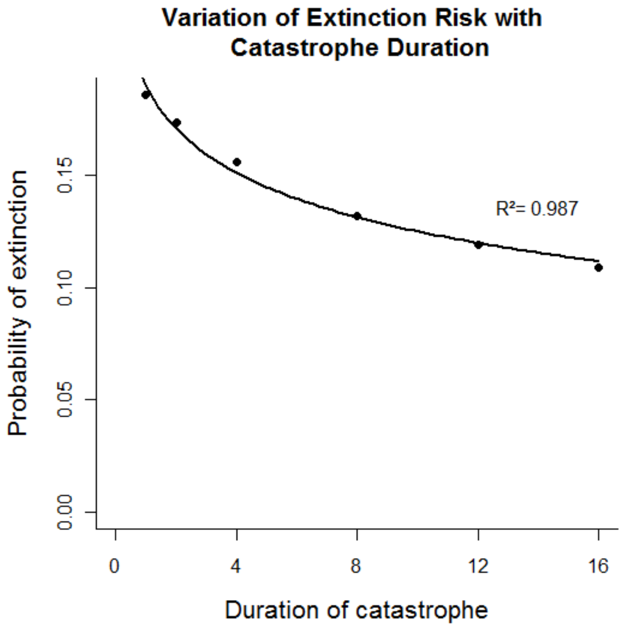

Table 3. Parameterization of the different models (effects on survival vs. fecundity and effects on adults vs. juveniles) involving variable *intensity* of catastrophes on the different vital rates. The probability of quasi-extinction obtained from 500,000 simulations is also shown in the table.

Model	**Juv Survival**	**Adult Survival**	**Adult Fecundity**	**Proba Quasi-Ext**
Classic	1/3	1/3	1/3	0.186
Survival only	$(1/3)^{4.5/3}$	$(1/3)^{4.5/3}$	1	*0.137*
Fecundity only	1	1	1/27	*0.126*
Adults only	1	$(1/3)^{4.5/3}$	$(1/3)^{4.5/3}$	**0.143**
Juveniles only	1/27	1	1	**0.100**

Figure 4. Illustration of the effect of catastrophe *intensity*. Population trajectory where only one catastrophe occurs during the 100 years (corresponding to a *frequency* of 1/100) and which *intensity* is 1/9. In this case, the catastrophe has an immediate effects (i.e., duration = 1 year).

