Approximating Persistence in a General Class of
Population Processes

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Abstract

We provide a general framework for estimating persistence in populations which may be affected by catastrophic events, and which are either unbounded or have very large ceilings. We model the population using a birth-death process modified to allow for downward jumps of arbitrary size. For such processes, it is typically necessary to truncate the process in order to make the evaluation of expected extinction times (and higher order moments) computationally feasible. Hence, we give particular attention to the selection of a cut-off point at which to truncate the process, and we present a simple method for obtaining quantitative indicators of the suitability of a chosen cut-off.

Keywords: Population process; catastrophes; hitting time; extinction.

1 Introduction

Birth, death and catastrophe processes have become familiar tools in the modelling of single-species population processes. By defining birth, death and catastrophe rates, and distributions of catastrophe sizes, it is possible to construct models of populations in which the behaviour of the population depends on its current size in an arbitrary manner. One early use of this approach is MacArthur and Wilson’s study of species colonising islands [11]. They employed a linear birth-death process (without catastrophes) in order to explore the persistence of populations that begin with just a single propagule, in an island environment from which they were previously absent (Chapter 4). These models were strictly bounded by the carrying capacity $K$ of the habitat, a value which could not be exceeded for any significant length of time. However, because the population had a positive growth rate on average, the carrying capacity also served as an equilibrium population size—the population would tend towards this value until, by chance, it went extinct—and hence the carrying capacity itself provided a major source of ‘density-dependence’ in the behaviour of the population.

Mangel and Tier [12, 14] presented a new approach to approximating quantities such as the expected persistence time for populations modelled by birth, death and catastrophe processes. They reasoned that it should be possible to find good approximations to

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the persistence times even in circumstances where a model does not prescribe a fixed and relatively small upper bound on the size of the population. They proposed truncating the process by choosing a cut-off point above which the population is assumed not to spend any significant amount of time, so that the persistence times calculated for this new, truncated model should give a reasonable approximation to the persistence of the original population. Evaluating measures of persistence, such as the expectation and other moments of the time to extinction, in this way requires only finding the solution to a single system of linear equations, and is therefore easily performed using any of a host of software packages (details of this approach, and examples of its application, are given in [12]). A significant advantage of this approach is that it separates density-dependence in birth and death rates from that introduced by the cut-off (although Mangel and Tier assumed, as MacArthur and Wilson did, that whenever the population goes beyond its new bounds, it is instantly returned, or ‘reflected’, back to the cut-off point). Because this procedure is purely numerical, with no a priori assumptions about the form of birth, death or catastrophe rates, more complicated forms of density-dependence can be incorporated into Markov chain models for populations.

Conceptually, it is clear that many populations are bounded by more or less fixed territorial areas, restricted habitat, or other hard limits that enforce a comparatively small ceiling on the size of the population. For example, a finite birth, death and catastrophe process has been applied to evaluating the persistence times, under two competing management programs, of the California spotted owl, Strix occidentalis occidentalis [1]. This species is limited in population size by the existence of a fixed number of potential nesting sites (indeed the number of occupied sites is the ‘population’ being modelled). In this, and other similar circumstances, evaluating measures of persistence times is simply a matter of solving the appropriate system of linear equations.

However, not all populations are bounded in such a definite way, either because any ceiling is very large or somewhat ‘fuzzy’, or because the population is not, in fact, strictly bounded. Rather, some unbounded populations may be ‘soft-limited’, by increasing mortality or decreasing birth rates above a carrying capacity, or by environmental influences, such as catastrophes. In these circumstances, it is often computationally infeasible to evaluate the persistence of a population for large initial sizes (although the persistence of large populations is often not of great interest). In order to evaluate the persistence of the population from smaller initial sizes, we must necessarily truncate the process in some way. But, it is not always clear what is an appropriate value for the cut-off. It should certainly be significantly larger than the largest initial size for which we wish to be sure of accurately estimating the persistence of the population. It should also capture all important aspects of the dynamics of the population; for example, if a population tended to become relatively stable around a particular size, it would be important that the cut-off be chosen well above that point. At the very least, “some amount of numerical experimentation” [12] would be required to obtain evidence that the evaluation of the quantities of interest does not depend significantly on the choice of cut-off. Yet, ideally, the cut-off should be justifiable in some quantitative way, and the truncation approach taken should be neither computationally intensive nor ad hoc.

We will present a quantitative approach to selecting an appropriate cut-off for populations without small, definite bounds. In Section 2, we describe a general birth, death and
catastrophe process for modelling populations that may be bounded, and which are subject to both demographic stochasticity and catastrophes. This model will be extended, in Section 3, to unbounded populations, which may be soft-limited above a carrying capacity or by catastrophic events. We will briefly address important differences between these and bounded population processes, and, drawing on the work of Brockwell [4], we will present a technique for calculating measures of persistence, an essential feature of which is a simple, direct method for selecting an appropriate cut-off. In Section 4, we illustrate the application of this technique with two examples, one being a comparison with known analytical results and another from the applied ecology literature. We conclude in Section 5 with a discussion of some of the advantages of this approach, as well as some applications.

2 Birth, death and catastrophe processes

We consider a population that is subject to both demographic stochasticity and catastrophic events. The population may consist of similar but distinct entities—individuals—whether they be individual organisms from a particular species, individual species within a taxon (for example [16]), occupied habitat patches, or, any other identifiable entity. Our goal is to calculate quantities related to the time it takes for the population to become extinct.

Birth, death and catastrophe processes (Brockwell et al. [3]) are a class of models that extend the familiar birth-death process (for example [11]) by the addition of catastrophic drops in population. Here and henceforth we will take ‘births’ to (potentially) include immigration, while ‘deaths’ and ‘catastrophes’ may include single or mass emigration. We construct a general birth, death and catastrophe process model for bounded populations as follows. Let \( X(t) \) be the state of the population process at time \( t \) (simply the size of the population). This can be any whole number of individuals, and thus the range of possible values for \( X(t) \) is \( \{0, 1, 2, \ldots\} \). We suppose that \( X(t) \) begins at some initial state \( X(0) \) at time 0, and then evolves according to a homogeneous, continuous-time Markov chain. The behaviour of the population over time is governed by the rates at which births, deaths and catastrophes occur, each of which may depend only on the current state \( i \). These rates will typically be specified as entries in the transition-rate matrix \( Q \). Keeping the model as general as possible, we will suppose that if \( X(t) = x \) (the population size is \( x \) at time \( t \)), then births occur at rate \( B(x) \) and single deaths occur at a rate \( D(x) \), each depending only on \( x \) (and not on \( t \)). Rates of catastrophe have a slightly more complicated structure. Each catastrophic event can cause a jump down of any size, determined independently in each case by the distribution \( F \) of catastrophe sizes: when the population size is \( x \), catastrophes (of any form) occur at a rate \( C(x) \), and the size of the catastrophe is \( k \) with probability \( F(k| x) \).

