Short communication

How to detect and visualize extinction thresholds for structured PVA models

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Abstract

An extinction threshold is a population size below which extinction risk increases to beyond critical values. However, detecting extinction thresholds for structured population models is not straightforward because many different population structures may correspond to the same population size. Moreover, the precise structure of real populations usually is not known. We therefore introduce a simple but effective protocol that allows the detection and visualization of extinction thresholds for models of structured populations without having to refer to population structure. The basic idea of this protocol is to record extinction risk "on the fly": every time a certain population size occurs during simulation, the remaining time to extinction is stored in a frequency distribution. Thus, the simulation model, not the modeller, generates the typical range of population structures linked to a certain population size. We apply the protocol to two examples to demonstrate the specific and general insights that can be gained. We argue that the protocol might also be useful for overcoming PVA's undue concentration on individual extinction risks.
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1. Introduction

A major task of conservation biology and population viability analysis (PVA) is to quantify extinction thresholds, i.e. population sizes below which extinction risk becomes so high that it is considered unacceptable (Shaffer, 1981; Soulé, 1986, 1987; Boyce, 1992; Burgman et al., 1993). In principle, this quantification is straightforward once an appropriate stochastic population model has been constructed: the model is repeatedly (e.g. 100 times) run over a certain time horizon (e.g. 50 years), and the extinction risk is quantified by dividing the number of model runs where extinction occurred within the time horizon by the total number of runs performed. This procedure is repeated for a

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range of initial population sizes. The extinction threshold is then the initial population size that leads to an extinction risk higher than a certain, predefined threshold level, e.g. 1% in 100 years.

This procedure is straightforward only for unstructured population models, i.e. models where the only state variable characterizing the population is the number of individuals. However, virtually all PVA models are structured, be it with respect to age, stage, social status, space or other aspects (e.g. Beissinger and West-phal, 1998; Stephan and Wissel, 1999; Griebeler and Gottschalk, 2000; Ebenhard, 2000; Todd et al., 2001). In turn, specifying the initial state of a population may involve quite a few degrees of freedom because the same initial number of individuals may correspond to completely different population structures. Obviously, the initial population structure may strongly affect extinction risk. For example, a cohort of senescent individuals and a cohort of juveniles will lead to different extinction risks. Moreover, in real populations the precise structure of the population is usually unknown.

We present a protocol that allows the extinction risk to be determined irrespective of the peculiarities of the initial population structure and that enables the visualization of the extinction threshold of a population. Below, we describe the protocol and then apply it to two example models, demonstrating the specific and general insights that can be gained using the protocol.

2. The protocol

The basic idea of the protocol is to run the population model until extinction and to use every population size occurring until extinction as a (virtual) initial population size. Thus, the population structure corresponding to a certain population size is specified not by the modeller (except at the very beginning of the simulation) but by the population dynamics themselves. The protocol consists of the following steps (see also the sample implementation in MATLAB®, which is provided in "Online Model" appendix to this article):

1. Specify the range of initial (or current) population sizes of interest, for example $N_0 \leq 30$ individuals.
2. Specify the time horizon T of interest, e.g. the risk of extinction over a time horizon of $t \leq 100$ years is considered.

3. Run the population model until extinction and store the resulting population dynamics $N(t)$. (To cope with parameter combinations where the risk of extinction is close to zero, it is useful to impose a limit to t, e.g. $t \leq 1000$ years.)
4. Then, scan $N(t)$. Each time a certain N_0 occurs in $N(t)$, two things are recorded: the occurrence of this population size is recorded and the time until the population becomes extinct (which is known from $N(t)$) is stored in a frequency distribution of extinction times. Population sizes outside the focal range as well as extinction times larger than T are not displayed in the plot but are counted as outliers instead. In this way, for each initial population size of interest, N_0, we generate a frequency distribution of extinction times.

   Since a single model run will only generate sparsely filled frequency distributions, steps 3 and 4 have to be repeated until a sufficient number of extinctions have been recorded for each population size of interest. We cannot give any general rules for how to compromise between computation time and required precision. Readers will have to establish their own criteria of what is 'enough' (e.g. 100 extinction events for each N_0).
5. The frequency distributions of extinction times are converted into probability distributions by dividing each bar of the distributions by the frequency with which the corresponding population size occurred during the analysis.
6. From these probability distributions the probability of extinction by time t after having started with initial population size N_0, i.e. $P_0(N_0, t)$, is calculated by cumulatively totalling the bars of the probability distributions. The plot of $P_0(N_0, t)$ (Fig. 1) then shows how the risk of extinction increases over time if initially (or currently, at time $t = 0$) the population has a certain size N_0.

