



Transient population dynamics and short-term sensitivity analysis of matrix population models

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Abstract

Demographic analysis methodologies which consider the transient dynamics of a population promise to be highly relevant for population conservation and management, but the present methods of analysis are still in the early stages of being developed. The methods require a knowledge of a population's initial stage-structure, and produce output which is complicated, and difficult to describe succinctly. This paper investigates whether the initial stage-structure is always required in order to obtain reliable information on the transient population dynamics. The paper also presents new methods for succinctly presenting the data from these near-term demographic analyses. The work of Fox and Gurevitch [Am. Naturalist 156 (2000) 242] is extended by deriving an analytical formula which decomposes their near-term sensitivity into two components: one which does not require the populations initial stage-structure to be measured, and one which does. This decomposition is used to estimate the sensitivity of the analysis to the initial population stage structure, without a knowledge of the population structure. The near-term sensitivity analysis is extended to look at several measures for the near-term sensitivity of population growth rate. These new measures allow the information contained in the analysis to be condensed, and for a comparison to be made between near-term and asymptotic sensitivity analyses. The methods are demonstrated by analysing empirical data on the cactus *Coryphantha robbinsorum*.

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1. Introduction

Demographic analysis is increasingly being used as a quantitative tool for guiding the management and conservation of populations (Mills et al., 1999; Bradbury et al., 2001). An important class of analysis methods uses population matrix models (Caswell, 2001). For example, matrix models have been used to inform the management of loggerhead sea turtles (Crowder et al., 1994; Heppell et al., 1996), guide the introduction of biological-control species (Křivan and Havelka, 2000), and to study the causes of the moas'

extinction (Holdaway and Jacomb, 2000). Whilst the majority of the literature on matrix population models considers their long-term, asymptotic population dynamics, this paper considers the analysis of their transient behaviour, and its application for conservation and population management.

The standard demographic analysis of a matrix model (Caswell, 2001) uses a time-scale which is intrinsically long-term, because it always considers populations that have reached their asymptotic growth rate. If carefully applied this asymptotic analysis is a useful and simple tool for guiding management (Mills et al., 1999). However, management and conservation issues are often concerned with time-scales that are short-term, and populations which need not have

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reached their asymptotic behaviour, so additional analysis methodologies which allow for short-term, transient effects would be particularly valuable. This issue was formally raised by Fox and Gurevitch (2000), who highlighted the mismatch between population biologists, who have moved away from a deterministic, equilibrium view of populations, and the widely used analysis methodologies, which predominantly estimate long-term, equilibrium quantities. The development of practical analysis methodologies which address the short-term dynamics of non-equilibrium populations would provide valuable guidance for many management issues.

Traditionally the damping ratio has been used to measure a population's rate of convergence towards asymptotic behaviour (Caswell, 2001), and several approaches have been proposed for measuring the distance between a population's stage distribution and its stable stage distribution (Keyfitz, 1968; Cohen, 1979). These measures can indicate whether an asymptotic analysis is applicable, but have not been used to help analyse the short-term, transient behaviour of a population. A general framework for analysing transient dynamics of non-equilibrium populations was presented by Fox and Gurevitch (2000), who called their approach 'near-term demographic analysis'. Near-term demographic analysis is a natural extension of the standard asymptotic analysis, and provides a general theoretical basis for short-term demographic analysis. Compared with the usual asymptotic analysis near-term demographic analysis has two main drawbacks: it requires more input data in the form of the initial stage-structure of the population, and its results are more complex to interpret. These additional complexities are, to some extent, unavoidable. The complex results are not readily comparable with the standard asymptotic analysis, require an understanding of the methodology for their careful analysis, and make it difficult or inappropriate to extract summary conclusions. The requirement of additional data means that existing data sets cannot be reanalysed, and could make data collection too costly or time consuming for a practical management project.