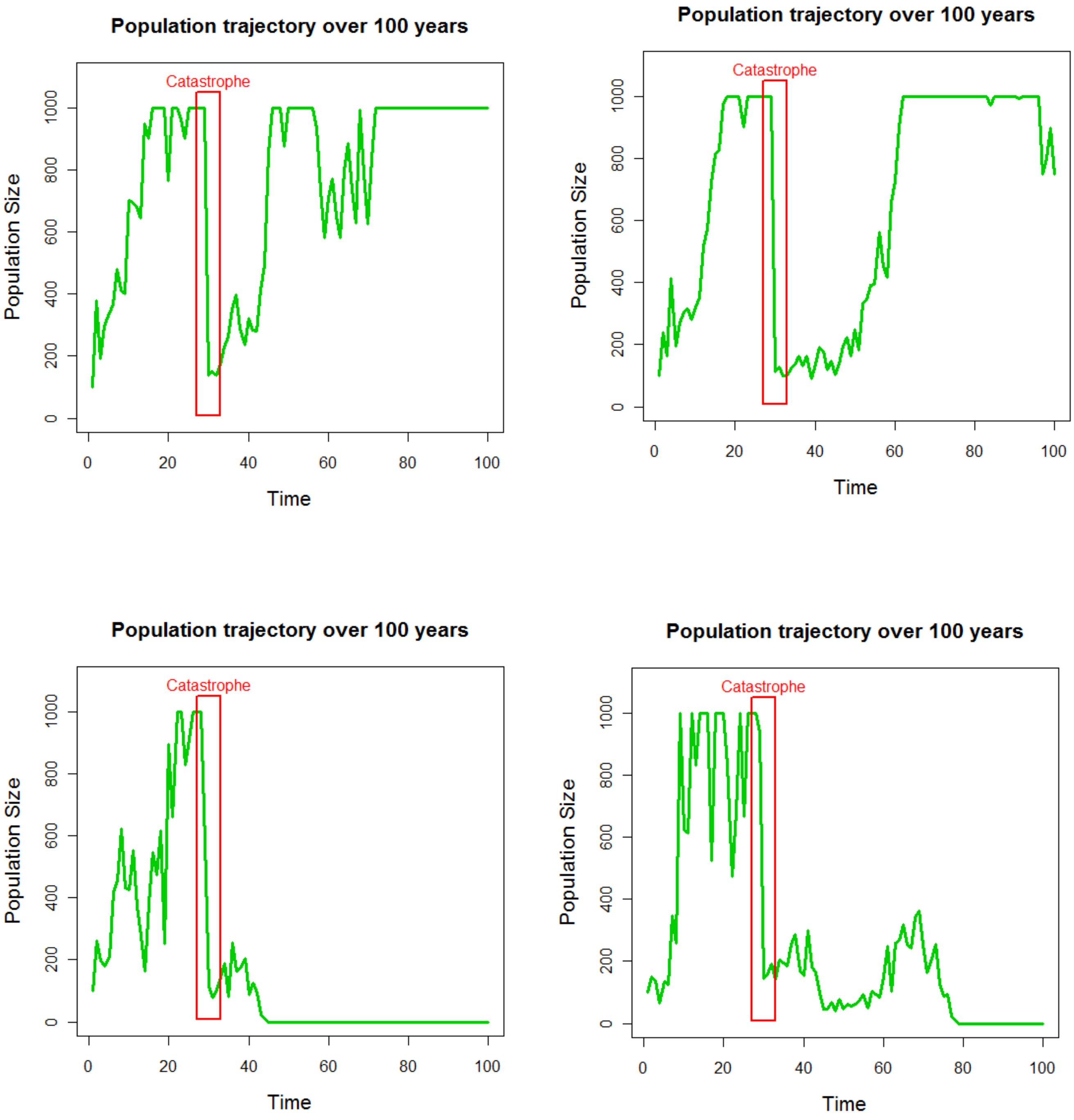

Figure 5. Illustration of the effect of catastrophe *frequency*. Population trajectory where three catastrophes occur (corresponding to a *frequency* of 3/100), in years 30, 50 and 70, but which *intensity* each time is 1/3. In this case, catastrophes have immediate effects (i.e., duration = 1 year).

