

Bounds on the dynamics of sink populations with noisy immigration

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Theoretical Population Biology, Volume 92, March 2014, Pages 88-96
<http://dx.doi.org/10.1016/j.tpb.2013.12.004>

Abstract

Sink populations are doomed to decline to extinction in the absence of immigration. The dynamics of sink populations are not easily modelled using the standard framework of per capita rates of immigration, because numbers of immigrants are determined by extrinsic sources (for example, source populations, or population managers). Here we appeal to a systems and control framework to place upper and lower bounds on both the transient and future dynamics of sink populations that are subject to noisy immigration. Immigration has a number of interpretations and can fit a wide variety of models found in the literature. We apply the results to case studies derived from published models for Chinook Salmon (*Oncorhynchus tshawytscha*) and blowout penstemon (*Penstemon haydenii*).

Keywords: Population ecology, projection model, sink population, immigration, Input-to-state stability

1 Introduction

Many populations are in a state of predictable decline in the absence of immigration, or of deliberate bolstering by conservation management strategies (Pulliam, 1988; Gonzalez and Holt, 2002; Holt et al., 2003; Roy et al., 2005; Matthews and Gonzalez, 2007). In many cases, such immigration events vary dramatically in magnitude or structure throughout the lifespan of the population. During natural metapopulation processes, numbers of immigrants introduced into sink populations (that is, populations which would decline in the absence of immigration) will vary according to annual variation in the size of source populations (Pulliam, 1988), or even according to prevailing wind directions (for example, Taylor and Reling (1986)), ocean currents (for example, Victor (1986)), or variation in the porosity of the between-population habitat matrix (Eriksson, 1996; Diffendorfer et al., 1995). Similarly, the translocation or reintroduction strategies of conservation managers may be at the mercy of annual fluctuations in the availability of stock from source populations or captive rearing programmes (Nelson et al., 2002). Yet it is critical to the conservation of sink populations that we are able to forecast features of future dynamics, and predict impacts of population management strategies. In this paper we provide a relevant modelling framework, and analyse populations in this framework.

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Here we choose to model (possibly time-varying or noisy) immigration into otherwise stably declining populations using matrix projection models with additive, positive inputs. Specifically, we append to the standard matrix Population Projection Model (PPM) (Caswell, 2001), a time-varying input

$$x(t+1) = Ax(t) + d(t), \quad x(0) = x_0, \quad t = 0, 1, 2, \dots, \quad (1.1)$$

where the input $d = d(\cdot)$ is componentwise nonnegative and vector-valued. This is a complementary formulation to that of Gonzalez and Holt (2002) and Holt et al. (2003), where typically the model is of the form (1.1) but with $A = A(t)$ time-varying and possibly nonlinear and $d(\cdot) = I$ a constant vector. The framework (1.1) is appropriate when immigration is described in absolute values (for example, 1000 individuals per annum) as opposed to proportional to the present population, which would be the result of modelling immigration as a perturbation to the projection matrix. The immigration rates $d(\cdot)$ may of course correspond to per capita emigration rates from source populations, but without knowledge of densities or even locations, and crucially, models for these populations such an approach would only obscure matters. It is also the case that population ecologists lack detailed quantitative information about $d(\cdot)$. Simply put, without knowledge of $d(\cdot)$ in (1.1), we cannot project the model to obtain predicted future population abundance. Notwithstanding the above uncertainty, it is reasonable, however, to assume that the immigration $d(\cdot)$ is bounded by some known (or estimated) quantities, that is

$$0 \leq d_m \leq d(t) \leq d_M, \quad t = 0, 1, 2, \dots, \quad (1.2)$$

where the above inequalities are understood componentwise and d_m and d_M are two known, nonnegative constant vectors. Since the behaviour of $d(\cdot)$ over time is unknown, we can only provide bounds for how the population develops over time.

The framework proposed here allows us to study not just asymptotic properties of sink populations subject to immigration, but also the transient propagation of immigration through time (Stott et al., 2011). More generally, the assumed linearity of the underlying model lends itself to the translation of analytical methods from systems and control theory. Such methods include: perturbation analysis, as originally developed in this context by Hinrichsen and Pritchard (1986a,b) and describing the behaviour of additive noise; and Input-to-State-Stability, developed by Sontag (2008) and collaborators.

Our goal is to provide analytic solutions to the upper and lower bounds of the envelope of future dynamics of these populations, rather than viewing noisy immigration as a component of a stochastic difference equation (as in Kesten (1973)) and then estimating means and variances in the density or growth rate of the sink population, as is performed in, for example, Sykes (1969). Our approach amounts to providing ‘best-and-worst’ case scenarios. We derive conservative (that is, wide) bounds that apply to all possible magnitudes of immigration, alongside tighter bounds that apply to a subset of immigration scenarios. We use two case studies to illustrate when and how immigration, and its propagation as transient dynamics, can promote persistence and growth of an otherwise declining population. The case studies also demonstrate the flexibility of the control theory approach, by considering demographic structuring in the immigration dynamics (for example, Robinson et al. (2008)). The case studies are chosen to demonstrate the relevance of our modelling strategy to both the understanding of natural sink dynamics, and to the design of conservation management strategies.

2 Methods and Results

2.1 Problem formulation

Our starting point is the matrix PPM with time-varying inputs (1.1). The quantity $x(t)$ denotes the population’s abundance at time-step t , and is a *structured* population, composed of N stages which typically refer to different ages or sizes whose life-history traits vary accordingly. As usual, \mathbb{R}^N denotes the set of real vectors with N components. The quantity $x_0 \in \mathbb{R}^N$ denotes the initial population, which may not be known in practice. The time increments usually coincide with the synchronisation of

important life–history events or the occurrence of a population census at a given date during the assumed time–step. The assumption of discrete time is common in population modelling, but analogous models for continuous time also exist (for a survey of such models see, for instance, Cushing (1998)).

The matrix A describes how an undisturbed population $x(t)$ in (1.1) changes over one time–step, using life–history information such as survival, growth/stage movement and fecundities of a population. Naturally the entries of A are constrained by biological limits. More precisely, we assume that A in (1.1) is an $N \times N$ matrix and is componentwise nonnegative and primitive. These assumptions are natural for such ecological systems (Stott et al., 2010) and imply that the conclusions of the Perron–Frobenius Theorem (Perron, 1907; Frobenius, 1912) hold. In particular, A has a dominant eigenvalue λ , which is real and positive, and as is well–known describes the long–term growth or decline of the undisturbed, ambient population (1.1). We say that A describes a sink (respectively neutral, source) population if $\lambda < 1$ ($\lambda = 1$, $\lambda > 1$). These three cases correspond to asymptotic decline, population stasis or asymptotic growth respectively.