This paper simplifies the near-term demographic analysis of Fox and Gurevitch (2000) by dividing the method into two components: one that is *independent* of a population's initial stage-structure, yielding near-term demographic information without the need

for additional data, and one that is *linearly dependent* upon the initial stage-structure of the population. This decomposition clearly shows how important an accurate knowledge of the population's initial stage-structure is for the accuracy of the near-term analysis. Finally, the results of the near-term analysis are expressed in terms of population growth rates, which allows the complex information from the analysis to be condensed into a succinct form. Expressing the sensitivities in terms of population growth rates allows the near-term analysis to be directly compared with the standard asymptotic sensitivity analysis.

2. Decomposing near-term sensitivity analysis

The time evolution of a stage-structured population with constant demographic parameters is described by:

$$\mathbf{n}(t) = \mathbf{A}^t \mathbf{n}(0) \quad (1)$$

where \mathbf{A} is the Leslie matrix containing the demographic parameters, $\mathbf{n}(0)$ the initial population structure and $\mathbf{n}(t)$ is the population structure at time t (Caswell, 2001). The standard analysis of a population described by Eq. (1) calculates the sensitivity of the growth rate of $\mathbf{n}(t)$ to changes in \mathbf{A} in the limit as t becomes infinite. Since the analysis looks at the limit as t becomes infinite it looks at the long-term, asymptotic behaviour of a population. A brief review of the standard asymptotic analysis can be found in Appendix B, whilst the conventions and notation used throughout this paper are explained in Appendix A and Table 1.

The near-term demographic analysis of Fox and Gurevitch (2000) calculates the sensitivity of the population structure to changes in the elements of the Leslie matrix a time t after the change. It therefore looks at the transient effects of a perturbation as well as the asymptotic behaviour. A transient analysis differs from an asymptotic analysis in two respects: firstly the effect of a perturbation can be followed from the instant the perturbation took place until the point at which the population has approached its new asymptotic growth rate, and secondly the initial population, prior to the perturbation, need not have a stable stage structure. As the time after the perturbation, t , increases the results of the near-term analysis approach those of an asymp-

Table 1
Summary of the notation used in the paper

Symbol	Description
A	Leslie matrix for a population
a_{kl}	An element of A
λ_i	The i th eigenvalue of A , ordered such that $\lambda_1 > \lambda_2 > \dots$
$\mathbf{w}^{(i)}$	The i th right eigenvector of A
W	Matrix of right eigenvectors, where each column is an eigenvector
$\mathbf{v}^{(i)}$	The i th left eigenvector of A
V	Matrix of left eigenvectors, where each column is an eigenvector
$\mathbf{n}(t)$	The population structure at time t
$\mathbf{n}(0)$	The initial population structure
$n_j(t)$	The j th component of $\mathbf{n}(t)$
$n(t) = \sum_j n_j(t)$	The total population size at time t
$c_i = \langle \mathbf{v}^{(i)}, \mathbf{n}(0) \rangle$	A measure of the proportion of $\mathbf{w}^{(i)}$ along $\mathbf{n}(0)$
$\mathbf{n}^{(i)}(t) = c_i \lambda_i^t \mathbf{w}^{(i)}$	The component of $\mathbf{n}(t)$ along $\mathbf{w}^{(i)}$
$n_j^{(i)}(t)$	The j th component of $\mathbf{n}^{(i)}(t)$
\bar{x}	The complex conjugate of the scalar x
\mathbf{x}^T	The transpose of vector \mathbf{x}
\mathbf{x}^*	The complex conjugate transpose of vector \mathbf{x}
$\ \mathbf{x}\ = \sum_i x_i $	The absolute sum of elements of vector \mathbf{x} (the L1-norm of \mathbf{x})
$\langle \mathbf{x}, \mathbf{y} \rangle = \sum_i \bar{x}_i y_i$	The scalar product of vectors \mathbf{x} and \mathbf{y}
$\mathbf{x}\mathbf{y} \equiv \mathbf{x} \otimes \mathbf{y}^*$	The vector direct product of vectors \mathbf{x} and \mathbf{y} giving a matrix $M_{ij} = x_i \bar{y}_j$

otic sensitivity analysis. The near-term sensitivity can be written as,

$$\frac{\partial \mathbf{n}(t)}{\partial a_{kl}} = \sum_i \frac{\partial \mathbf{n}^{(i)}(t)}{\partial a_{kl}} \tag{2}$$