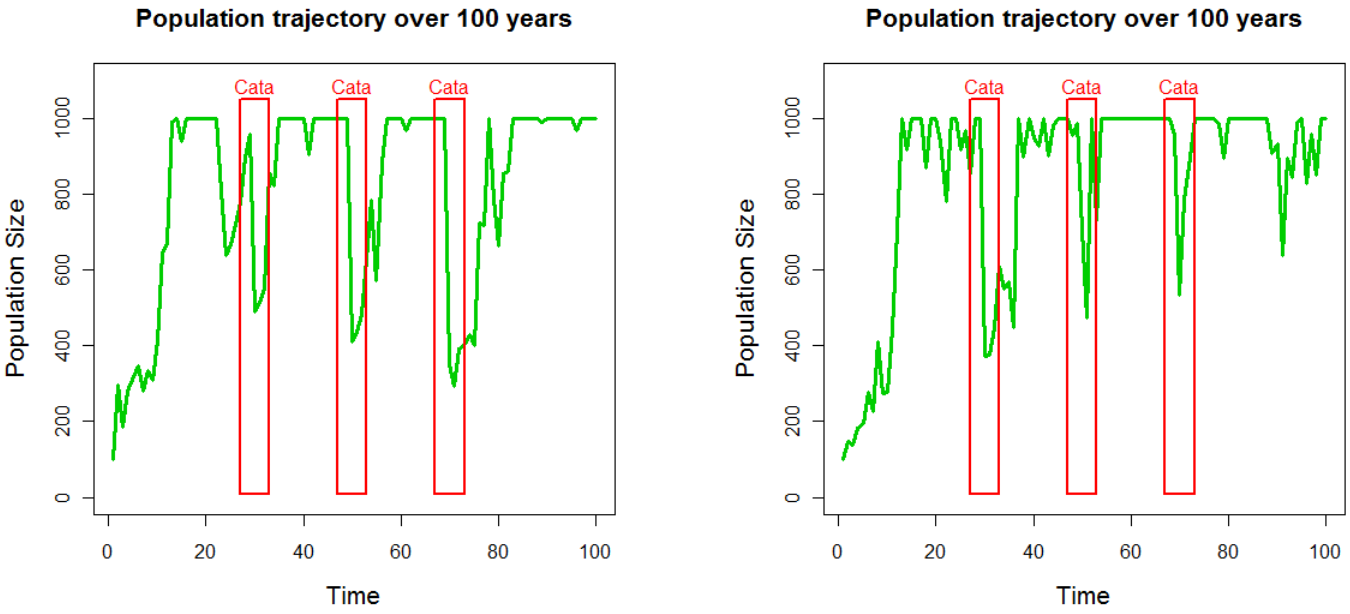

Figure 6. Illustration of the effect of catastrophe duration. Population trajectory where only one catastrophe occurs during the 100 years (corresponding to a *frequency* of 1/100), but which duration is 8 years. The global *intensity* is 1/9 (i.e., annual *intensity* is $(1/9)^{1/8}$).

Table 4. Mean age distribution, reproductive values and mean relative reproductive potential of the modeled population.

Age class	Mean Age Distribution	Reproductive Value	Mean Relative Reproductive Potential
Age 1	0.72	1.00	**0.72**
Age 2	0.15	5.42	**0.84**
Age 3	0.07	5.20	0.37
Age 4	0.04	4.65	0.17
Age 5	0.02	3.31	0.07

Table 5. Relative decrease of total population size and different subset of reproductive potential (RP) for each catastrophe scenario. The associated probability of quasi-extinction is also shown.

Model	Proba Quasi-Ext	Population size	RP juveniles	RP age 2	RP age 3:5
classic	**0.186**	- 54.3%	-43%	-42%	-49%
Survival only	**0.137**	+ 15%	+44%	-63%	-69%
Fecundity only	**0.126**	- 66.6%	-91%	+118%	+76%
Adults only	**0.143**	- 59.7%	-65%	+80%	-68%
Juveniles only	**0.100**	+ 22.4%	+33%	-91%	+84%

Table 6. Relative decrease of reproductive potential of each age class for each catastrophe scenario.

Age class	Classic	Survival only	Fecundity only	Adults only	Juveniles only
age 1	-43%	**+44%**	*-91%*	-65%	+33%
age 2	-42%	-63%	+118%	**+80%**	*-91%*
age 3	-46%	-68%	+105%	-67%	+115%
age 4	-49%	-68%	+72%	-68%	+77%
age 5	-52%	-71%	+52%	-70%	+59%