The elements of the transition-rate matrix \( Q \), denoted \( q_{ij} \), correspond to the rates at
which the population jumps to \( j \) from its current state \( i \). These values are given by

\[
q_{ij} = \begin{cases} 
B(i), & j = i + 1, \\
D(i) + C(i)F(1|i), & j = i - 1, 1 \leq i, \\
C(i)F(k|i), & j = i - k, k \leq i, \\
-H(i), & j = i, \\
0, & \text{otherwise}, 
\end{cases}
\]  

(1)

where \( H(i) \) is always chosen so that each row of \( Q \) sums to 0.

For the present context we will introduce two further quantities to this general model. First, all populations at or below \( x_e \) are considered to be extinct. It may be that \( x_e = 0 \), if we are interested in the persistence of the population prior to its total extinction, but \( x_e \) may be greater than 0 if we are interested in looking at persistence before some form of effective extinction (functional or quasi-extinction). Second, there may be a population ceiling \( N \) such that the rates \( q_{ij} \) are non-zero only when \( i \leq N \). This implies that, whenever the population begins at or below \( N \) (as we shall always assume), it will remain at or below \( N \), a definite hard limit to the population size. We will say that the process is \textit{bounded} whenever a ceiling \( N \) limits the size of the population, in which case \( B(x) = 0 \) for some \( x > x_e \), or otherwise the process is \textit{unbounded}.

Before proceeding, we make note of a number of assumptions about the model. First, we make the technical assumption that the process is stable (meaning that all transition rates are finite). This will be satisfied for most reasonable population models (however, see [8]). Second, we will require that the states above \( x_e \) form a communicating class: for any pair of states, \( i \) and \( j \), both greater than \( x_e \), and less than or equal to \( N \) if the process is bounded, it must be possible for the process to reach \( i \) from \( j \) and \textit{vice versa}. This condition, which is often implicit in ecological models, holds (for example, but not exclusively) whenever the birth and death rates are non-zero:

\[
B(x) > 0, \quad \text{for all } x_e < x < N, \\
D(x) > 0, \quad \text{for all } x_e < x \leq N.
\]

Finally, if \( x_e \) is the state at or below which the population is considered to be extinct, we require

\[
q_{ij} > 0, \quad \text{for some } i > x_e \text{ and } j \leq x_e,
\]

so that it is possible for the population to reach an extinct state (otherwise, it would persist forever). Note that extinction must be possible (but not necessarily certain) from all initial population sizes; there must be at least one sequence of possible transitions leading to extinction from any non-extinct state. Conversely, the population may or may not be able to recover from below the extinction level \( x_e \), but this detail will not affect calculations of persistence as they are treated in the remainder of this paper.

## 3 Persistence in unbounded populations

In order to extend the basic model to the case of unbounded populations, we need only suppose that there is no ceiling; that is, \( B(i) > 0 \) for all \( i > x_e \). The model now has no hard
upper bound $N$, but otherwise it inherits all the features of the previous model.

### 3.1 Explosions and non-extinction

The most important differences between bounded and unbounded models concern their behaviour over long time scales or at large population sizes. Bounded population models of the type we consider are well behaved in the sense that the expected time to extinction is finite for any initial state, but there is no such guarantee for unbounded models. In particular, unbounded models may exhibit two kinds of behaviour that may affect persistence times: explosion and non-extinction. Explosions occur when the state of the process reaches infinity in a finite time. Although explosivity is often of some theoretical interest, it is easily ruled out if we can establish that the population is certain to become extinct in finite time. Even if a process is not explosive, extinction might not be certain. However, the probability of extinction $p_i$, starting in state $i$, can be calculated as the minimal non-negative solution to the system of equations

$$
\sum_{k=0}^{i+1} q_{ik} p_k = 0, \quad i \geq x_e,
$$

$$
p_i = 1, \quad i \leq x_e.
$$

(See, for example, Theorem 3.3.1 of Norris [15].)

Results of Brockwell [5] show that, for birth, death and catastrophe processes, if extinction is certain from any non-extinct state, then extinction is certain from all non-extinct states, and we may then attempt to calculate the expected time to extinction. We will delay addressing the problem of solving equations (2), because that discussion will benefit from a more general treatment of measures of persistence times for unbounded models.

### 3.2 Measures of persistence

We could find approximate measures of persistence times for unbounded populations by introducing an artificial ceiling $n$ and letting $B(x) = 0$ for $x \geq n$ (as in, for example, Mangel & Tier [12, 14]), so that $n$ takes the role of a limit on the population that cannot be exceeded. We refer to this approach to estimating measures of persistence as ‘truncation-by-reflection’ (TBR) because setting $B(x) = 0$, for $x \geq n$, is equivalent to reflecting the process back to $n$ as soon as it exceeds that value. One of its drawbacks is that selecting an appropriate value of $n$ may be difficult.

Here we develop an alternative technique for approximating measures of persistence, which we will term truncation-by-absorption (TBA). Truncation-by-absorption allows for the worst-case scenario when calculating measures of persistence which provide conservative estimates that are always between 0 and the true values, a property not shared by approximations computed using truncation-by-reflection. In the case of approximating the expectation and higher moments of the time to extinction, we actually obtain approximations by calculating quantities related to the time until either extinction occurs or the population hits $n+1$ (thus letting the population also go ‘extinct’ when it gets large). Here,
the worst-case scenario is that extinction occurs as soon as the population exceeds \( n \). When calculating the probability of extinction, however, TBA specifies that extinction will never occur if the population exceeds \( n \), as the population becomes trapped above its ceiling value. (In this case only, we do not equate the absorbing ceiling with the extinct states.) Probabilities calculated in this way are again conservative estimates. In contrast, probabilities of extinction calculated using truncation-by-reflection are always equal to 1.

As we will note, TBA has numerical properties which simplify the process of finding a suitable cut-off \( n \) and assist in accurately approximating measures of persistence. On the other hand, finding accurate approximations using only truncation-by-reflection may be computationally intensive where there is a large difference between the smallest appropriate cut-off \( n \) and the extinction level \( x_e \), and particularly in cases where a suitable \( n \) is (initially) unknown. In such cases it may be difficult to experiment with ceiling values and confirm that the choice of ceiling does not significantly affect the results. We will demonstrate that our approach gives a much clearer picture of the suitability of potential cut-offs.

We will present the concept of truncation-by-absorption as an approach to approximating measures of persistence for unbounded populations, but will first note that it may also be of use with bounded models in which the population ceiling is very large. In such cases, in order to obtain complete solutions in a reasonable time (covering all initial population sizes below the true ceiling \( N \)), we may need to employ complicated numerical techniques, implemented on high-end computer hardware, due simply to the size of the resultant systems of equations. However, in many cases we do not require complete solutions: it may not be of great interest to compute measures of persistence times for large initial populations, and it may be more efficient to find approximate solutions for a subset of initial population sizes, between the extinction level and an initial size significantly smaller than the ceiling. In such instances, the procedures developed below for unbounded models may be employed without modification to approximate measures of persistence for initial states much smaller than \( N \).