where

$$\frac{\partial \mathbf{n}^{(i)}(t)}{\partial a_{kl}} = \frac{\partial c_i}{\partial a_{kl}} \lambda_i^t \mathbf{w}^{(i)} + c_i t \lambda_i^{t-1} \frac{\partial \lambda_i}{\partial a_{kl}} \mathbf{w}^{(i)} + c_i \lambda_i^t \frac{\partial \mathbf{w}^{(i)}}{\partial a_{kl}} \tag{3}$$

and c_i is the proportion of $\mathbf{n}(0)$ which lies along the i th eigenvector. Expressions for c_i and its derivative are given by Eqs. (A.6) and (A.7), respectively.

One practical difficulty with near-term demographic analysis is that it requires the initial population structure, $\mathbf{n}(0)$, to be known (this additional information is required in order to calculate the coefficient c_i). Determining a population’s initial structure would require considerable effort, thus restricting the range of practical applications. However, this view may be overly

pessimistic, because it is not clear how sensitive the results of a near-term demographic analysis are to the initial population structure. If we could calculate this sensitivity we could predict when a detailed knowledge of $\mathbf{n}(0)$ is unnecessary for acceptably reliable results. Near-term analysis could then be usefully applied in a wider set of scenarios without a large increase in the data collection effort.

The sensitivity of the near-term demographic analysis to a population’s stage structure can be quantified by decomposing Eq. (2) into two terms: one which requires no additional data about the initial population structure, and the other which is linearly dependent on data about the initial population structure. The derivation of this decomposition is given in Appendix C, with the result being

$$\frac{\partial \mathbf{n}(t)}{\partial a_{kl}} = \underbrace{S(t) \frac{\mathbf{n}(0)}{\|\mathbf{w}^{(1)}\|}}_{\text{independent of } \mathbf{n}(0)} + \underbrace{\Delta S(t) \Delta \mathbf{n}}_{\text{linearly dependent on } \mathbf{n}(0)} \tag{4}$$

where

$$\Delta \mathbf{n} = \mathbf{n}(0) - \frac{\mathbf{n}(0)}{\|\mathbf{w}^{(1)}\|} \mathbf{w}^{(1)} \tag{5}$$

is the deviation of the initial population structure away from the stable stage structure. The vector $S(t)$ quantifies the contribution that the stable stage structure makes to the transient sensitivity. It is the component of the near-term sensitivity which requires no data about the initial population structure. The matrix $\Delta S(t)$ quantifies the contribution that initial deviations from the stable stage distribution make towards the near-term sensitivity. This matrix describes the component of the near-term sensitivity which requires additional data about the initial population structure. Expressions for these two quantities are derived in Appendix C, with the results being

$$S(t) = t \lambda_1^{t-1} \frac{\partial \lambda_1}{\partial a_{kl}} \mathbf{w}^{(1)} + \sum_{m>1} \frac{\lambda_1^t - \lambda_m^t}{\lambda_1 - \lambda_m} \bar{v}_k^{(m)} w_l^{(1)} \mathbf{w}^{(m)} \tag{6}$$

$$\Delta S(t) = \sum_m t \lambda_m^{t-1} \frac{\partial \lambda_m}{\partial a_{kl}} \mathbf{w}^{(m)} \otimes \mathbf{v}^{(m)*} + \sum_{n \neq m} \frac{\lambda_m^t - \lambda_n^t}{\lambda_m - \lambda_n} \bar{v}_k^{(m)} w_l^{(n)} \mathbf{w}^{(m)} \otimes \mathbf{v}^{(n)*} \tag{7}$$