If undisturbed, the standard PPM is a mean–field model in the sense that two individuals in any given population stage are identical and have identical futures. Furthermore, the model (1.1) *without* $d(\cdot)$ omits any stochasticity present in the system, such as that caused by environmental fluctuations. In our formulation, the input $d(\cdot)$ represents stochasticity through immigration, with each vector $d(t) \in \mathbb{R}^N$. The input $d(\cdot)$ could represent managed immigration (and so is *known* and under *our* control). Alternatively, $d(\cdot)$ might be unknown (and so *not* under our control). Such a modelling framework is used in mathematical systems and control theory (see, for example, Sontag (1998)) but seems to have received less attention in ecological applications.

For any two vectors $a = [a_1, a_2, \dots, a_N]^T \in \mathbb{R}^N$ and $b = [b_1, b_2, \dots, b_N]^T \in \mathbb{R}^N$, where superscript T denotes matrix transposition, we write $a \leq b$ when $a_i \leq b_i$ for all $i = 1, 2, \dots, N$. For a matrix B , we write $B \geq 0$ if every entry of B is nonnegative.

2.2 Results

In the presence of immigration $d(\cdot)$, the solution $x(t)$ of (1.1) is given by

$$x(t) = A^t x_0 + \sum_{j=0}^{t-1} A^j d(t-j-1), \quad t = 1, 2, \dots \quad (2.1)$$

The first term on the right hand side of (2.1) is the contribution to $x(t)$ from the initial population x_0 . The second term contains the contribution to $x(t)$ from the immigration term $d(\cdot)$. We comment here that the immigration vectors $d(\cdot)$, and their extremal values d_m and d_M should be modelled to all take the same units as the population $x(t)$. So when $x(t)$ denotes numbers of individuals in each stage class, the immigration vector $d(t)$ should denote the number of new arrivals. Alternatively, owing to the linearity of the model (1.1), when $x(t)$ denotes proportions of the population, relative say to the initial population distribution $\|x_0\|_1$, then so should $d(t)$.

We restrict our attention throughout this work to sink populations where, in the absence of immigration, the population is asymptotically declining at rate λ^t with $\lambda < 1$. We seek to quantify how immigration affects these dynamics. When $\lambda \geq 1$, the population grows asymptotically and nonnegative inputs only make the population larger. Since $A \geq 0$ and $\lambda < 1$ we have

$$0 \leq \sum_{j=0}^{t-1} A^j = I + A + \dots + A^{t-1} = (I - A)^{-1}(I - A^t), \quad t = 1, 2, \dots, \quad (2.2)$$

and

$$\sum_{j=0}^{\infty} A^j = (I - A)^{-1}, \quad (2.3)$$

where I is the $N \times N$ identity matrix. If immigration is constant in time, say with value d_* , or converges to d_* , then the first term on the right hand side of (2.1) converges to zero and the second term converges to the constant vector $x_* = (I - A)^{-1}d_*$. In words, the population given by (2.1) converges to $(I - A)^{-1}d_*$. If $d_* = 0$, then $x_* = 0$, so that if immigration declines to zero in time then so does the population. Conversely, if d_* is positive, then so is x_* , and in this case the population does not die out (even though A predicts decline to extinction without immigration).

However, as already stated, such quantitative information regarding $d(\cdot)$ is usually not available and hence we only assume that $d(\cdot)$ is bounded as in (1.2). Using the nonnegativity of all the terms, we can bound the solution x in (2.1) from above and below by

$$A^t x_0 + \sum_{j=0}^{t-1} A^j d_m \leq x(t) \leq A^t x_0 + \sum_{j=0}^{t-1} A^j d_M. \quad (2.4)$$

Using the fact that $\lambda < 1$ we can compute the sums in (2.4) explicitly to give

$$A^t x_0 + (I - A)^{-1}(I - A^t)d_m \leq x(t) \leq A^t x_0 + (I - A)^{-1}(I - A^t)d_M, \quad (2.5)$$

where we have used (2.2). Both of the bounds in (2.5) are composed of a nonnegative time-varying component from the initial state x_0 , and a nonnegative time-varying component from the immigration term. Since $\lambda < 1$, the former terms are decreasing asymptotically whilst the latter are increasing. As we proceed to demonstrate, these bounds can often be written as a single time-varying component and a constant additive term. The upper bound in (2.5) is itself bounded from above by $A^t x_0 + (I - A)^{-1}d_M$ so that

$$x(t) \leq A^t x_0 + (I - A)^{-1}d_M. \quad (2.6)$$

The expression (2.6) holds for any d_M satisfying (1.2), but is more conservative (that is, worse) than that in (2.5).

A less conservative upper bound than that in (2.6) can be reformulated from the expression in (2.5). If d_M and x_0 are such that $\bar{x}_0 := x_0 - (I - A)^{-1}d_M$ is nonnegative, meaning that the long-term effect of the largest level of immigration is not larger than the initial ambient population, then we can rewrite the upper bound for $x(t)$ in (2.5) as

$$x(t) \leq A^t \bar{x}_0 + (I - A)^{-1}d_M. \quad (2.7)$$

The first term in the upper bound (2.7) is identical to that of (2.1), but with a perturbed nonnegative initial population \bar{x}_0 . The second term in (2.7) is simply an additive constant vector, which can be computed.

A similar treatment applies to the lower bound in (2.5). Again, if d_m and x_0 are such that $\underline{x}_0 := x_0 - (I - A)^{-1}d_m$ is nonnegative then

$$x(t) \geq A^t \underline{x}_0 + (I - A)^{-1}d_m. \quad (2.8)$$

Notice that as $d_M \geq d_m$ then $\bar{x}_0 \leq \underline{x}_0$ meaning that if $\bar{x}_0 \geq 0$ then $\underline{x}_0 \geq 0$ as well.

The bounds (2.7) and (2.8) actually hold for *any* d_M and d_m (that satisfy (1.2) as assumed throughout) but they become most useful when $\bar{x}_0, \underline{x}_0 \geq 0$. Indeed, since the terms $(I - A)^{-1}d_M$ and $(I - A)^{-1}d_m$ in (2.7) and (2.8) respectively are constant, we can understand the time-varying behaviour of the bounds, particularly the transient behaviour, by simply considering $A^t \bar{x}_0$ and $A^t \underline{x}_0$. Techniques for describing, quantifying and estimating transient behaviour of $A^t x$ for $x \geq 0$ include the concepts of reactivity, Neubert and Caswell (1997), population inertia, Koons et al. (2007), the Kreiss bound, Townley et al. (2007); Townley and Hodgson (2008). The paper of Stott et al. (2011) provides a review of this material, introduces new metrics, and proposes a framework for studying transient behaviour.