In this protocol, the population structure at the beginning of each simulation has to be specified by the modeller. To avoid possible artefacts of this initial structure, an initial time interval may be ignored in each simulation. Our experience is that in most models, the "memory" of initial conditions is forgotten after, say, 20 years, but especially for very long-lived species, it might be necessary to ignore a longer initial time interval (Armbruster et al., 1999).
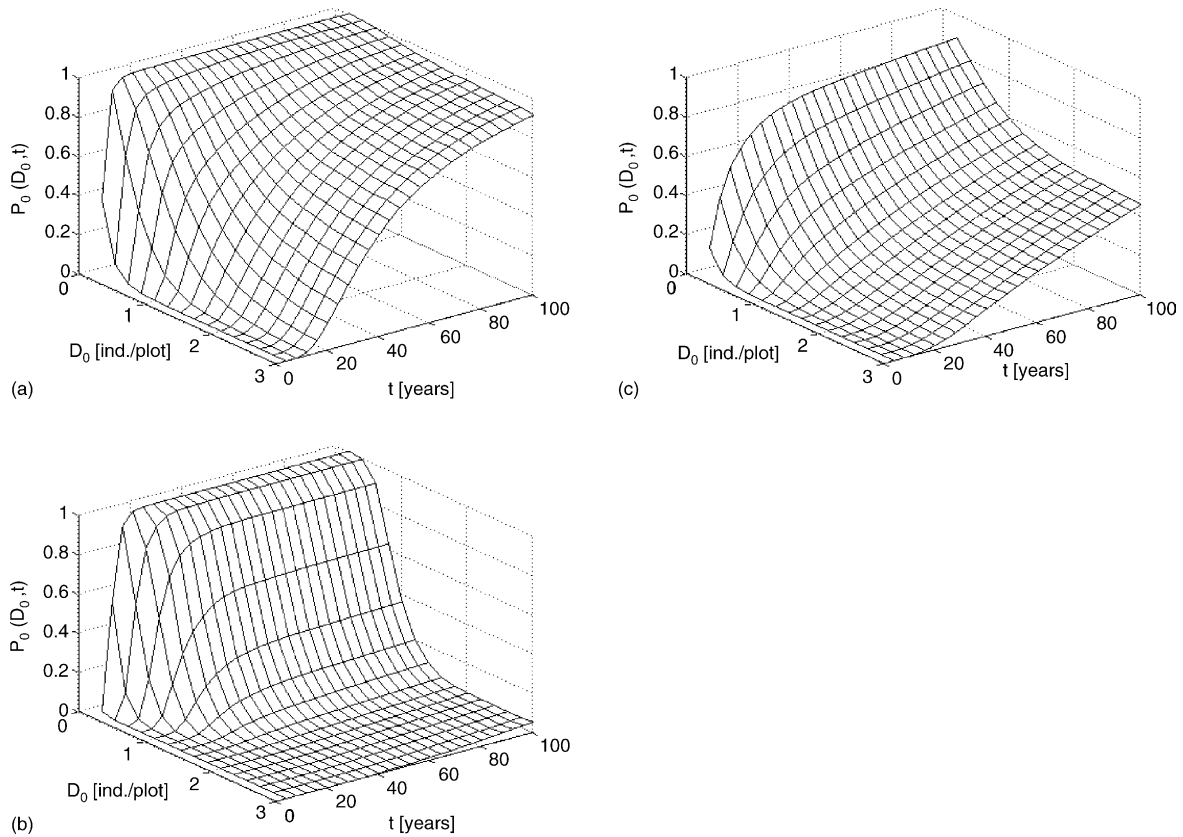
Fig. 1. Probability $P_0(D_0, t)$ of extinction by time t if the population at time $t = 0$ has the density D_0 (individuals/plots). The model evaluated is an individual-based, spatially explicit model of the wall lizard (*Podarcis muralis*). (a) Reference parameter set, viz. isolated population and habitat capacity of $K = 10$ plots; (b) $K = 40$ plots; (c) $K = 10$, but immigration of one adult of randomly chosen sex within 2 years (modified after Hildenbrandt et al., 1995; note that the minimum density considered is 0.2 individuals/plot).