### 3.2.1 Approximating measures of persistence.

Anderson [2] considered the following system of equations (derived from the Laplace transform of the time \( \tau \) to extinction; see Appendix A.1), which encapsulates both (2) and the equations for the moments of persistence times:

\[
\sum_{k=0}^{i+1} q_{ik} w_k = -\gamma_i, \quad i \geq x_e,
\]

\[
w_i = c, \quad i \leq x_e.
\]  

For example, the expected extinction times \( T_i = \text{E}(\tau|X(0) = i) \) constitute the minimal non-negative solution to the above system when \( \gamma_i = 1 \) and \( c = 0 \):

\[
\sum_{k=0}^{i+1} q_{ik} T_k = -1, \quad i \geq x_e,
\]

\[
T_i = 0, \quad i \leq x_e.
\]
These equations are generalisations of the linear equations for measures of persistence times for bounded populations (for example, Mangel and Tier [12]), and, indeed, comprise a finite system when there is a finite upper bound \( N \). Table 1 gives values of \( \gamma_i \) and \( c \) needed in (3) to recover any moment of the persistence times, as well as the probability of eventual extinction.

<table>
<thead>
<tr>
<th>Measure</th>
<th>( \gamma_i )</th>
<th>( c )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Probability of eventual extinction</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Expected time to extinction, ( T_i )</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>( m )-th moment of time to extinction, ( T_i^{(m)} )</td>
<td>( mT_i^{(m-1)} )</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 1: Values of \( \gamma_i \) and \( c \) for some measures of persistence times.

Following the program laid out by Brockwell [4, 5] and Anderson [2], it is easy to see that systems of equations of this kind all have the same form of solution: a sequence \( \{w_i, i \geq 0\} \) is a solution to (3) if and only if it has the form

\[
 w_i = \kappa u_i - v_i, \quad i \geq 0, 
\]

where \( \kappa \) is a positive constant and the sequences \( \{u_i, i \geq 0\} \) and \( \{v_i, i \geq 0\} \) are the (unique) solutions to the systems of equations

\[
\begin{align*}
 i+1 \sum_{k=0}^{i+1} q_{ik} u_k &= 0, \quad i \geq x_e + 1, \\
 i+1 \sum_{k=0}^{i+1} q_{ik} v_k &= -\gamma_i, \quad i \geq x_e + 1,
\end{align*}
\]

with \( u_i = 0 \) and \( v_i = -c \) for \( 0 \leq i \leq x_e \), and \( u_{x_e+1} = 1 \) and \( v_{x_e+1} = 0 \) (we note that both \( \{u_i\} \) and \( \{v_i\} \) are non-decreasing sequences). By varying \( \kappa \) we obtain a family of solutions to (3), and the value of \( \kappa \) that determines the minimal non-negative solution is given by

\[
 \kappa = \sup_{i \geq x_e+1} \kappa_i, 
\]

where \( \kappa_i = v_i/u_i \); that is, \( \kappa \) is the least upper bound on the sequence \( \{v_i/u_i\} \). It is possible to show (see Appendix A.1) that \( \sup_{i \geq x_e+1} \kappa_i = \lim_{i \to \infty} \kappa_i \), and so we can make the approximation

\[
 \kappa \approx \kappa_{n+1}, 
\]

and proceed by solving the systems (6) with \( i \) in the range \( 0, \ldots, n \), where \( n \) is some given cut-off value. Note that solving the system over this range produces values \( u_0, \ldots, u_{n+1}, v_0, \ldots, v_{n+1} \), and hence \( \kappa_{x_e+1}, \ldots, \kappa_{n+1} \). Note also that since the coefficients \( q_{ik} \) are common to both systems of equations, we need only solve one system directly. Back substitution can then be used to solve the other.
3.2.2 Choosing an appropriate cut-off

The quality of our approximation will vary depending on the choice of the cut-off \( n \), and selecting an optimal value is of utmost importance in finding accurate approximations to measures of persistence. It can be chosen initially by taking an informed guess as to the likelihood that the truncated population might reach \( n \) from an initial size \( x_e + 1 \); this likelihood (or, its contribution to persistence times) should be small. At the very least, \( n \) should be large enough to ensure that no new structure appears in the dynamics of the process for states above \( n \), unless those states are unlikely to be encountered.

The probability of reaching \( n \). Truncation-by-reflection and truncation-by-absorption each take a different approach to the behaviour of populations at the ceiling; TBA assumes that the population goes extinct immediately after exceeding the ceiling or cut-off \( n \), allowing extinction directly from the cut-off, while TBR assumes that the population immediately returns to \( n \) after exceeding that value, effectively preventing births or immigration. Although they represent fundamentally different approaches to approximating a population process, they are closely related. Let \( R_i(n) \) and \( A_i(n) \) be the expected times to extinction under TBR and TBA, respectively, when the cut-off is \( n \), and let \( P_i(n) \) be the probability that the population, starting with \( i \) individuals, ever exceeds \( n \) (that is, it hits \( n + 1 \) at least once before going extinct). Then

\[
R_i(n) = A_i(n) + R_n(n)P_i(n)
\]

(see Appendix A.2). So, the expected time to extinction under TBR, starting in state \( i \), is equal to the expected time to extinction under TBA, plus the expected time to extinction from the ceiling \( n \) multiplied by the probability that the ceiling is exceeded at least once.

The above equation is most useful when put in the form

\[
P_i(n) = \frac{R_i(n) - A_i(n)}{R_n(n)}, \quad (9)
\]

because it demonstrates the importance of the TBA approximation in estimating the probability of eventual extinction. Under TBA, the process either goes extinct by dropping below \( x_e + 1 \), or it becomes trapped forever in state \( n + 1 \), and hence the probability \( P_i(n) \) is just 1 minus the estimate of the probability of extinction.

The approximate probability of extinction, under TBA, is an important indicator of the suitability of the cut-off \( n \); if this quantity is small, then \( P_i(n) \) will be large and the cut-off is likely to be reached. (Furthermore, we do not need to calculate this quantity separately. Given approximations by both TBR and TBA, we can calculate these probabilities according to equation (9).) Hence, by examining \( P_i(n) \) over the range of initial states \( x_e + 1 \) to \( n \), we can determine the range of initial states for which \( n \) may be an appropriate cut-off. If \( P_i(n) \) is close to zero, then \( n \) may be suitable for \( i \).

The accuracy of approximations. The conclusions presented immediately above are qualified (for example, giving cases where \( n \) may be suitable for \( i \)), because the approach is
not entirely foolproof. Suppose, for example, that in a particular population process eventual extinction is certain, but that the expected time to extinction is infinite, in which case there is no good choice of cut-off for approximating the expected extinction time. Nonetheless, a particular cut-off may seem appropriate for a small range of initial values because $P_i(n)$ is very small, while the approximation is entirely incorrect.

Fortunately, we can also obtain an indicator of the accuracy of our approximation to $\kappa$. By plotting $\kappa_i$ against $i = x_e + 1, \ldots, n + 1$, we are able to see whether $\kappa_i$ approaches an upper bound over this range. Additionally, we may estimate the rate of convergence of $\kappa_i$ to $\kappa$ over $x_e + 1 \leq i \leq n + 1$ by plotting $\Delta \kappa_i = |\kappa_{i+1} - \kappa_i|$ against $i$ on a log-linear scale. If $\Delta \kappa_i$ is linear in $i$ on that scale, then this will suggest that the differences are converging to 0 geometrically fast, and hence that $\kappa_i$ is converging rapidly to $\kappa$. Indeed, we can estimate the rate of convergence $\delta$ from the log-linear plot and hence obtain an estimate of the error $|\kappa - \kappa_{n+1}|$.