For example, using reactivity of A^t given by $\rho(t) := \|A^t\|_1$ (the largest column sum of A^t), we have that

$$\|x(t)\|_1 \leq \rho(t)\|\bar{x}_0\|_1 + \|(I - A)^{-1}d_M\|_1, \quad t = 1, 2, \dots,$$

where the one–norm $\|y\|_1$ of a vector y is given by the sum of the absolute values of the components of y .

Alternatively, the population inertia (Koons et al., 2007) of the matrix PPM $x(t+1) = Ax(t)$ is an asymptotic ratio of the population density from initial population distribution x_0 compared to that from the stable stage structure (that is, from $x_0 = w$, with w a positive right eigenvector of A corresponding to the dominant eigenvalue; the asymptotic growth rate). The population inertia depends on the initial population distribution and is known to be bounded over all x_0 from below and above by the *attenuated inertia* (denoted $\underline{\rho}_\infty$) and *amplified inertia* (denoted $\bar{\rho}_\infty$) given by

$$\underline{\rho}_\infty = \frac{v_{\min}\|w\|_1}{v^T w} \quad \text{and} \quad \bar{\rho}_\infty = \frac{v_{\max}\|w\|_1}{v^T w}, \quad (2.9)$$

respectively. The terms v and w in (2.9) are positively scaled left and right eigenvectors of A corresponding to the asymptotic growth rate of A and v_{\min} and v_{\max} are the smallest and largest entries of v respectively. We refer the reader to Stott et al. (2011) for full details. The upshot is that when $\underline{x}_0, \bar{x}_0 \geq 0$, for large t the population density is bounded by

$$\lambda^t \underline{\rho}_\infty \|\underline{x}_0\|_1 + \|(I - A)^{-1} d_m\|_1 \leq \|x(t)\|_1 \leq \lambda^t \bar{\rho}_\infty \|\bar{x}_0\|_1 + \|(I - A)^{-1} d_M\|_1. \quad (2.10)$$

As an illustrative example, we have graphed sample upper and lower bounds in Figure 1(iii) below. In Figures 1(i), 1(ii) we have highlighted the two decompositions of these bounds, as described by (2.5) and (2.7) for the upper bound (respectively (2.5) and (2.8) for the lower bound).

- Figure 1(i) contains $A^t x_0$ plotted as a solid line and the time–varying components $(I - A)^{-1}(I - A^t)d_m$ and $(I - A)^{-1}(I - A^t)d_M$ in squares and circles respectively. These are the components of (2.5). Without immigration the population density $A^t x_0$ is converging to zero.
- Figure 1(ii) contains $A^t \bar{x}_0$ and $A^t \underline{x}_0$ plotted in solid–circles and solid–squared respectively and constant terms $(I - A)^{-1}d_M$ and $(I - A)^{-1}d_m$ plotted in dashed lines. These are the components of (2.7) and (2.8).

The sums of the lines in Figures 1(i), 1(ii) are equal and form the bounds in (2.5) which are plotted in Figure 1(iii). The population density is bounded between the solid–circled and solid–squared lines. Crucially, it is evident that for small times the bounds are dominated by the transient behaviour of $A^t \bar{x}_0$ and $A^t \underline{x}_0$ and, as $\lambda < 1$, for large t the terms $(I - A)^{-1}d_M$ and $(I - A)^{-1}d_m$ dominate. These latter terms provide asymptotic bounds for the population.

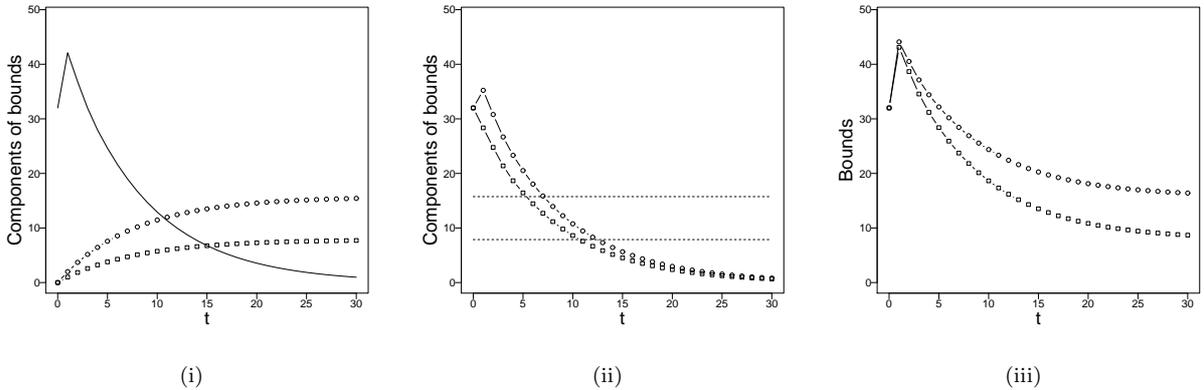


Figure 1: Sample population bounds and their decompositions. See the main text for a detailed description.

Remark 2.1. [(i)]

1. Although the above bounds give estimates of how large or small components of the population can be, we highlight that these bounds *are achieved* for constant immigration $d(t) = d_M$ or $d(t) = d_m$ for all t . These are the most extreme inputs permitted in this framework.
2. When $d_m = 0$ then the lower bounds for $x(t)$ in (2.5) and (2.8) collapse to $A^t x(0)$, that is, we learn nothing new. However, in general this by no means ensures that the population dies out. Here one would need to use specific (for example, probabilistic) information about the immigration terms $\{d(j)\}_{j=0}^t$ to derive the likelihood of the population $x(t+1)$ dipping below arbitrarily small population densities.
3. The upper bounds on the population are independent of the minimal immigration magnitude d_m , and similarly the lower bounds are independent of the maximal immigration magnitude d_M . Such an observation should be used in informing management decisions. For example, for a modelled population where conservation is the goal, efforts should be directed to making d_m as large as possible. Conversely, when seeking to manage for an invasive species; limiting how large d_M can be is desirable. In general, the closer d_m and d_M are, the tighter the envelope of population projections.