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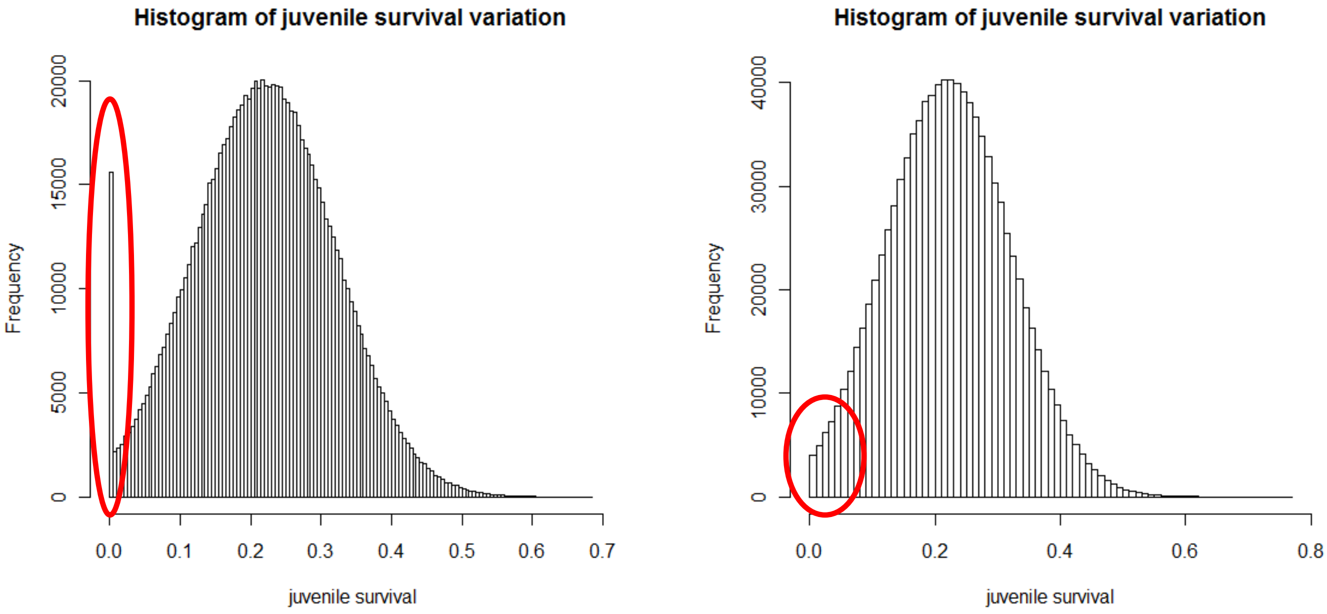
Appendix 1. Modeling of environmental stochasticity of vital rates as a multivariate Normal distribution

In this study, I modeled environmental stochasticity by a multivariate Normal distribution of adult survival, juvenile survival and the natural logarithm of birth rate (the birth rate having itself a log-normal distribution). The mean and standard deviation (SD) of log (birth rate) were chosen as to correspond to a mean of 3.9 and a SD of 1.5 for the birth rate in its original scale. The mean and SD were respectively 0.48 and 0.1 for adult survival and 0.22 and 0.1 for juvenile survival. Survival being a probability, it must be restricted to take only values between 0 and 1. A simulated sample of one million of values for each vital rate shows that adult survival never take values outside the [0, 1] range (max = 0.973, min = 0.003) and that juvenile survival never take values above 1 (max = 0.695). However, juvenile survival takes values below zero about 1.4% of the time (it is due to the low mean of 0.22, with a SD of 0.1). To avoid such cases, two solutions were envisaged: (1) setting the value to zero when the draw happen to be below zero; or (2) draw a new value when the draw happen to be below zero. The first solution is not satisfying in our case because it artificially increases the proportion of zeros in the distribution, which is thus not normal anymore (see Fig. 1a). Therefore, the second solution was preferred and thus used for population trajectory simulations, because it trunked the distribution at zero without modifying the shape of the distribution (see Fig. 1b). Figure 2 shows that the distributions of adult survival and fecundity are satisfying. Table 1 shows the mean and standard deviation obtained for each parameter with this modeling.

Table 1. Mean and standard deviation for each vital rate obtained from 1 million simulations.