3. Example applications

We apply our protocol to two PVA models of different complexity. We are not going to describe these models and their results in detail, because here we focus only on the protocol. The first, more complex model describes small populations of the wall lizard, *Podarcis muralis* (Hildenbrandt et al., 1995). The purpose of the model was to assess the extinction risk of a population inhabiting an artificial habitat that was constructed as a mitigation measure (Bender et al., 1996). The model is individual-based (Uchmański and Grimm, 1996) and spatially explicit. The territorial behaviour of *P. muralis* is taken into account by a set of behavioural rules. The spatial unit, or 'plot', of the model is defined as the minimum size of a male territory.

Fig. 1a shows the plot of $P_0(D_0, t)$ for the reference parameter set of the model (Bender et al., 1996). The capacity of the habitat is very small, i.e. only 10 plots. In this scenario, extinction risk is very high for all the initial population densities observed (here, to compare scenarios with different habitat capacities, initial densities D_0 are considered instead of initial numbers). If we increase habitat capacity to 40 plots, an extinction threshold becomes visible at an initial density of about 1.5 individuals/plot (Fig. 1b). If initial density is smaller, extinction risk is still unacceptably high. For initial densities larger than 1.5 individuals/plot, the extinction risk is low (about 0.05 or 5% after 100 years). Interestingly, beyond the extinction threshold, initial density has only marginal influence on extinction risk. This is an indicator of the 'established phase'

of the population, which is characterized by a quasi-stationary distribution of the population's state variables and by a constant risk of extinction per short time interval. From theoretical arguments (Wissel et al., 1994; Grimm and Wissel, 2004) and from experience with more than 20 structurally different PVA models we know that the established phase and the occurrence of extinction thresholds is a general phenomenon that does not depend on the details of the PVA models.

The risk of extinction of populations starting with very low densities, i.e. smaller than 0.4 individuals/plot, is only marginally affected by the increase in habitat capacity. Populations below the extinction threshold are not 'established' in the sense that they do not realize the full potential to persist provided by their habitat (Fig. 1a and b). This situation changes if instead of an increased habitat capacity we consider a scenario identical to the reference scenario of Fig. 1a but with the immigration of one adult individual every 2 years. Although the extinction risk after 100 years is generally still too high because the habitat is too small, immigration reduces the extinction risk at very low densities.

The example of Fig. 1 shows that our protocol and the resulting plot of $P_0(N_0, t)$ provide a simultaneous perception of the dependence of extinction risk on time and initial population size. However, sometimes a two-dimensional slice through the plot at a fixed time, e.g. $t = 100$, may be sufficient or even more informative if different scenarios are to be compared. Therefore, in Fig. 2, $P_0(N_0, 100)$ is presented for a second example model, which describes a population of capercaillie (*Tetrao urogallus*) in the Bavarian Alps (Grimm and Storch, 2000). The purpose of this model was to assess minimum area requirements for viability. The model is much simpler than the first example model: it is age-structured, includes demographic and environmental noise, and assumes a ceiling capacity K: if population size N exceeds K, randomly chosen individuals are removed until $N = K$.

Comparing the plot of $P_0(N_0, 100)$ for different ceiling capacities K (Fig. 2) reveals that a minimum capacity of about 250 individuals is needed to have a risk of extinction after 100 years of less than 5%, and for a risk less than 1%, $K = 500$ is needed. Only for $K \geq 250$ is the population able to reach the 'established phase', i.e. a range of population sizes where extinction
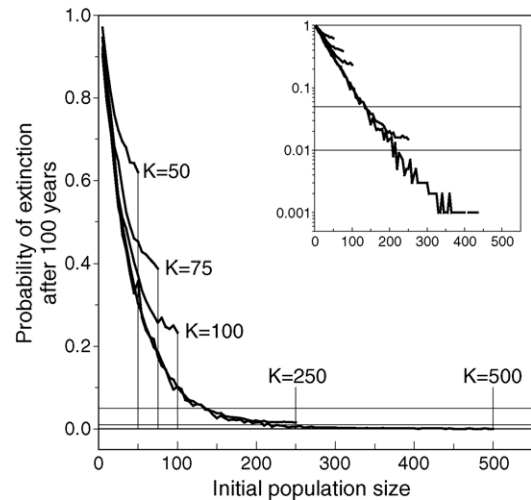

Fig. 2. Probability $P_0(N_0, 100)$ of extinction after 100 years versus initial population size N_0 for different values of the habitat capacity K (individuals). The inset shows the same curves, but with logarithmic P_0-axis. The threshold risks of 5 and 1%, respectively, are marked by the two parallels to the time axis. The model evaluated is of capercaillie (*Tetrao urogallus*) in the Bavarian Alps (modified after Grimm and Storch, 2000).