2.3 Structured immigration and outputs

Tighter bounds in (2.4)–(2.8) can be obtained when more information about immigration is available. So far we have been considering unstructured immigration. Structured immigration is accommodated by replacing $d(t)$ in (1.1) by $b\delta(t)$, where $\delta(t) \in \mathbb{R}$ is a (possibly unknown) scalar (denoting magnitude) and $b \in \mathbb{R}^N$ is a known nonnegative vector (denoting direction). For example, immigration into the first stage class of a matrix PPM with five stages is given by

$$b = [1 \ 0 \ 0 \ 0 \ 0]^T.$$

The condition (1.2) is replaced by

$$\delta_m \leq \delta(t) \leq \delta_M, \quad t = 0, 1, 2, \dots, \quad (2.11)$$

so that the fixed scalars δ_m and δ_M determine the interval of immigration magnitudes. To make the modifications to the bounds presented so far the terms $d(t)$, d_m and d_M are replaced by $\delta(t)b$, $\delta_m b$ and $\delta_M b$ respectively. For example, (2.7) and (2.8) become

$$A^t \underline{x}_0 + \delta_m (I - A)^{-1} b \leq x(t) \leq A^t \bar{x}_0 + \delta_M (I - A)^{-1} b, \quad t = 0, 1, 2, \dots.$$

Taking the above suggestions into consideration, the model (1.1) can be extended to accommodate structured immigration and an *observation* $y(t)$:

$$\left. \begin{aligned} x(t+1) &= Ax(t) + b\delta(t), & x(0) &= x_0 \\ y(t) &= Cx(t), \end{aligned} \right\} \quad t = 0, 1, 2, \dots \quad (2.12)$$

The symbol C in (2.12) denotes a M by N matrix, which includes the special case when $C = c^T$ is a row vector so that $y(t) = c^T x(t)$ is a scalar. In systems and control, the term y is called an output or measurement of (2.12) and is a linear combination of the components of the population $x(t)$. For example, if measurements of the i^{th} stage class of a population are taken then $C = c^T$ is given by

$$c^T = \underbrace{[0 \ \dots \ 0 \ 1 \ 0 \ \dots \ 0]}_{i^{\text{th}} \text{ entry equal to one}}, \quad \text{so that } y(t) = c^T x(t) = x_i(t).$$

Similarly, if total population abundance, $\|x(t)\|_1$, is measured at each time-step t then $C = [1 \ \dots \ 1]$ so that

$$y(t) = [1 \ \dots \ 1] x(t) = \sum_{i=1}^N x_i(t) = \|x(t)\|_1. \quad (2.13)$$

The inclusion of C allows us to see how different aspects of the population change in the presence of immigration $d(\cdot)$. If C is nonnegative then it respects the inequalities derived thus far. So for structured immigration, bounded as in (2.11), we have

$$CA^t x_0 + \delta_m \sum_{j=0}^{t-1} CA^j b \leq y(t) \leq CA^t x_0 + \delta_M \sum_{j=0}^{t-1} CA^j b, \quad (2.14)$$

and as $\lambda < 1$ this gives

$$CA^t x_0 + \delta_m C(I - A)^{-1}(I - A^t)b \leq y(t) \leq CA^t x_0 + \delta_M C(I - A)^{-1}(I - A^t)b. \quad (2.15)$$

Similarly, the bounds (2.7) and (2.8) become

$$CA^t \underline{x}_0 + \delta_m C(I - A)^{-1}b \leq y(t) \leq CA^t \bar{x}_0 + \delta_M C(I - A)^{-1}b. \quad (2.16)$$

The estimates (2.14)–(2.16) are valid for all $t = 0, 1, 2, \dots$.

2.4 Incorporating uncertainty

Ecological models are inherently uncertain and are prone to both environmental and demographic (through vital rates) stochasticity (Tuljapurkar, 1990). Furthermore, the matrices used in population projection models are usually fitted statistically to data (see Caswell (2001, Chapter 6) and the references therein) which leads to differences between ‘true’ and modelled vital rates. Such uncertainty is overlooked in (1.1) by using a fixed matrix A .

So how can we incorporate into our framework for handling immigration parametric uncertainty in the matrix specifying the projection model? One approach, identical in spirit to our earlier handling of uncertain, but bounded, immigration is to assume that A is unknown, but to assume that we have known, or estimated, bounds for A so that

$$0 \leq A_m \leq A \leq A_M. \quad (2.17)$$

The matrices A_m and A_M in (2.17) are assumed known. For example, survival rates might not be known precisely but lower and upper bounds on survival might be available. More generally, the condition (2.17) would allow us to capture lower and upper estimates of vital rates. Since $\lambda(A_m) \leq \lambda(A) < 1$ (by, for example, Berman and Plemmons (1979, p.27)), the lower bounds presented thus far now hold with A replaced by A_m . For instance, the lower bound in (2.5) becomes

$$x(t) \geq A_m^t x_0 + (I - A_m)^{-1}(I - A_m^t)d_m. \quad (2.18)$$

If $\lambda(A_M) < 1$, then the upper bounds also hold with A replace by A_M . For example:

$$x(t) \leq A_M^t x_0 + (I - A_M)^{-1}(I - A_M^t)d_M. \quad (2.19)$$

Moreover, we can replace A in (1.1) by a time-dependent matrix $A(t)$ and the bounds (2.18) and (2.19) hold, provided that $A(t)$ satisfies (2.17) for every $t = 0, 1, 2, \dots$.

Analogously to Remark 2.1, the ‘smaller’ the difference between A_m and A_M in (2.17), the tighter the resulting population projection envelope, that is, the better the estimates become. Crucially, however, the above bounds are tight in the sense that if $A = A_m$ or $A = A_M$ for all t then the inequalities in (2.18) and (2.19) are in fact equalities.

2.5 Time- and spatial- averaged behaviour

So far we have been viewing additive immigration in (1.1) as a deterministic, but essentially unknown, process and thus concentrated on establishing bounds for the resulting population which hold for *any* immigration sequence (that is bounded in the sense of (1.2) or (2.11)).

It is possible to take a more stochastic approach and view immigration as a random process so that $d(\cdot)$ is a sequence of random variables and thus so is the population $x(t)$, which itself satisfies a stochastic difference equation (see, for example, Kesten (1973) or Shaikhet (1996)). Such an approach to matrix projection modelling has been addressed in Sykes (1969). In this situation it is natural to ask what are the statistical moments of such a population? Assuming that the sequence $d(\cdot) = b\delta(\cdot)$ is IID (independent and identically distributed) with expected value $\bar{\delta}^*$, we write $z(t) := \mathbb{E}(x(t))$, the expected value of $x(t)$. Using the linearity of expectation we compute that $z(t)$ satisfies the deterministic difference equation

$$\begin{aligned} z(t+1) &= \mathbb{E}(x(t+1)) = \mathbb{E}(Ax(t) + b\delta(t)) = A\mathbb{E}(x(t)) + b\mathbb{E}(\delta(t)) \\ &= Az(t) + b\bar{\delta}^*, \quad t = 0, 1, 2, \dots, \end{aligned} \quad (2.20)$$

with asymptotic limit

$$\lim_{t \rightarrow \infty} \mathbb{E}(x(t)) = (I - A)^{-1}b\bar{\delta}^*. \quad (2.21)$$

Notice that the dynamics (2.20) governing $\mathbb{E}(x(t))$ (the expectation of the PPM with random immigration) are in fact the same as those governing the population subject to constant immigration taking its expected value (the PPM subject to expected immigration). That is where we replace $d(t) = b\delta(t)$ in (1.1) by its expected value for every t . As such the limit (2.21) is the same for both populations.