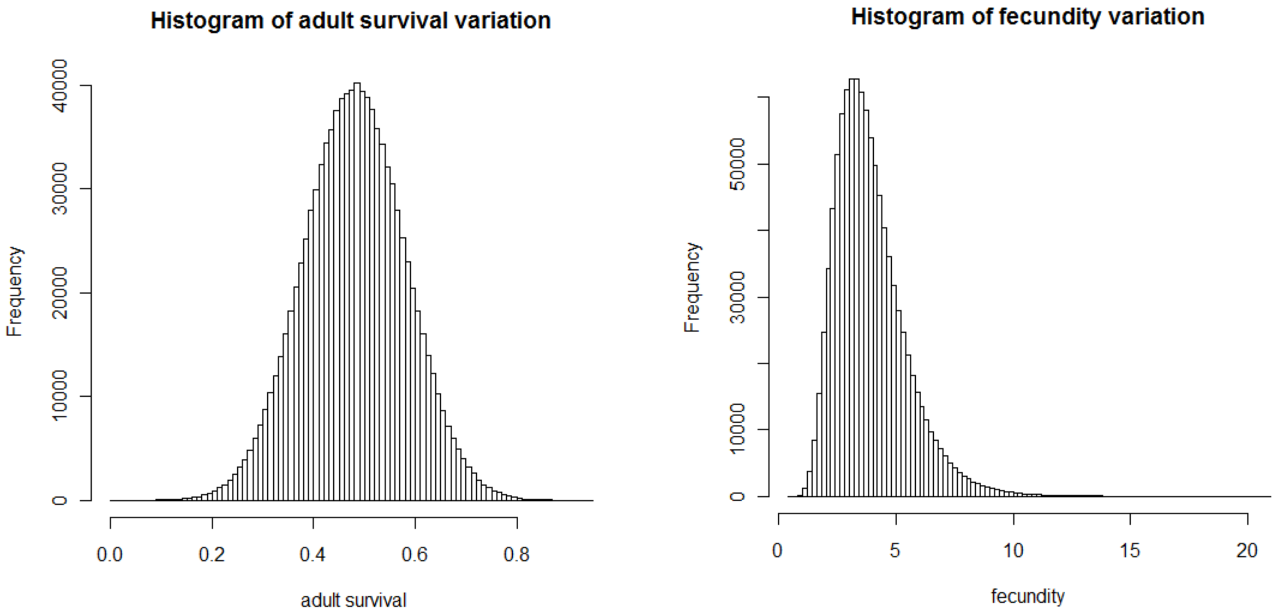
	mean	SD
Fecundity	3.9315	1.4893
Adult Survival	0.4833	0.0968
Juvenile Survival	0.2236	0.0960

Figure 1. Distribution of the one million simulated sample of juvenile survival under two different models: a) values that fall below zero are set to zero; one can see that this modeling generate a peak at zero in the distribution (red circle), which is thus not normal anymore. b) when the value of juvenile survival fall below zero, vital rates values are redrawn; in this case, we see that the distribution is correctly trunked at zero, with no peak (red circle); the distribution is normal.


a.