Assuming that convergence is monotonic and approximately geometric for $i$ above some level $g$, and using well-known properties of geometric series (see Appendix A.2 for details), we can establish that

$$|\kappa - \kappa_{n+1}| \approx \frac{\delta^{n+1-g} \Delta \kappa_g}{1 - \delta},$$

where, for example,

$$\delta \approx \frac{\Delta \kappa_n}{\Delta \kappa_{n-1}}.$$  \hfill (11)

(We may, alternatively, estimate $\log \delta$ and then $\delta$ from the linear portion of the log-linear plot of $\Delta \kappa_i$.) Then, if the convergence of $\kappa_i$ to $\kappa$ is approximately geometric for $i > g = n - 1$, we may take

$$|\kappa - \kappa_{n+1}| \approx \frac{\delta^{n+2} \Delta \kappa_{n-1}}{1 - \delta},$$

which will be small if $n$ is a suitable cut-off.

One might be tempted to add this difference to $\kappa_{n+1}$ in order to improve its accuracy as an approximation to $\kappa$. However, it is important that our approximation does not exceed $\kappa$, for otherwise the computed measures of persistence will be greater, and may be considerably greater, than the true values. Small errors in excess of $\kappa$ can quickly compound to very large errors in the quantities being calculated, while small errors short of $\kappa$ are less of a problem, since we know that in this case our approximate values are bounded between 0 and the (strictly positive) true value.

Note that finding a good choice of the cut-off $n$ by checking $P_i(n)$ and the accuracy of $\kappa_{n+1}$ only ensures that the approximation is accurate for initial size $x_e + 1$. Although $P_i(n)$ may suggest a range of values over which $n$ could be appropriate, checking the accuracy of $\kappa_{n+1}$ only confirms $n$ as appropriate for an initial size $x_e + 1$. Usually, we are interested in finding accurate approximations for a range of initial population sizes, from $x_e + 1$ up to some size $m$. Fortunately, we may use the same approach to find a cut-off appropriate to the initial size $m$. Suppose that the extinction level is $m - 1$. Then, if a cut-off $n$ is suitable for extinction level $m - 1$, the event that the process hits $n$ after starting at $m$ does not contribute greatly to the persistence time at or above $m$. This persistence time is also measures persistence above the original extinction level $x_e$, and hence if $n$ is suitable
for approximating persistence above $m - 1$, with initial state $m$, then it is suitable for approximating persistence above $x_e$, with an initial state between $x_e + 1$ and $m$. Conversely, we note that while it is possible to use $\kappa_{n+1}$ to derive the value of a measure of persistence for an initial population of $n + 1$ individuals, from (5), $w_{n+1} = 0$ if we approximate $\kappa$ by $\kappa_{n+1}$. Hence, it is reasonable to expect the accuracy of the approximation $w_i$ to become very bad as the initial state approaches $n + 1$.

In the case, then, where extinction is certain but occurs in infinite mean time, the above approach to assessing the accuracy of $\kappa_{n+1}$ should not show $\kappa_i$ converging to any limiting value. Then, while it is impossible to demonstrate conclusively (using numerical techniques) that $\{\kappa_i\}$ diverges, apparent divergence provides evidence that the cut-off is either much too small, or that in fact $\kappa = \infty$ and no suitable cut-off exists. When such ambiguity remains, it may be necessary to gain a better theoretical understanding of the particular type of population process in order to determine whether a suitable cut-off can be found.

4 Examples

4.1 Comparison with analytical results

We will first illustrate our approach to estimating persistence with reference to the unbounded general catastrophe model discussed in Cairns and Pollett [6]. Because explicit results are available in certain special cases of this model, we can assess the accuracy of our technique. Suppose that the transition rates (1) have the specific form

$$q_{ij} = \begin{cases} 
\rho \beta^{i-1} a, & j = i + 1, \\
\rho \beta^{i-1} b (1 - q) q^{i-j-1}, & 0 < j < i, \\
\rho \beta^{i-1} b (1 - q) \sum_{k \geq i} q^{k-1}, & j = 0, \\
-\rho \beta^{i-1}, & j = i, \\
0, & \text{otherwise},
\end{cases}$$

for $i, j \geq 0$. In terms of birth, death and catastrophe rates, for $x \geq 1$:

$$B(x) = \rho \beta^{x-1} a,$$
$$D(x) = 0,$$
$$C(x) = \rho \beta^{x-1} b,$$

with catastrophe size distribution

$$F(k|x) = \begin{cases} 
(1 - q) q^{k-1}, & 1 \leq k < x, \\
(1 - q) \sum_{j \geq x} q^{j-1}, & k = x.
\end{cases}$$

In this model, all events occur at a common rate $\rho \beta^{x-1}$ dependent on the current size $x$ of the population, where $\rho$ and $\beta$ both positive. Further, given that some change in the population occurs, the size of the jump has a fixed distribution: jumps up (births) occur
with probability $a$, and the jumps down (deaths and catastrophes) occur with probability $b = 1 - a$ and with a size according to a geometric distribution with parameter $0 \leq q < 1$. Cairns and Pollett [6] give conditions for certain extinction and finite expected times to extinction for the above model (see Appendix A.4). By considering a number of particular cases of this model, we will show that the procedure outlined in the previous section does indeed produce accurate estimates of persistence.

(Note that while we do not propose this model as suitable for faithfully modelling any particular type of population, it is representative of the most general class of birth, death and catastrophe processes for which explicit expressions are available for the probability of, and expected time to, extinction.)

If we take $\rho = 2$, $\beta = 1.04$, $q = 0.05$ and $a = 0.6$, then extinction is not certain. For this case we evaluated the extinction probabilities by setting $\theta = 0$, $\gamma_i = 0$ for all $i$, and $c = 1$. Figure 1 is a plot of $\kappa_i$ against $i$. We see that $\kappa_i$ converges quickly to the theoretical value of around 0.7018 (given by (30); Appendix A.4).

If instead we take $a = 0.4$, then extinction is certain in finite mean time. We evaluated the expected extinction times by setting $\theta = 0$, $\gamma_i = 1$ for all $i$, and $c = 0$. The theoretical value of $\kappa = T_i$ is 2.1242 (from (31); Appendix A.4), and Figure 2(a) shows that $\kappa_i$ does indeed approach this value. Figure 2(b) demonstrates that the differences $\Delta \kappa_i = \kappa_{i+1} - \kappa_i$ become linear on a log-linear scale, indicating that $\kappa_i$ is converging to $\kappa$ (approximately) geometrically. We can obtain a rough approximation to the rate of convergence $\delta$ as per
(11) by examining the last few estimates of $\kappa$ (namely, $\kappa_{31}$, $\kappa_{30}$ and $\kappa_{29}$) and find the error using (10). From the data for Figure 2(a), $\delta \approx 0.6581$ and thus the error is

$$\kappa - \kappa_{31} \approx \frac{\delta^2 (\kappa_{30} - \kappa_{29})}{1 - \delta} \approx 2.664 \times 10^{-5}.$$ 

(a) (b)

Figure 2: (a) $\kappa_i$ approaches its upper bound; (b) the linearity of $\Delta \kappa_i$ on a log-linear scale indicates geometric convergence.