The expected values $\mathbb{E}(x(t))$ considered so far are averages taken over space, that is the range of values the random variable can take at each time-step. An alternative is to compute the time-average of a single realisation of the population over t steps, which is defined by

$$\bar{x}(t) = \frac{1}{t} \sum_{j=0}^{t-1} x(j),$$

and is itself a random variable. The sequence of time-averages of the population satisfy a difference relation, which we do not give here but it is straightforward to demonstrate, invoking the Strong Law of Large Numbers, that the time and spatial averages coincide asymptotically (almost surely), so that

$$\lim_{t \rightarrow \infty} \bar{x}(t) = (I - A)^{-1}b\bar{\delta}^* = \lim_{t \rightarrow \infty} \mathbb{E}(x(t)). \quad (2.22)$$

The first equality in (2.22) can alternatively be seen as a strong Ergodic Theorem. These conclusions do not mirror those of Gonzalez and Holt (2002), Holt et al. (2003), Roy et al. (2005), Matthews and Gonzalez (2007), where persistence of declining and sink populations subject to immigration has also been studied both theoretically and experimentally. There it is established that, broadly speaking, time-varying vital rates and constant immigration give rise to populations that are in expectation larger than the mean model would suggest. This so-called ‘inflationary effect’ is further exaggerated by positive autocorrelation in the vital rates. We refer the reader to the above mentioned articles for more details. We believe that the crucial difference between the differing conclusions is that the uncertainty in the models considered here appears additively in the form of unknown immigration, as opposed to multiplicatively in the form of time-varying vital rates.

We finish this section by commenting on the second moments of the population, when viewed as a sequence of random variables. A more involved calculation gives that the covariance matrix of $x(t)$ converges to

$$C_\infty - (\bar{\delta})^2(I - A)^{-1}bb^T(I - A)^{-T},$$

as $t \rightarrow \infty$, where C_∞ is the unique positive definite solution of

$$C_\infty = AC_\infty A^T + (\bar{\delta})^2 b^T (I - A)^{-T} A^T + (\bar{\delta})^2 A (I - A)^{-1} b^T + ((\bar{\delta})^2 - \sigma^2) bb^T,$$

(see Ran and Reurings (2002)) and $\sigma^2 = \text{var}(d(t))$. The matrix C_∞ can be found as the limit of the iterative scheme

$$C(t+1) = AC(t)A^T + \bar{\delta}bz^T(t)A^T + \bar{\delta}Az(t)b^T + ((\bar{\delta})^2 - \sigma^2)bb^T \quad t = 0, 1, 2, \dots,$$

where recall that $z(t) = \mathbb{E}(x(t))$. In particular, the variance of $x(t)$ converges to a finite and computable quantity.

3 Examples

Example 3.1. The paper by Kareiva et al. (2000) considers the management of a declining population of Chinook Salmon (*Oncorhynchus tshawytscha*) in the Columbia River Basin of North America. Part of this species' decline is attributed to damming of the river basin, and the resulting prevention of migration. For example, the Hell's Canyon Dam has completely blocked salmon passage and eliminated much spawning habitat. While increasing the Chinook Salmon population may take many simultaneous and interconnected intervention strategies, we consider how the population might change subject to a conservation measure or ecological change leading to reintroduced immigration into the population. We will use the model presented in Kareiva et al. (2000), which is a 5×5 matrix PPM for female salmon, with each stage denoting age in years and is given by

$$A = \begin{bmatrix} 0 & 0 & 0.326 & 5.02 & 39.7 \\ 0.0131 & 0 & 0 & 0 & 0 \\ 0 & 0.8 & 0 & 0 & 0 \\ 0 & 0 & 0.790 & 0 & 0 \\ 0 & 0 & 0 & 0.673 & 0 \end{bmatrix}, \quad (3.1)$$

with dominant eigenvalue $\lambda = 0.7602 < 1$. We consider adding immigration into the largest stage class; spawning females, so that

$$b = [0 \ 0 \ 0 \ 0 \ 1]^T. \quad (3.2)$$

Kareiva et al. (2000) does not provide estimates of a suitable initial population x_0 and so for our simulations we assume that the population is initially at the stable distribution

$$x_0 = [93.3932 \ 1.6064 \ 1.6905 \ 1.7559 \ 1.5540]^T, \quad (3.3)$$

(the positive right eigenvector corresponding to the eigenvalue λ) when immigration is included. Again, in absence of suitable data, we have normalised w so that its components sum to 100 (so that the components of $x(t)$ correspond to percentages of population density relative to the initial population distribution). In this case

$$(I - A)^{-1}b = [53.9849 \ 0.7059 \ 0.5647 \ 0.4459 \ 1.3000]^T, \quad (3.4)$$

and therefore $\bar{x}_0 := x_0 - (I - A)^{-1}d_M \geq 0$ if $\delta_M \leq 1.20$, that is, at most 1.2% of the initial population density immigrates in each stage.

Figure 2 contains the bounds (2.5) for this example plotted with two sample projections $x(t)$ subject to uniformly distributed and periodic immigration with values bounded between $\delta_m = 1.6$ and $\delta_M = 10$. The simulations are intended to be illustrative and the immigration bounds have been chosen with this in mind. The aboved calculated threshold $\delta_M = 1.2$ is not used as we deem it too small to effectively illustrate the material presented. As noted in Remark 2.1 (i), the bounds of the envelope are attained for sustained extremal (maximal or minimal) immigration, so the estimates are sharp. Note that although qualitatively the bounded regions are very similar in appearance we draw attention to the hugely variable scales on the y -axes. This is to be expected as the term $(I - A)^{-1}b$ in (3.4) that appears in the bounds in (2.5) is biased towards the first stage class. Intuitively, since immigration acts on the most reproductive stage class, even small additions will result in a substantially larger juvenile population in the next time-step. Note also that the projected trajectories and the bounds coincide in Figure 2 (b)–(e) for the first few time-steps. This is again because immigration is acting on the final stage-class, the Leslie matrix (Leslie, 1945) structure of A ensures a delay before the effect of these immigrants is felt in the earlier stage classes.