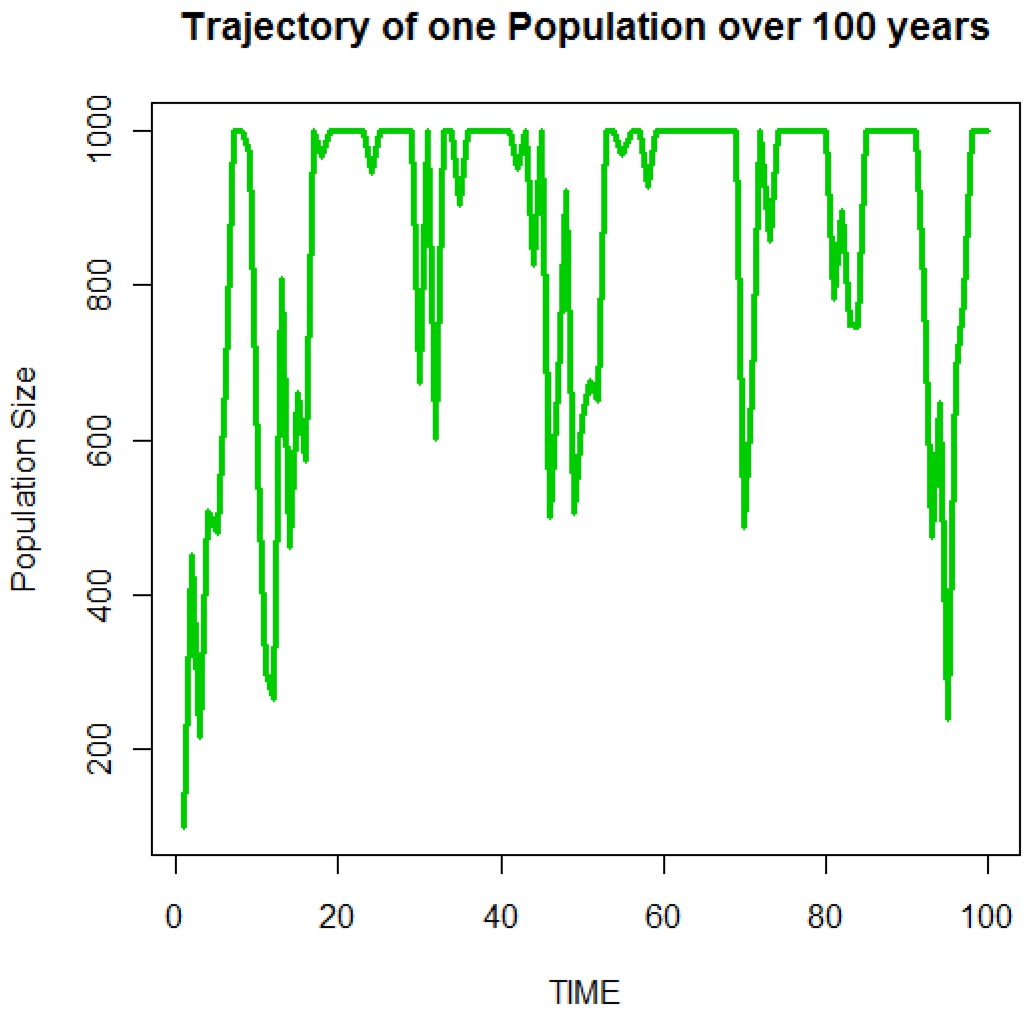
b.

Figure 2. Distribution of the one million simulated sample of adult survival (a) and birth rate (b).


a.

b.

Appendix 2. Example of a population trajectory simulated with the basic model without catastrophe.



Appendix 3. Results from 500 simulations of population trajectories of the “classic” scenario of catastrophe (i.e., immediate mortality) with “classic” modeling (Model A) and the modeling I used in this study (Model B). Model A is a model where the effect of a catastrophe can only be specified as a direct reduction of population size, whereas in Model B, the effect of a catastrophe is specified as a decrease of each vital rate for a given duration. In this example, for model B, duration was set to 1 year, the *intensity* of catastrophes was the same for all vital rates and was equal to *intensity* of model A (1/3), and the *frequency* of catastrophes was equal to that of model A. We see that the results are exactly the same, which mean that the “classic” model of catastrophe can be specified in this more general model (model B).

Statistics	**Model A**		**Model B**	
	Mean	*SD*	*Mean*	*SD*
Time to Quasi-Extinction	39.26	28.91	39.26	28.91
Final Population Size	643.39	342.18	643.39	342.18
Probability of Quasi-Extinction	0.366		0.366	

Appendix 4. Complete set of results from the different set of models.