risk is only marginally affected by population size; for $K = 50$, 75, and 100 initial population size has strong influence on extinction risk (see the orders of magnitudes of extinction risk shown in the inset of Fig. 2). Fig. 2 also helps distinguish between the two aspects of MVP (minimum viable population; Shaffer, 1981) which often seem to be mixed up in the literature, minimum area requirement and minimum population size. Capacity K often represents the size of the area inhabited by the population, and thus the comparative plot of $P_0(N_0, 100)$ for *different* values of K, helps determine the minimum area requirement of the population for viability. Once this minimum area, or K, respectively, is given, the plot of $P_0(N_0, 100)$ for, say, $K = 500$ indicates the threshold, or minimum, population size. Below this threshold, extinction risk is higher than in the established phase.

A difference between the plots in Figs. 1b and 2 is that the population in Fig. 1b shows a plateau of high extinction risk at very low densities, whereas in Fig. 2 such a plateaus does not exist. The plateau indicates an Allee effect in the model of Fig. 1: a critical density of wall lizards is needed to establish the territorial system and warrant reproduction and survival. Below

this density, persistence is impossible and variation in density is irrelevant.

4. Discussion

The aim of this paper is to introduce a protocol that determines and visualizes extinction thresholds for structured population models. The plot of $P_0(N_0, t)$ for an entire time horizon or a certain time, e.g. $t = 100$, visualizes the existence of the 'established phase' of the population in which the extinction risk per short time interval is constant (but not necessarily small). The plot helps distinguish conceptually between two aspects of MVP: minimum area requirements and critical population sizes. The plot also shows that the extinction risks of populations, which for some reason (e.g. natural or anthropogenic catastrophic events) are smaller than the extinction threshold, are largely insensitive to the capacity of the habitat (Fig. 1a and b). The problem of such small populations is to cross the threshold and thereby reach the established phase. In such critical situations, immigration from other populations helps reduce the extinction risk (Fig. 1c). Note that our plot only helps visualize extinction threshold, but does not introduce a metric to detect such thresholds. If in a certain PVA the dependence of the threshold on certain parameters or management options would be a main question, such a metric could easily be developed and tested using our plot. With a tested metric, the extinction threshold contours could be plotted on a single 2D figure for a set of scenarios to show how model parameter variation affects the overall extinction risk behaviour as a function of time and population initial condition.

Our protocol is not designed to replace other quantifications of persistence and viability (e.g. Burgman et al., 1993; Akçakaya, 1995; Beissinger and Westphal, 1998; Groom and Pascual, 1998; Grimm and Wissel, 2004), but to provide an additional tool. The protocol offers three main advantages: first, we can apply it to all kinds of models of structured stochastic population models and can thus use it as a unifying means to evaluate models of extinction theory and PVA (another unifying quantity, the 'intrinsic mean time to extinction', is introduced by Grimm and Wissel, 2004). Second, the full plot of how the risk of extinction depends on time and current population size helps overcome PVA's

overconcentration on individual numbers, such as the risk of extinction after 20 or 50 years. Each assessment of viability is necessarily bound to a certain time horizon and a certain threshold risk of extinction that one is willing to accept. However, the choice of both the time horizon and the threshold risk is arbitrary and, consequently, different horizons and thresholds are used in the literature. In contrast, presenting the full plot of $P_0(N_0, t)$ demonstrates that an absolute assessment of viability is impossible. Third, the plot of $P_0(N_0, t)$ visualizes the probabilistic nature of the dynamics of small populations: once a population is in the established phase, i.e. is larger than the extinction threshold, the risk of extinction is constant for small time intervals. This means that the risk of extinction increases approximately linearly over time as long as the risk is small (Grimm and Wissel, 2004). The constant, non-zero risk of extinction implies that there is always the risk of the population size dropping below the extinction threshold. Then, the population size has a certain probability of returning to the established state, or continuing to decrease until extinction (Wissel et al., 1994).

The protocol presented here is easy to implement and can be seamlessly applied to existing models, provided that the time series $N(t)$ are available (see "Online Model" appendix). The only slight disadvantage might be the considerable amount of computing time due to the number of model runs needed to populate the frequency distribution. Therefore, we believe that, given the potential insights gained from the protocol, it will be useful to apply the protocol and see whether it helps to answer the questions studied. There are, of course, situations where the effect of a certain initial population size structure on extinction risk is of interest, for example when populations are reintroduced. Our protocol does not deal with such situations.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2005.05.016.

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