For the random immigration considered here large regions of the envelope are 'visited' by the resulting population trajectories. We have also plotted the population projection subject to the spatial averaged mean of immigration, in this instance $\delta(t) = \delta^* = \frac{\delta_m + \delta_M}{2}$, as immigration has been assumed uniformly distributed. For such constant immigration it follows that (as in (2.21)) $x(t)$ converges to

$$\begin{aligned} \delta^*(I - A)^{-1}b &= 5.8 [53.9849 \ 0.7059 \ 0.5647 \ 0.4459 \ 1.3000]^T \\ &= [313.1123 \ 4.0942 \ 3.2753 \ 2.5862 \ 7.5400]^T, \end{aligned}$$

with $\|\delta^*(I - A)^{-1}b\|_1 = 330.6080$, corresponding to over 200% increase in population density relative to that of the original population.

The bounds as presented can be used to help inform management decisions. For example, what is the minimum per time-step immigration level that maintains an asymptotic population density no smaller than that of the original population? Recall that asymptotically $x(t)$ is bounded from below by

$$(I - A)^{-1}b\tilde{\delta}_m,$$

where $\tilde{\delta}_m$ is the to-be-determined lower bound for immigration. Insisting that asymptotic population density is at least that of the original population amounts to ensuring that $\|(I - A)^{-1}b\tilde{\delta}_m\|_1 \geq 100$ so that with $\mathbb{1}^T = [1 \ 1 \ 1 \ 1 \ 1]$

$$\mathbb{1}^T(I - A)^{-1}b\tilde{\delta}_m \geq 100 \quad \iff \quad \tilde{\delta}_m \geq \frac{100}{\mathbb{1}^T(I - A)^{-1}b} = 1.7543.$$

Alternatively, note that at stable distribution, the adult stage class (stage class five) comprises roughly 1.6% of the population structure. What is the minimum per time-step immigration level that asymptotically doubles this proportion? Such a requirement amounts to choosing $\tilde{\delta}_m$ now so that

$$b^T(I - A)^{-1}b\tilde{\delta}_m \geq 3.2 \quad \iff \quad \tilde{\delta}_m \geq \frac{3.2}{b^T(I - A)^{-1}b} = 2.4615.$$

Such a minimum level of immigration ensures that the asymptotic population structure is no smaller than

$$(I - A)^{-1}b\tilde{\delta}_m = [132.8840 \ 1.7376 \ 1.3900 \ 1.0976 \ 3.2000]^T,$$

which note that has total density $\|(I - A)^{-1}b\tilde{\delta}_m\|_1 = 140.3090$, that is roughly 40% larger than the initial population density.

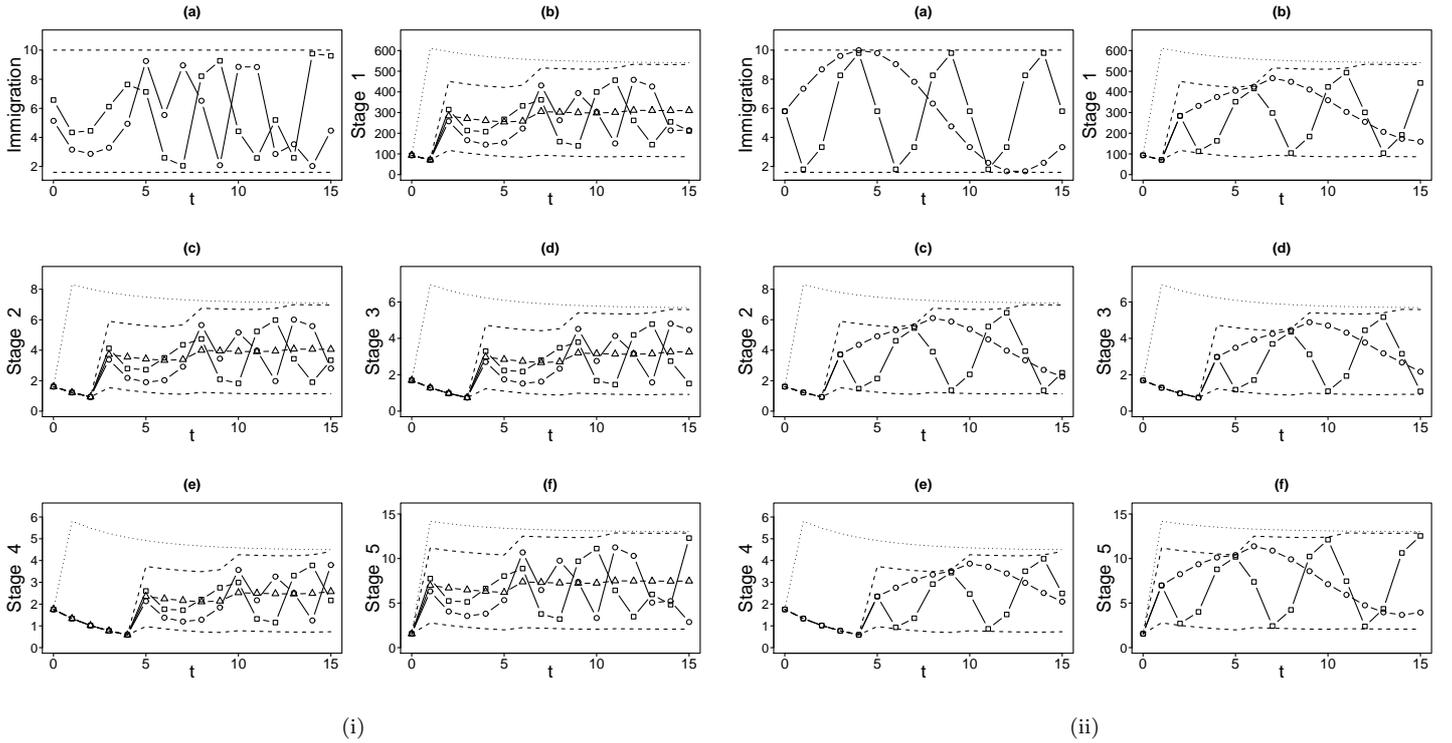


Figure 2: Results of Example 3.1. (i) Uniformly distributed immigration. (ii) Periodic immigration. In each subplot **(a)** contains two sample immigration trajectories and the lines $y = \delta_m = 1.6$ and $y = \delta_M = 10$. The resulting projected stages 1–5 are plotted in **(b)**–**(f)** respectively. The dashed and dotted lines are the bounds (2.5) and (2.6) respectively. The lines in (i) **(b)**–**(f)** with triangles are the stages of the population subject to the mean immigration $\delta(t) = \frac{\delta_m + \delta_M}{2}$ for all $t = 0, 1, 2, \dots$.

Example 3.2. Kottas (2012) considers the viability of endangered populations of blowout penstemon (*Penstemon haydenii*), a perennial plant species that is endemic to the Sandhills of Nebraska and the northeast Great Divide Basin in Wyoming. Blowout penstemon’s habitat is limited to eroded areas on hillsides or depressions, called blowouts. The viability of penstemon is dependent on blowout suitability, particularly the formation of vegetative cover, as above-ground penstemon cannot persist in an environment consisting largely of grasses that have compact growth and an efficient root system. Until the beginning of the 20th century traditional agriculture allowed penstemon to persist by eliminating this vegetative cover and cultivating additional blowout formation.