Table 1: Results of the series of simulations with varying *frequency*. *Intensity* was set to 1/3 for all parameters and duration was 1.

model 0

***Frequency* = 0**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	825	255.8	30	1000	**0.069**
Time Quasi-Ext	31.9	28	3	100	

model 1.4

***Frequency* = 1/200**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	808.2	268.7	30	1000	**0.093**
Time Quasi-Ext	34.1	28.8	3	100	

model 1.3

***Frequency* = 1/100**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	791.3	280.1	30	1000	**0.121**
Time Quasi-Ext	35.6	29.2	2	100	

model 1.2

***Frequency* = 1/50**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	757.4	299.9	30	1000	**0.186**
Time Quasi-Ext	37.9	29.5	3	100	

model 1.1

***Frequency* = 1/20**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	665.1	337.1	30	1000	**0.432**
Time Quasi-Ext	40	29.1	2	100	

Table 2: Results of the series of simulations with varying i*ntensity* (*intensity* was equal for all parameters). *Frequency* was set to 1/50, and duration was 1.

model 0

No Catastrophe	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	825	255.8	30	1000	**0.069**
Time Quasi-Ext	31.9	28	3	100	

model 1.5

***Intensity* = 1/2**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	787	280.8	30	1000	**0.118**
Time Quasi-Ext	35.6	28.9	3	100	

model 1.2

***Intensity* = 1/3**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	757.4	299.9	30	1000	**0.186**
Time Quasi-Ext	37.9	29.5	3	100	

model 1.6

***Intensity* = 1/5**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	729	319.9	30	1000	**0.32**
Time Quasi-Ext	39.7	29.7	2	100	

model 1.7

***Intensity* = 1/10**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	712.3	335	30	1000	**0.524**
Time Quasi-Ext	39.4	29.4	2	100	

Table 3: Results of the series of simulations with varying duration of catastrophes. *Frequency* was set to 1/50 and *intensity* to 1/3.

model 1.2

***Duration* = 1**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	757.4	299.9	30	1000	0.186
Time Quasi-Ext	37.9	29.5	3	100	

model 2.1

***Duration* = 2**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	761.1	297.6	30	1000	0.174
Time Quasi-Ext	38.1	29.4	3	100	

model 2.2

***Duration* = 4**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	766.2	293.5	30	1000	0.156
Time Quasi-Ext	38.1	29.1	3	100	

model 2.3

***Duration* = 8**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	775.8	287.5	30	1000	0.132
Time Quasi-Ext	38.2	28.9	3	100	

model 2.5

***Duration* = 12**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	781.5	283.7	30	1000	0.119
Time Quasi-Ext	38.2	29	3	100	

model 2.4

***Duration* = 16**	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	786.1	280.3	30	1000	0.109
Time Quasi-Ext	37.9	29	3	100	

Table 4: Results from models representing catastrophes having effects on: (1) both survival and fecundity (model 1.2); (2) survival only (model 3.1); (3) fecundity only (model 3.2).

model 1.2

All parameters	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	757.4	299.9	30	1000	**0.186**
Time Quasi-Ext	37.9	29.5	3	100	

model 3.1

Survival only	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	782.8	283.9	30	1000	**0.137**
Time Quasi-Ext	36.2	29.2	3	100	

model 3.2

Fecundity only	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	793.3	277.6	30	1000	**0.126**
Time Quasi-Ext	33.1	29	2	100	

Table 5: Results from models representing catastrophes having effects on: (1) both adults and juveniles (model 1.2); (2) adults only (model 4.1); (3) juveniles only (model 4.2)

model 1.2

All parameters	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	757.4	299.9	30	1000	**0.186**
Time Quasi-Ext	37.9	29.5	3	100	

model 4.1

Adults only	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	779.9	286.1	30	1000	**0.143**
Time Quasi-Ext	35.2	29.4	2	100	

model 4.2

Juveniles only	mean	SD	min	max	Proba Quasi-Ext
Final Pop Size	800.8	271.8	30	1000	**0.100**
Time Quasi-Ext	34.2	28.7	3	100	