This result can also be rewritten in terms of the eigenvector components, which will be of use when the

near-term sensitivity of the population growth rate is considered. In this case, the component of Eq. (4) along the i th eigenvector is

$$\frac{\partial \mathbf{n}^{(j)}(t)}{\partial a_{kl}} = \mathbf{S}^{(i)}(t) \frac{n(0)}{\|\mathbf{w}^{(1)}\|} + \Delta \mathbf{S}^{(i)}(t) \Delta \mathbf{n} \quad (8)$$

with $\mathbf{S}^{(i)}(t)$ being,

$$\mathbf{S}^{(1)}(t) = t \lambda_1^{t-1} \frac{\partial \lambda_1}{\partial a_{kl}} \mathbf{w}^{(1)} + \lambda_1^t \sum_{m>1} \frac{\bar{v}_k^{(m)} w_l^{(1)}}{\lambda_1 - \lambda_m} \mathbf{w}^{(m)} \quad (9a)$$

$$\mathbf{S}^{(i)}(t) = -\lambda_i^t \frac{\bar{v}_k^{(i)} w_l^{(1)}}{\lambda_1 - \lambda_i} \mathbf{w}^{(i)}, \quad \text{for all } i > 1 \quad (9b)$$

and $\Delta \mathbf{S}^{(i)}(t)$ being

$$\begin{aligned} \Delta \mathbf{S}^{(i)}(t) &= t \lambda_i^{t-1} \frac{\partial \lambda_i}{\partial a_{kl}} \mathbf{w}^{(i)} \otimes \mathbf{v}^{(i)*} \\ &+ \sum_{m \neq i} \frac{\lambda_i^t}{\lambda_i - \lambda_m} [\bar{v}_k^{(i)} w_l^{(m)} \mathbf{w}^{(i)} \otimes \mathbf{v}^{(m)*} \\ &+ \bar{v}_k^{(m)} w_l^{(i)} \mathbf{w}^{(m)} \otimes \mathbf{v}^{(i)*}] \end{aligned} \quad (10)$$

Eqs. (6) and (7) can be related to Eqs. (9) and (10) by the expressions

$$\mathbf{S}(t) = \sum_i \mathbf{S}^{(i)}(t) \quad (11a)$$

$$\Delta \mathbf{S}(t) = \sum_i \Delta \mathbf{S}^{(i)}(t) \quad (11b)$$

Both $\mathbf{S}(t)$ and $\Delta \mathbf{S}(t)$ are functions of time and the elements of the Leslie matrix (specifically the eigenvectors and eigenvalues of the Leslie matrix), and are therefore independent of the population's initial stage structure. This means that they can be calculated with the same data that is used for a standard asymptotic analysis. This raises the possibility of being able to assess the sensitivity of a near-term analysis to the initial population structure before detailed information on the population structure is known. When the first term of Eq. (4) greatly exceeds the second term then a knowledge of the initial stage structure is relatively unimportant. The ratio of $\Delta \mathbf{S}(t)$ to the first term in Eq. (4) can be used as a quantitative measure of the importance of collecting data on the initial stable stage structure. MATLAB routines to calculate these and other quantities used in this paper can be obtained from the author.

2.1. Transient sensitivity of a population with a stable stage structure

If a population initially has a stable stage structure then $\Delta \mathbf{n} = 0$, and the transient sensitivity requires no information about the initial population vector. All the required information is contained in the right-eigenvector of the dominant eigenvalue (the initial population vector can be written as $\mathbf{n}(0) = n(0) \mathbf{w}^{(1)} / \|\mathbf{w}^{(1)}\|$). In this case a near-term demographic analysis can be made using exactly the same data that would be required for an asymptotic sensitivity analysis.

2.2. Sensitivity immediately after a perturbation ($t = 1$)

One time-step after a perturbation, the matrix $\Delta \mathbf{S}(1)$ is zero except for one element, $\Delta S_{kl}(1) = 1$ (where the subscripts k and l correspond to the element of the Leslie matrix being perturbed, see Appendix C). Therefore, only one element of the initial population vector is needed to determine the sensitivity in Eq. (4). The expression for $\mathbf{S}(t)$ is also particularly simple when $t = 1$, being $\mathbf{S}(1) = w_l^{(1)} \sum_i \bar{v}_k^{(i)} \mathbf{w}^{(i)}$. If the k th element of $\mathbf{S}(1) / \|\mathbf{w}^{(1)}\|$ is small compared with the l th element of $\Delta \mathbf{n} / n(0)$, then the initial departure away from a stable stage structure dominates the near-term sensitivity of the population size to perturbations in a_{kl} . If the reverse is true then data on the initial population structure adds little to the accuracy of the near-term sensitivity analysis.