As a grazing economy replaced traditional agriculture, vegetative cover began to increase and the environment for penstemon began to decrease. Additionally, factors such as reduced fire frequency lead a reduction in bare, blowing sand, restricting penstemon to isolated patches with decreasing suitability, with little opportunity for remaining viable seeds to migrate to a different habitat. Since blowout penstemon populations are enhanced by transplanting seeds and seedlings into previously unoccupied blowouts, which has increased the number of plants and the number of blowout populations overall, we are especially concerned with variability in factors influencing blowout formation. This variability in blowout formation is reflected in the immigration vector $d(t) = \delta(t)b$, with b given by (3.5).

Since a dispersed population will be initially concentrated exclusively on seeds and seedlings we will assume in this example that dispersed populations are exclusively leftover viable seeds from a previous environment. Thus, the vector b will take the form

$$b = [1 \quad 0 \quad 0 \quad 0]^T. \quad (3.5)$$

The projection matrix for blowout penstemon in Kottas (2012) is given by

$$A = \begin{bmatrix} 0.003 & 0 & 0.167 & 0 \\ 0.008 & 0.451 & 1.348 & 0 \\ 0 & 0.146 & 0.471 & 0.195 \\ 0 & 0 & 0.210 & 0.334 \end{bmatrix}, \quad (3.6)$$

with $\lambda = 0.94 < 1$. We consider the scenario where a recently-formed and previously unoccupied blowout is colonised by seeds from other dispersing penstemon populations after time $t = 0$, with the number of colonising seeds varying from $\delta_m = 1.5 \times 10^5$ and $\delta_M = 1.5 \times 10^7$ (the reason for these values will become apparent in a subsequent paragraph). Thus, the initial population vector x_0 in this case study is equal to the zero vector. In Figure 3 we plot the population in each demographic stage (seeds, seedlings, flowering adults and vegetative adults) for two different immigration trajectories and immigration sequences coming from two different processes. The first process models IID uniform random immigration with mean $\frac{\delta_m + \delta_M}{2}$. The second process models deterministic periodic immigration with the same mean. Note that, in both cases, the variability in the last three demographic stages (Figure 3 (c)–(e)) is rather small, mimicking that of the PPM with constant (averaged) immigration, while the variability in the seed bank (Figure 3 (b)), is large. As in Example 3.1, this is to be expected, as the term

$$(I - A)^{-1}b = [1.0063 \quad 0.0629 \quad 0.0020 \quad 0.0062]^T,$$

is dominated by the seed and seedling stages of the population. Similarly with Example 3.1, the population envelope can be largely filled, depending on the immigration that is assumed to occur. Notice, however, that fluctuations in population density are dissipating as one moves from looking at the seed bank to the seedling, flowering adult and vegetative adult stages, respectively. This result provides a noticeable contrast with the result in Example 3.1. There the effects of a particular immigration regime is qualitatively apparent throughout the stage space. This is because immigration enters into the population at a reproductive stage, while in the examples illustrated in Figure 3, immigration enters into the population at a non-reproductive stage, and thus the impact of immigration on other stages is slower and less pronounced.

In the same vein as in Example 3.1, the bounds derived in this manuscript can be used to help establish some benchmarks needed for population restoration and/or conservation. Kottas (2012, pp.18–20) outlines an approved set of specific criteria that must be met for penstemon to be reclassified from

endangered to threatened. These criteria included having a collection of populations “each with a minimum of 300 plants at low points of population fluctuations, that are documented to be naturally-reproducing and self-sustaining”. In our framework, satisfying this criterion would amount finding δ_m so that

$$c^T(I - A)^{-1}b\delta_m \geq 300,$$

where $c^T = [0 \ 0 \ 1 \ 0]$. Since $c^T(I - A)^{-1}b = 0.0020$ the minimum immigration level δ_m needs to exceed 1.5×10^5 seeds in order to ensure a population consisting of at least 300 naturally-reproducing and self-sustaining plants.