Using the approximation $\kappa \approx \kappa_{31}$, we find the expected extinction times depicted in Figure 3. The deviation of the numerical approximation from the true values observed for initial sizes close to the cut-off $n = 30$ is consistent with our interpretation of this technique: the process may also be absorbed above $n$. However, for low initial populations (and recalling that $\kappa = T_1 = 2.1242$), the true error in $\kappa$ is $2.641 \times 10^{-5}$, which agrees closely with the estimate of the error assuming geometric convergence. These values correspond to a relative error of approximately 0.0013%, indicating that (at least for initial population sizes much lower than the cut-off) our technique is capable of finding accurate approximations for extinction probabilities and expected extinction times.

We reiterate that while the approximation obtained using TBA may be very accurate, it is best for initial populations not far above the extinction level $x_e$, and may be expected to deteriorate as the initial population increases. Close to the cut-off $n$, the accuracy of the approximation may be very poor indeed; however, this is a problem also for approximations obtained by TBR; neither approach faithfully represents the process near the ceiling. Once again, the advantage of TBA is that it is ‘reliably’ inaccurate, in that it is always between 0 and the true values.
4.2 A model for Crabeater Seal populations

While the method of approximating measures of persistence that we have presented has been developed for unbounded populations without a hard ceiling, it is also useful in quantifying the effect of a known or hypothesised ceiling on the dynamics of a population. We will illustrate this use of truncation-by-absorption by considering a model based on data for crabeater seal \((Lobodon carcinophagus)\) populations wintering on ice in the Crown Prince Gustav Channel, Antarctica. Nine populations of between 50 and 2000 individuals were studied by Laws and Taylor [10], and, Wilcox and Elderd [19] use these and other data on the rate of disease outbreaks in seals to formulate a model for a crabeater seal population with a ceiling of between 1000 and 2000 individuals. The purpose of their model was to investigate the effects of density-dependent catastrophes, in this case due to disease, on persistence times. It will also serve, here, as a useful example for comparing different types of truncation, and for investigating the role of ceilings in population models.

Crabeater seals appear to be susceptible to outbreaks of disease with high mortality rates, but which are uncommon in small populations. The rate of outbreak is “density dependent” in the sense that, above a certain threshold size, outbreaks become much more common and disease becomes an important factor in the persistence of the population. Wilcox and Elderd [19] use the disease mortality data of Laws and Taylor [10] to estimate the threshold population size \(x_{th}\) to be approximately 400 individuals. In their model, this threshold marks the transition of the rate of disease outbreaks from a value close to 0, for populations much below \(x_{th}\), to a rate of either \(c = 0.05\) or \(c = 0.115\) for populations much
above the threshold. (These values for the rates are the maximum likelihood estimate, and the upper bound of a 95% confidence interval for that estimate, respectively, from data for harbour seals. Wilcox and Elderd [19] proposed these estimates as a first approximation to the rate of disease outbreak for crabeater seals, as there was little data on the frequency of disease outbreaks for the species.) The threshold was reflected in the model through a catastrophe rate $C(x)$ of the form

$$C(x) = c \left( \frac{x^\Gamma}{x^\Gamma + x_{th}^\Gamma} \right),$$

where $\Gamma = 30$ ensured that the rate makes a rapid transition from 0 to the maximum rate about $x_{th} = 400$, as shown in Figure 4.

The average mortality rate due to outbreaks of disease was assumed to be constant, and the catastrophe size distribution $F(x - j|x)$ was binomial in all cases, with a probability of survival of 0.15 (corresponding to the mean per capita mortality rate of 0.85 given by Laws and Taylor [10]). At least two individuals were assumed to die in any disease outbreak, however, so the population after an outbreak was binomially distributed between 0 and $x - 2$, with intensity parameter $p = 0.15$, and hence

$$F(x - j|x) = \begin{cases} \frac{(x-2)}{j} p^j (1-p)^{x-2-j}, & 0 \leq j \leq x - 2, \\ 0, & \text{otherwise}. \end{cases}$$

Figure 4: Rates of disease outbreak around the threshold value of $x_{th} = 400$. The rates vary between 0 below $x_{th}$ and $c = 0.05$ (solid) or $c = 0.115$ (dashed) above $x_{th}$.

To estimate the birth and death rates, $B(x)$ and $D(x)$, the population was assumed to produce approximately 1 offspring per female per year (and an even sex distribution was
assumed), such that in the absence of deaths, the population would grow by a factor of 1.5 each year. Hence, $B(x)$ was derived from $\exp[B(x)/x] = 1.5$, and death rates were derived from $B(x)$ and the annual population growth rate $\lambda$ of either 1.01 or 1.05. Thus,

$$B(x) = x \log(1.5), \quad \text{and}$$

$$D(x) = x \log(1.5/\lambda).$$

Although Wilcox and Elderd assumed that the populations were bounded, it is still informative to consider an unbounded version of their model. We will begin by considering the problem of estimating the probability of extinction, for if extinction were not certain, then the population would tend towards any proposed ceiling value, no matter how large. Brockwell [5] gives a necessary and sufficient condition for certain extinction in an unbounded population model with linear birth and death rates $xB$ and $xD$, respectively, and binomial catastrophes, with intensity parameter $p$, that occur at a constant rate $c$. Extinction is certain if and only if

$$D - c \log p \geq B.$$  \hspace{1cm} (18)

While the catastrophe rates $C(x)$ used in the crabeater seal model are not constant, they are roughly constant (roughly equal to $c$) for population sizes significantly larger than $x_{th} = 400$ individuals. If the condition

$$\log \left( \frac{1.5}{\lambda} \right) - c \log p > \log(1.5)$$ \hspace{1cm} (19)

is satisfied, then there exists a state $m$ such that the process is certain to drop below $m$ in a finite time, if it starts above $m$. This is a direct consequence of its similarity to Brockwell’s linear birth-death model with binomial catastrophes, for which (19) would be sufficient for certain extinction, and hence certainty in dropping below any state $m$. In models of this type, the converse also holds: if the process is certain to drop below some finite size (for example, $m$), given that it starts above that size, then extinction is certain regardless of the value of $x_e$. Hence, (19) is also a sufficient condition for the certain extinction in the unbounded crabeater seal model. It is easy, then, to show that extinction is indeed certain for all combinations of the parameters $c = 0.05, 0.115$ and $\lambda = 1.01, 1.05$.