2.3. Sensitivity long after a perturbation ($t = \infty$)

As the time after a perturbation increases the near-term sensitivity of the population size, given by Eq. (4), approaches the following limit

$$\lim_{t \rightarrow \infty} \frac{1}{tn(t)} \frac{\partial \mathbf{n}(t)}{\partial a_{kl}} = \lambda_1^{-1} \frac{\partial \lambda_1}{\partial a_{kl}} \left[\frac{\mathbf{w}^{(1)}}{\|\mathbf{w}^{(1)}\|} + (\mathbf{w}^{(1)} \otimes \mathbf{v}^{(1)*}) \frac{\Delta \mathbf{n}}{n(0)} \right] \quad (12)$$

Eq. (12) shows that the asymptotic sensitivity of the population size depends upon the initial population structure, $\Delta \mathbf{n} / n(0)$. Initial conditions therefore have consequences for the long-term as well as the transient population dynamics (initial conditions only af-

fect the asymptotic sensitivity of the population size, not the population growth rate). The importance of initial departures from a stable stage structure upon the asymptotic sensitivity of the population size can be roughly gauged by calculating $(\mathbf{w}^{(1)} \otimes \mathbf{v}^{(1)*}) \Delta \mathbf{n} / n(0)$. If this quantity exceeds one then the information held in $\Delta \mathbf{n}$ is likely to make an important contribution to the asymptotic sensitivity of the population size.

3. The near-term sensitivity of the population growth rate

Near-term demographic analysis incorporates all the eigenvectors of the Leslie matrix into the demographic analysis, whereas the standard asymptotic sensitivity analysis uses only the dominant eigenvalue. In a standard asymptotic sensitivity analysis all stages have the same growth rate, equal to the dominant eigenvalue, making the definition of population growth rate unambiguous (Caswell, 2001). For the near-term sensitivity analysis the choice of population growth rate is not so clear because there are several possible measures of transient growth rate. One possibility is not to try and calculate a transient growth rate and instead to calculate the sensitivity of each eigenvalue, which is the approach taken by Fox and Gurevitch (2000). Alternatively, the sensitivity of a weighted average of the eigenvalues can be used to define an average growth rate. Two useful averages are the average growth rate of the i th stage, $\langle \lambda \rangle_i$, and the average growth rate for the entire population, $\langle \lambda \rangle$. The average growth rate of the i th stage can be defined as

$$\langle \lambda \rangle_i = \sum_j \lambda_j \frac{n_i^{(j)}(t)}{n_i(t)} \tag{13}$$

and using Eq. (13) the average growth rate for the entire population can be defined as

$$\langle \lambda \rangle = \sum_i \langle \lambda \rangle_i \frac{n_i(t)}{n(t)} \tag{14}$$

Differentiating Eqs. (13) and (14) with respect to a_{kl} gives the sensitivity of these growth rates to changes in a_{kl} ,

$$\frac{\partial \langle \lambda \rangle_i}{\partial a_{kl}} = \sum_j \frac{\partial \lambda_j}{\partial a_{kl}} \frac{n_i^{(j)}(t)}{n_i(t)} + \frac{\lambda_j - \langle \lambda \rangle_i}{n_i(t)} \frac{\partial n_i^{(j)}(t)}{\partial a_{kl}} \tag{15}$$

and

$$\frac{\partial \langle \lambda \rangle}{\partial a_{kl}} = \sum_i \frac{\partial \langle \lambda \rangle_i}{\partial a_{kl}} \frac{n_i(t)}{n(t)} + \frac{\langle \lambda \rangle_i - \langle \lambda \rangle}{n(t)} \frac{\partial n_i(t)}{\partial a_{kl}} \tag{16a}$$

$$= \sum_{i,j} \frac{\partial \lambda_j}{\partial a_{kl}} \frac{n_i^{(j)}(t)}{n(t)} + \frac{\lambda_j - \langle \lambda \rangle}{n(t)} \frac{\partial n_i^{(j)}(t)}{\partial a_{kl}} \tag{16b}$$

where the sensitivity of $n^{(j)}(t)$ is given by Eq. (8). Eqs. (15) and (16) allow the transient sensitivity of the population growth rate to be calculated from the transient sensitivity of the population size.