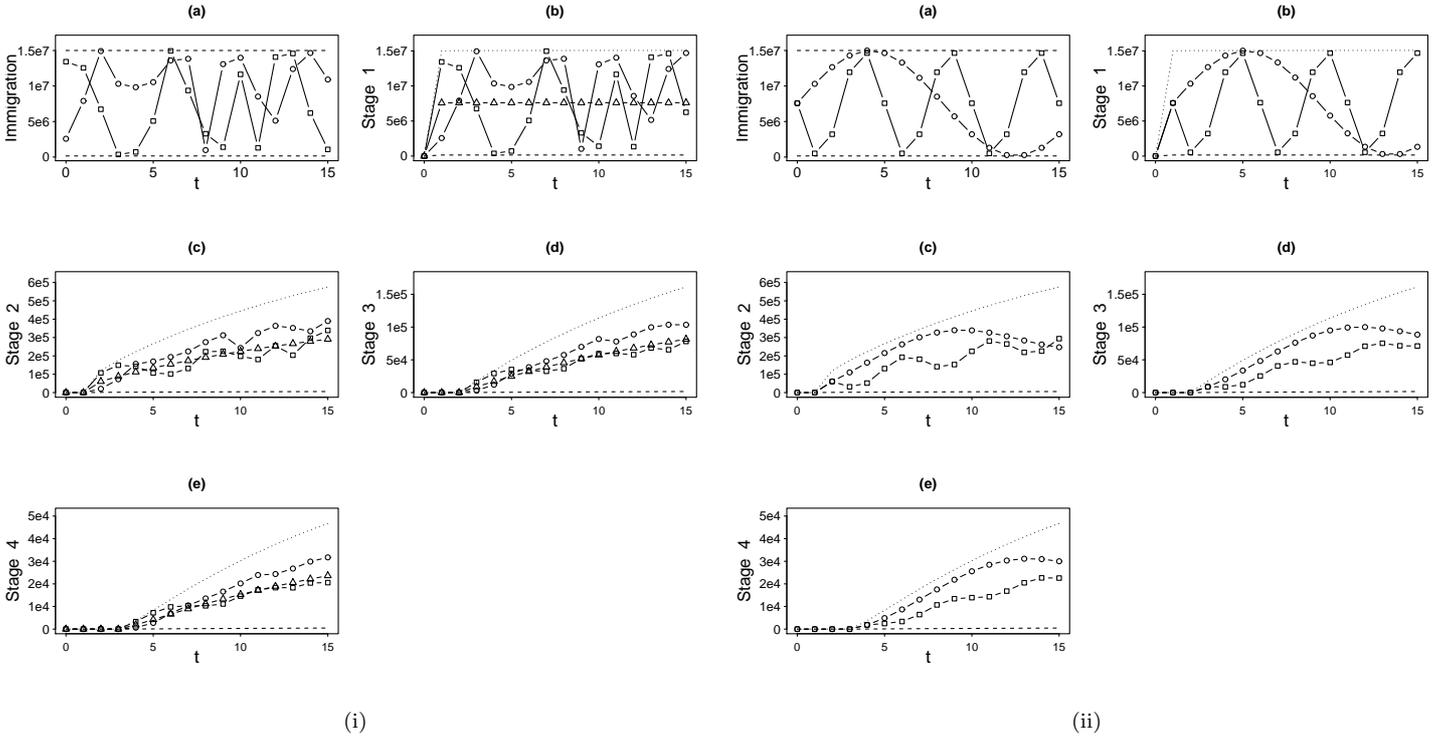


Figure 3: Results of Example 3.2. (i) Uniformly distributed immigration. (ii) Periodic immigration. In each subplot (a) contains two sample immigration trajectories and the lines $y = \delta_m = 1.5 \times 10^5$ and $y = \delta_M = 1.5 \times 10^7$. The resulting projected seed bank, seedling, flowering adult and vegetative adult population stages are plotted in (b)–(e) respectively. The dashed and dotted lines are the bounds (2.5) and (2.6) respectively. The lines in (i) (b)–(e) with triangles are the stages of the population subject to the mean immigration $\delta(t) = \frac{\delta_m + \delta_M}{2}$ for all $t = 0, 1, 2, \dots$

4 Discussion

The dynamics of stage-structured populations can display diverse and complicated behaviour over time, owing to the influence of transient amplification and attenuation (Stott et al., 2011); phenomena that is further exaggerated by immigration. When immigration is stage structured and time-varying, but crucially bounded, one approach to describe the resulting population envelope is to simulate repeatedly over a range of parameter values and derive statistical moments (means, variances) of growth rates and future densities (Engen et al., 1998; Tenhumberg et al., 2008). Such an approach is computationally intensive – in a five stage model the range of unstructured immigration is the five dimensional hypercube $[\delta_m, \delta_M]^5$. To project just 1000 simulations along each of the “edges” of the hypercube requires $1000^5 = 10^{15}$ simulations, and even this will still not fully describe the possible range of population trajectories. The alternative approach we have taken is to describe, analytically, the upper and lower bounds of the resulting population projection envelope. We have appealed to the philosophy of systems and control theory and used the assumed linearity (that is, assumed density independence) and componentwise nonnegativity of the model to determine bounds for future population densities and future densities of specific demographic stages.

How might the bounds derived be useful? The first important observation is that immigration in the present has impacts for the future of a population. As noted in Example 1, immigration into the adult stage class provides a substantial boost to future generations via the offspring of this reproductive stage. The results presented provide tools for describing long term effects of sustained immigration. Second, the formulae provide estimates for “best” and “worst” case scenarios that can be used as guides for management strategies. In emergency situations, conservation biologists often rely on captive rearing, translocations and species reintroductions, to bolster or recover populations of declining or locally-extinct species (Sarrazin and Barbault, 1996). Such conservation programmes are expensive, laborious and risk the welfare of endangered species. Hence we consider it important to forecast the future dynamics resulting from conservation interventions, and optimise reintroduction campaigns to maximise the probability of long-term population persistence. Conservation strategists might consider time-varying reintroductions, or focus on specific lifestages of the endangered organism, to exploit transient dynamics and best achieve their goals. Trade-offs between the magnitude, structure and timing of reintroductions might help to design management programmes, or adjust them adaptively, to help deal with financial or logistical constraints (Martínez-Abraín et al., 2011).

The envelope of trajectories of disturbed sink populations can also be useful for the design of biological control strategies. Biocontrol agents are introduced to crops, greenhouses or natural environments to control pest, weed or invasive populations. It has been argued that when such a strategy works, the biocontrol agents themselves are destined to decline to local extinction (Shea and Possingham, 2000). It is conceivable, however, that as biocontrol agent numbers reach low levels their efficacy is sufficiently reduced to allow the pest to persist or for new outbreaks of the pest occur. The bounds derived could help inform release programmes by predicting the required additional biocontrol agent to avoid their local extinction over a given time period. As with conservation management strategies, exploration of structured introductions could help to maximise the persistence of the biocontrol agents alongside the minimisation of the costs of introduction or satisfaction of logistical constraints.

We have additionally extended the treatment of immigration on sink populations to the case when there is uncertainty or density or time dependence in the underlying demographic parameters. In reality, environmental fluctuations will influence not just the magnitude of immigration but also the demographic parameters of the ambient population (Tuljapurkar and Haridas, 2006) and thus machinery to handle such stochasticity is required. As demonstrated, the material presented here extends to such a situation when an estimate on the size of the perturbations is known. As with all robustness type tools, the price we have to pay for greater model uncertainty is more conservative (that is, wider) estimates of population trajectories.

Defining and refining these bounds is important for our understanding of population ecology and life-history evolution. The bounds on sink populations with additive immigration can be used to measure or forecast the contribution of subpopulations to the global dynamics of metapopulations (Kawecki and

Holt, 2002). This can aid the analysis of patterns in the evolution of dispersal strategies. Dispersive species, for example, might benefit from focussing their dispersal into lifestages that contribute most to transient amplification, yielding short term population growth even when long-term decline is inevitable (Tenhumberg et al., 2009). Such evolution to exploit transient dynamics might be called “making the best of a bad job”, whereby dispersing lifestages take a gamble that environmental conditions will improve to allow long-term population increase before the sink population goes extinct. According to our bounds, repeated additive immigration can reverse the decline of sink populations. This phenomenon was also seen in Gonzalez and Holt (2002); Holt et al. (2003); Roy et al. (2005) and Matthews and Gonzalez (2007) for models with uncertain (and often autocorrelated) life-history traits and constant immigration. Our results additionally show that the demographic structure of these ingress events can make a large difference to the resulting envelope of population densities. Microparasites could also evolve to exploit positive growth via additive immigration: even though within-host dynamics, or between-host transmission, are predicted to decline in the long-term, microparasites could persist sufficiently long, thanks to a combination of transient amplification and immigration, to allow adaptation to the “sink” host population and subsequent disease emergence (Holt and Gomulkiewicz, 1997; Antia et al., 2003; Benmayor et al., 2009).

Acknowledgement

Chris Guiver is fully supported and Dave Hodgson, Richard Rebarber and Stuart Townley are partially supported by EPSRC grant EP/I019456/1.

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