Figure 5 reproduces the results of Wilcox and Elderd [19] for initial populations of up to 1000 individuals. The plots show the persistence times above a quasi-extinction level of $x_e = 30$ for the crabeater seal model, for each of the various combinations of values of the growth rate $\lambda$ and the outbreak rate $c$. The marked dip in the plots for $\lambda = 1.01$ (Figure 5(a) & (b), dashed lines) corresponds to increased mortality for initial populations close to $x_{th} = 400$, and is due to the increased rate of disease outbreak around the threshold, following which the population is likely to be fairly close to the level of quasi-extinction. Populations with sizes smaller than $x_{th}$ are not subject to such frequent outbreaks of disease, and are likely to climb closer to $x_{th}$ before experiencing any mortality due to disease, and hence are expected to persist for longer. Conversely, larger populations are likely to be further from $x_e$ after an outbreak of disease, and hence are expected to persist for longer after such an event.
Figure 5: Comparison between approximate expected persistence times for initial populations between 31 and 1000 individuals, calculated using truncation-by-reflection (dashed) or by-absorption (solid), with cut-off $n = 1000$, for various combinations of parameters $\lambda$ and $c$. The results of the two approximations differ greatly for $\lambda = 1.05$ ((c) and (d)), as the largest contribution to the persistence times comes from the event that the process goes extinct after reaching the cut-off $n$. 

(a) $\lambda = 1.01$, $c = 0.05$

(b) $\lambda = 1.01$, $c = 0.115$

(c) $\lambda = 1.05$, $c = 0.05$

(d) $\lambda = 1.05$, $c = 0.115$
The persistence times for $\lambda = 1.05$ (Figure 5(c)&(d), dashed lines) follow a very different trend. As noted in [19], while there appears to be a slight dip near $x_{th}$, the expected time to (quasi-) extinction is relatively constant above about 100 individuals. In this case, we observe no strong dependence of the persistence times on the initial population. In order to see the effect of the population ceiling, we may compare the persistence times calculated assuming a bounded population (or truncation-by-reflection; Figure 5, dashed lines) with those calculated using truncation-by-absorption (Figure 5, solid lines). The solid lines in Figure 5(a)&(b), give the persistence times for TBA for $\lambda = 1.01$, which for initial populations much smaller than the ceiling are comparable to those calculated using TBR (dashed lines). The solid lines in Figures 5(c)&(d), however, are very much less than those given by the dashed lines, a discrepancy which is accounted for by observing that TBA returns values that are expected times until the population either goes extinct or exceeds its ‘ceiling’. We may conclude that, regardless of the initial size of the population, there is a high probability that the population will reach its ceiling value, and the largest component of the expected time to extinction (for initial populations greater than about 100 individuals) is the time taken to drop below $x_e$ from the population ceiling. (Even after an outbreak of disease that occurs when the population is at the ceiling, it is likely to return to the ceiling again before going extinct.)

This behaviour is not so easy to see when we consider only the results of calculations of persistence time for the bounded population. Recall also the interpretation of the convergence of $\kappa_i$ to $\kappa$: if $\kappa_{n+1}$ is close to $\kappa$, then the event that the population goes above $n$ from $x_e + 1$ does not contribute significantly to its persistence, and the process with approximate ceiling $n$ accounts for most of the likely paths of the original model. Figure 6(b) shows the values $\kappa_i$ for $\lambda = 1.05$. There is a clear lack of evidence for convergence of $\kappa_i$ to the limiting value $\kappa$ over the range $i = x_e + 2, \ldots, 2001$. We may interpret this as another indication that it is likely the population will hit its ceiling value (perhaps even many times), and that this event has a significant effect on the persistence of the population. Conversely, for the case $\lambda = 1.01$, $\kappa_i$ begins to converge by about $i = 1000$ (Figure 6(a)), particularly for the higher catastrophe rate $c = 0.115$.

The true probability of eventual extinction is 1 in the crabeater seal model, for all combinations of the parameters $\lambda$ and $c$ considered in [19]. However, by examining the probability $P_i(n)$ of exceeding the ceiling, for the four combinations of parameter values, we can better judge the suitability of the chosen cut-off of 1000 individuals, and the range over which we would expect that cut-off to be appropriate. Figure 7 shows values of $P_i(n)$ for the four combinations of values of $\lambda$ and $c$. Only in the two cases where $\lambda = 1.01$ does the cut-off of 1000 individuals appear to be appropriate over any range of initial population sizes. When $\lambda = 1.01$ and $c = 0.05$, we could expect reasonable accuracy for initial populations of only just above the extinction level of 30 individuals; $P_{31}(1000) = 0.0019$ and $P_{32}(1000) = 0.0037$. By an initial population size of 36, the chance of exceeding the ceiling prior to extinction is greater than 1%, accounting for a 6.2% difference between the TBR and TBA estimates. Although this difference is relatively small, Figures 7 and 6(a) indicate that a cut-off larger than 1000 may be more appropriate; for example, $\kappa_i$ appears to be converging by a cut-off of about 2000 individuals. When $c = 0.115$, the chance of exceeding the cut-off remains under 1% for initial populations up to 560 individuals, corresponding a difference between
the two approximations of 1.1%. The convergence evident in Figure 6(a) supports the conclusion that 1000 individuals is an appropriate cut-off in this case.

In contrast to the above, in neither of the cases where \( \lambda = 1.05 \) is the cut-off of 1000 individuals suitable (as was clear from the plot in Figure 6(b)). The chance that the population would exceed the cut-off, when starting just above the extinction level, is about 11.3% when \( c = 0.115 \) and 11.9% when \( c = 0.05 \). Although it is difficult to estimate a suitable cut-off by examination of the probabilities \( P_i(n) \), we should anticipate that a cut-off very much larger than 1000 individuals would be required to obtain accurate estimates of the expected time to extinction in the \( \lambda = 1.05 \) cases. Figure 6(b) shows that even at a cut-off of 2000 individuals, there is no sign of convergence in \( \kappa_i \).

In fact, in some circumstances there may be no suitable cut-off. Eventual extinction is certain, so \( P_i(n) \) must go to zero for a sufficiently large value of \( n \), but the values \( \kappa_{n+1} \) may never truly converge as \( n \) gets large because the expected time to extinction may be infinite. Unfortunately, the mathematical understanding of linear birth-death processes subject to binomial catastrophes is somewhat limited. Brockwell’s result on the probability of eventual extinction (equation (18), above) is one of the few explicit results on processes of this form. One open problem is to derive necessary and sufficient conditions for the expected time to extinction to be finite (even if extinction is certain, this quantity may be infinite, as in some of the cases considered in [6]).

This example illustrates the important role that population ceilings may play in persistence, particularly in rapidly growing populations with (relatively) small ceilings. In the case of crabeater seals, for the higher population growth rate of \( \lambda = 1.05 \), the size of the population ceiling is important because populations are very likely to reach it, virtually regardless of their initial size, and because such behaviour may reduce the effect on persis-

![Figure 6](image)

**Figure 6**: \( \kappa_i \) for \( i = x_e + 2, \ldots, 2001 \) for \( c = 0.05 \) (solid) and \( c = 0.115 \) (dashed) with (a) \( \lambda = 1.01 \), and (b) \( \lambda = 1.05 \).
tence of the strong dependence of the catastrophe rate on the current population size. In particular, we may use the convergence of $\kappa_i$ to $\kappa$ over a range of values $i = x_c + 2, \ldots, n + 1$ to assess the importance of the population ceiling in governing the behaviour of the population. This example also illustrates the importance of the convergence of $\kappa_i$ to $\kappa$ as an indicator of the suitability of a chosen ceiling for the truncation of an unbounded population process. Where $\kappa_{n+1}$ is close to $\kappa$, the chosen ceiling is likely to be suitable, and both TBR and TBA should produce similar persistence times (at least, for initial population sizes much less than the ceiling value), such as in the cases where $\lambda = 1.01$. When $\kappa_i$ does not appear to have converged to $\kappa$, the cut-off $n$ is not suitable for calculating persistence times (for unbounded populations or populations with ceilings much larger than $n$), and the two methods for calculating persistence times will not agree closely, for example in the cases where $\lambda = 1.05$.