In the long-term as $t \rightarrow \infty$ all measures of population growth rate are equal to the dominant eigenvalue ($\lim_{t \rightarrow \infty} \langle \lambda \rangle_i = \lim_{t \rightarrow \infty} \langle \lambda \rangle = \lambda_1$). This implies that the second terms in Eqs. (15) and (16a) asymptotically approach zero. Furthermore, the population stage structure, $\mathbf{n}(t)/n(t)$, asymptotically approaches the dominant right-eigenvector, $\mathbf{w}^{(1)}/\|\mathbf{w}^{(1)}\|$, so that the asymptotic sensitivities of all population growth rates agree with the standard asymptotic sensitivity analysis,

$$\lim_{t \rightarrow \infty} \frac{\partial \langle \lambda \rangle}{\partial a_{kl}} = \lim_{t \rightarrow \infty} \frac{\partial \langle \lambda \rangle_i}{\partial a_{kl}} = \frac{\partial \lambda_1}{\partial a_{kl}} \tag{17}$$

unlike the asymptotic sensitivity of the population size, which is influenced by the initial population structure (Eq. (12)).

Looking at the transient population dynamics, the near-term sensitivities of $\langle \lambda \rangle_i$ and $\langle \lambda \rangle$ differ from each other and the asymptotic result. The sensitivity of $\langle \lambda \rangle_i$ gives detailed information about each stage. The sensitivity of $\langle \lambda \rangle$ contains less information, but does provide a simple summary statistic which still contains information about the transient effects of a perturbation upon the population growth rate.

4. Example

As an example of our approach to near-term demographic analysis, the decomposition of Eq. (4), we use the model of the cactus *Coryphantha robbinsorum* presented by Fox and Gurevitch (2000). The life-cycle of this cactus, along with the transition rates (labelled as site A by Fox and Gurevitch, 2000) is shown in Fig. 1. The initial population structure is assumed to be $\mathbf{n}(0) = (10, 5, 2)^T$. So initially there are twice as many small juveniles as large juveniles, and five times

