



Bounds on the dynamics of sink populations with noisy immigration



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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*).

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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 pro-

vide a relevant modelling framework, and analyse populations in this framework.

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 non-negative 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

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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, non-negative 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 non-negative 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 non-negative.

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 non-negative inputs only make the population larger. Since $A \geq 0$ and $\lambda < 1$ we have

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

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 other 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

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