5 Discussion

We have presented the method of truncation-by-absorption for Markovian models, and, building on the work of Brockwell [5] and Anderson [2], we have used it to evaluate measures of the persistence times of populations (primarily in an ecological context). In applications of Markov chains to ecological modelling, it is common to impose some fixed upper bound on the population, either as some hypothesised ceiling derived from knowledge of the population’s habitat, or as a simple cut-off to facilitate the evaluation of quantities of interest. In the latter case, the truncation of the state space is usually accompanied by an assumption

![Figure 7: Values of $P_i(1000)$ for parameters: $\lambda = 1.01$ and $c = 0.115$ (solid line); $\lambda = 1.01$ and $c = 0.05$ (dashed); $\lambda = 1.05$ and $c = 0.115$ (dotted); $\lambda = 1.05$ and $c = 0.05$ (dash-dot).]
that the boundary is reflecting: the process may reach the cut-off, but can never exceed it or become stuck there. In contrast, truncation-by-absorption posits ‘extinction’ if the process ever exceeds the cut-off. At first this seems to be counter-intuitive, since an absorbing ceiling is an unreasonable assumption for most population models, but truncation, for the purpose of calculating measures of persistence times, need not mirror the effects of a physical population ceiling. Rather, its purpose is to help in evaluating approximations to these quantities that accurately represent the true values, as the cut-off becomes large. As we have demonstrated, truncation-by-absorption presents two major advantages over truncation-by-reflection.

1. The parameterisation of solutions in terms of \( \kappa = \sup_{i \geq x} \kappa_i \), and the ease with which we may approximate \( \kappa \), provides a relatively simple procedure by which we can assess the accuracy of a truncation from the solution to a single system of equations (6) without resorting to ad hoc comparisons between results for a variety of cut-offs. We may employ both graphical and quantitative indicators of the suitability of a cut-off, by assessing the convergence of \( \kappa_i \) graphically, by estimating the error \( |\kappa - \kappa_{n+1}| \) under the assumption of approximately geometric convergence, and by examining the probability that the population will exceed the cut-off.

2. Truncation-by-absorption incorporates the worst-case scenario in which the population goes extinct as soon as it exceeds the cut-off \( n \), and hence provides conservative estimates of persistence that are always bounded above by the true values. Although in most cases measures of persistence calculated using truncation-by-reflection will converge, as the cut-off gets large, to the true values of the underlying unbounded models, these values are not similarly bounded.

Nevertheless, we also note that, just as both bounded and unbounded population models are useful, so are both reflecting and absorbing cut-offs in truncated state spaces. In our analysis of the crabeater seal model of Wilcox and Elderd [19], we compared the expected time to quasi-extinction (in which the population drops below 30 individuals) from each form of truncation. Wilcox and Elderd proposed the model as a tool for investigating the effect of catastrophes on persistence times, but by comparing persistence times calculated using truncation-by-absorption with those obtained assuming a reflecting boundary, we were able to investigate the effect of the hypothesised population ceiling. Even if the ceiling \( N \) of a model is a well-defined physical bound, comparing exact measures of persistence with those computed using truncation-by-absorption (with an artificial ceiling of \( n = N - 1 \)) will indicate the effect of the ceiling on the persistence of the population. In a conservation context, for example, this could allow managers to better understand the effect of manipulating the population ceiling on the persistence of a population.
A Appendix

A.1 Approximating $\kappa$

A useful theoretical representation of the distribution of the hitting time $\tau$ of the extinct states is its Laplace-Stieltjes transform, conditional on the process starting in state $i$:

\[
x^*_{i}(\theta) = \begin{cases} 
E(e^{-\theta \tau} | X(0) = i), & \theta > 0, \\
\Pr(\tau < \infty | X(0) = i), & \theta = 0.
\end{cases}
\]

These quantities satisfy the system of equations

\[
\sum_{k=0}^{i+1} q_{ik} x^*_k(\theta) = \theta x^*_i(\theta), \quad i \geq x_e,
\]

\[
x^*_i(\theta) = 1, \quad i \leq x_e,
\]

(20)

and, if we can rule out explosivity, (20) has a unique solution satisfying $0 \leq x^*_i(\theta) \leq 1$ for all $i$ (see Section 9.2 of Anderson [2]). Note that (2) is obtained on setting $\theta = 0$, and in fact, we can recover all moments of the persistence times by taking derivatives of $x^*_i(\theta)$ at $\theta = 0$.

Anderson considered the equation

\[
\sum_{k=0}^{i+1} q_{ik} w_k = \theta w_i - \gamma_i, \quad i \geq x_e,
\]

\[
w_i = c, \quad i \leq x_e,
\]

(21)

which encapsulates (20) and also allows calculation of the probability of eventual extinction and moments of extinction times. (Note that Anderson had $x_e = 0$ and $\gamma_i = \gamma$ for all $i$. The simple extension here covers functional extinction and allows for the evaluation of higher-order moments of persistence times.)

The system (21) can be solved by finding sequences $\{u_i, i \geq 0\}$ and $\{v_i, i \geq 0\}$ that satisfy the systems

\[
\sum_{k=0}^{i+1} q_{ik} u_k = \theta u_i, \quad i \geq x_e + 1,
\]

(22)

\[
\sum_{k=0}^{i+1} q_{ik} v_k = \theta v_i - \gamma_i, \quad i \geq x_e + 1,
\]

with $u_i = 0$ and $v_i = -c$ for $0 \leq i \leq x_e$, and $u_{x_e+1} = 1$ and $v_{x_e+1} = 0$. Any solution to (21) can then be written in the form

\[
w_i = \kappa u_i - v_i, \quad i \geq 0,
\]

(23)
where \( \kappa = w_1 \) determines which particular solution is represented. When calculating moments of persistence or the probability of eventual extinction, it is the \textit{minimal, non-negative} solution to (21) that is of interest (see Anderson [2], §9.2).

Because solutions to (22) are unique for a given set of parameters, the primary goal in applying this method is the determination of \( \kappa \). If \( \sup_{i > x_e + 1} \kappa_i \) is indeed finite, this supremum is either \textit{attained} for some finite value of \( i > x_e + 1 \), or else it is \textit{equal to} \( \lim_{i \to \infty} \kappa_i \). We would hope that, at the very least, we could accurately \textit{approximate} \( \kappa \) by finding a cut-off point \( n \) at which

\[
\max_{x_e + 2 \leq i \leq n+1} \kappa_i \approx \kappa. \tag{24}
\]

However, we can show the supremum \textit{equals} the limit, in the present context of evaluating either the probability of eventual extinction or any of the moments of the persistence times, all of which require \( \theta = 0 \). (We will not attempt to do this for the general case \( \theta \geq 0 \).)

First recall that our process is assumed to have finite rates, that jumps upward are limited to size 1, and that the ‘extinct’ states \( i \leq x_e \) are accessible from states above \( x_e \). If, from (3), \( w_j = 0 \) for some \( j > x_e \), then the probability of eventual extinction (or some moment of the persistence time, whichever we are considering), starting from state \( j \), must be 0. On the one hand, a zero probability of eventual extinction for a particular \( j > x_e \) would imply that functionally extinct population sizes are not accessible from \( j \), above \( x_e \), in violation of an assumption. On the other hand, if any of the moments of the persistence time, starting in state \( j \), were zero, then, by a generalisation of Markov’s inequality, the persistence time would be almost surely zero, which would correspond to an immediate jump from state \( j \) to some extinct state \( k \leq x_e \), thus violating our assumption that rates are finite. So, there can be no \( j < \infty \) such that the supremum is attained at \( j \), and hence

\[
\kappa = \sup_{i > x_e + 1} \kappa_i = \lim_{i \to \infty} \kappa_i,
\]

at least when \( \theta, c \) and \( \{\gamma_i\} \) are such that the minimal, non-negative solution to (3) corresponds to the probability of eventual extinction or some moment of the persistence times. Note that we can use the limit rather than the limit supremum because \( \kappa_i (= v_i/u_i) \) is the ratio of two non-decreasing sequences.

A.2 Suitability of cut-off \( n \)

We can break down the expected time to extinction, in the case of the original process, into components derived by conditioning on whether or not the population exceeds the proposed ceiling \( n \) before extinction occurs (this is, whether it reaches state \( n + 1 \)). Assume that \( X(0) = i \leq n \). Define \( \eta_n \) to be the first time at which the process exceeds \( n \) (that is, hits \( n + 1 \)), so that \( \eta_n < \infty \), or \( \eta_n = \infty \), if the population exceeds the ceiling, or never exceeds the ceiling, respectively. Let \( \tau_R \) be the time at which the process drops below \( x_e + 1 \), calculated using TBR. Then,

\[
E_i[\tau_R] = E_i[\tau_R|\eta_n < \infty]Pr_i(\eta_n < \infty) + E_i[\tau_R|\eta_n = \infty]Pr_i(\eta_n = \infty).
\]

(We write \( E_i \) or \( Pr_i \) expectation and probability conditional on \( X(0) = i \).) We can further decompose the first term on the left-hand side since, by the Markov property, the time to
extinction starting in state \(i\), given that the process hits the ceiling \(n\) at least once, is the sum of the time it takes to hit \(n\) and the time to extinction starting in state \(n\). Hence,

\[
E_i[\tau_R] = (E_i[\eta_n|\eta_n < \infty] + E_n[\tau_R]) \Pr_i(\eta_n < \infty) + E_i[\tau_R|\eta_n = \infty] \Pr_i(\eta_n = \infty). \tag{25}
\]

Now note that the time \(\tau_A\) to extinction under the TBA regime should be the minimum of \(\tau_R\) and \(\eta_n\), and, because \(\eta_n\) is the smaller value if and only if \(\eta_n < \infty\),

\[
E_i[\tau_A] = E_i[\min(\tau_R, \eta)] = E_i[\eta_n = \infty] \Pr(\eta_n = \infty) + E_i[\eta_n|\eta_n < \infty] \Pr(\eta_n < \infty). \tag{26}
\]

Hence, on substituting (26) into (25), it becomes clear that

\[
E_i[\tau_R] = E_i[\tau_A] + E_n[\tau_R] \Pr_i(\eta_n < \infty). \tag{27}
\]

That is, the expected time to extinction in the TBR case is the expected time under TBA, plus a quantity accounting for the possibility that the process hits its ceiling before it goes extinct. So, knowing any three of these quantities we can calculate the fourth; for example, by calculating expected times to extinction under TBR and TBA for \(x_i + 1 \leq i \leq n\), we can calculate an estimate of the probability of eventual extinction. Note that \(\eta_n < \infty\) only if the process is absorbed above \(n\) (and not at or below \(x\)). Thus, \(1 - \Pr_i(\eta_n < \infty)\) is the estimate of the probability of eventual extinction starting in state \(i\), under TBA.

We also note that since all terms in (27) are (strictly) positive for a finite ceiling \(n\), we obtain the inequality \(E_i[\tau_A] < E_i[\tau_R]\), further evidence that \(E_i[\tau_A]\) is a conservative estimate of the true expected time to extinction. However, it also becomes clear that since \(\Pr_i(\eta_n < \infty) \downarrow 0\) as \(n \to \infty\) whenever extinction is certain, \(E_i[\tau_R]\) may in fact converge to \(E_i[\tau]\) under the same limit (provided \(E_n[\tau_R]\) is not increasing ‘too fast’). Note that this does not mean that \(E_n[\tau_R]\) will converge to \(E_n[\tau]\); although the values of \(E_n[\tau_R]\) certainly look more plausible than those of \(E_n[\tau_A]\) (which are typically close to zero), they are not necessarily more accurate.

### A.3 Accuracy of \(\kappa_{n+1}\)

In order to assess the suitability of the cut-off \(n\) and estimate the error in approximating \(\kappa\) by \(\kappa_{n+1}\), we note that if the convergence of \(\kappa_i\) to \(\kappa\) is approximately geometric for any \(i \geq g\) (for some \(g\)), and \(\delta\) is the rate of convergence, then we have

\[
\log \Delta \kappa_i \approx \log \Delta \kappa_g + (i - g) \log \delta,
\]

and hence, for any \(g \leq h < n\) (where \(n\) is the cut-off value),

\[
\delta \approx \left| \frac{\kappa_{h+2} - \kappa_{h+1}}{\kappa_{h+1} - \kappa_h} \right| = \frac{\Delta \kappa_{h+1}}{\Delta \kappa_h}. \tag{28}
\]

We might take \(h = n - 1\) in (28), but in any case, we may estimate \(\delta\) from the linear portion of the log-linear plot of \(\Delta \kappa_i\). Then, assuming convergence is monotonic and using well known properties of geometric series, for \(n > g\) we will have

\[
|\kappa - \kappa_{n+1}| \approx \frac{\delta^{n+1-g} \Delta \kappa_g}{1 - \delta}, \tag{29}
\]

which will be small if \(\kappa_{n+1}\) is to be a good approximation to \(\kappa\).
A.4 Results from Cairns and Pollett [6]

For the model given by (13), extinction is certain to occur in a finite time if \( R = a - b/(1 - q) \leq 0 \), and when this is not the case, the probability of extinction is given by

\[
p_j = 1 - \frac{R(1 - q - (h - q)h^j)}{a(1 - h)}, \quad j \geq 0,
\]

where \( h = q + b/a \). Further, when \( \beta \neq 1 \), the expected extinction times are finite if \( \beta > 1/h \), and are given by

\[
T_i = \frac{1 - q - (\varepsilon - q)\varepsilon^{i-1}}{\rho(b - a(\varepsilon - q))(1 - \varepsilon)}, \quad i \geq 1,
\]

where \( \varepsilon = 1/\beta \).

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References