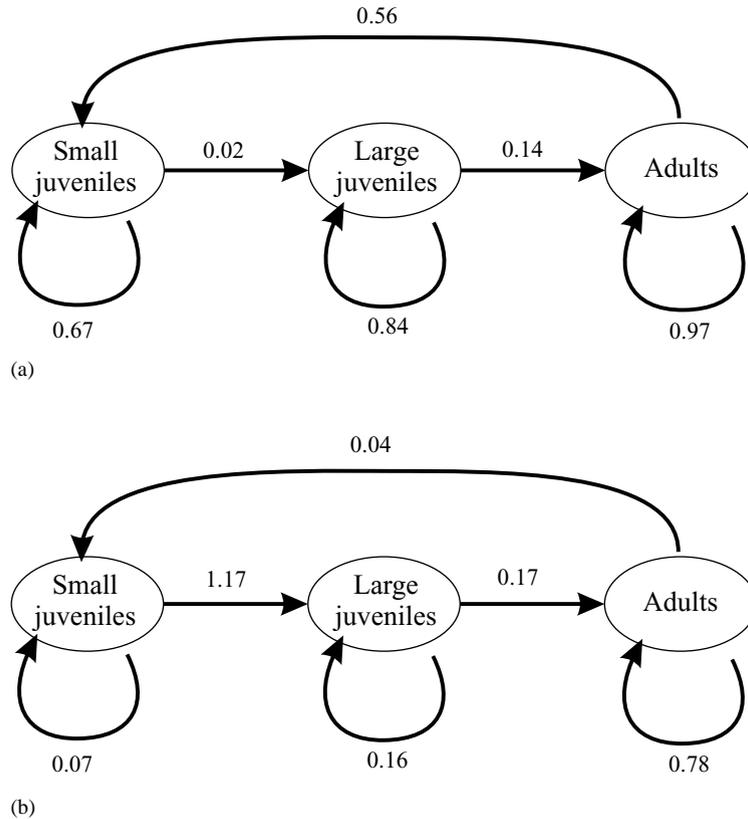


Fig. 1. Panel (a) shows the life cycle graph and transition rates for a population of *Coryphantha robbinsorum* (Fox and Gurevitch, 2000). Panel (b) shows the sensitivity of the long-term growth rate, λ_1 to fluctuations in each transition rate, $d\lambda_1/da_{kl}$.

as many small juveniles as adults. Compared with the asymptotic stage-structure (the asymptotic stage-structure is $\mathbf{n}_{\text{eq}}(0) \approx (10, 1, 6)^T$), the initial population has an excess of large juveniles and a deficit of adults.

4.1. Sensitivities of the population size

First consider the effect of perturbing a single transition rate: the transition between large juveniles and adults (this element of the Leslie matrix is $a_{32} = 0.14$). The sensitivity of the population size of each stage, as a function of time, can be calculated using Eq. (4) and is shown in Fig. 2 (as explained by Fox and Gurevitch, 2000, sensitivities have been time corrected by dividing by t). The bold lines show the exact transient sensitivities whilst the light lines show the transient sensitivities under the assumption that the initial

population has a stable stage structure (i.e. $\Delta \mathbf{n} = 0$, so that only the first term of Eq. (4) is non-zero).

As explained earlier, at $t = 1$ there is only one non-zero sensitivity, and for a perturbation of a_{32} the non-zero sensitivity is for the adult stage. Before carrying out the sensitivity analysis, some idea about the importance of the initial population structure can be gained by considering $S(1)/\|\mathbf{w}^{(1)}\|$ which is equal to $(0, 0, 0.07)^T$. Therefore, if the initial stage structure of the population differs from the stable stage structure by more than just 0.07 (i.e. if $\Delta \mathbf{n}/n(0) > 0.07$) then data on this initial population structure will be important. Because 0.07 is small we conclude that it is likely in this case that the population's initial stage structure will dominate the transient sensitivity at $t = 1$ for the transition from large juveniles to adults. This is confirmed by calculating the second element of $\Delta \mathbf{n}/n(0)$ which is 0.22, greatly exceeding 0.07. Further confir-

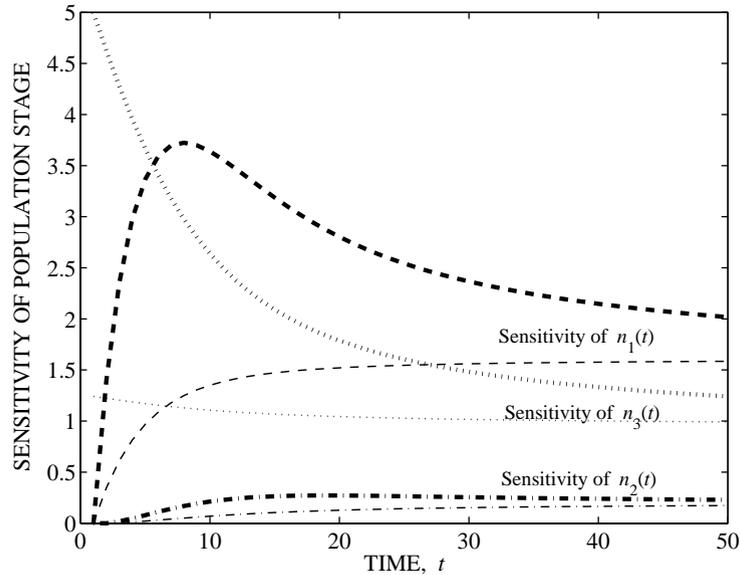


Fig. 2. The sensitivity of the population size of each stage (Eq. (4)) divided by the time, as a function of time after a perturbation in the transition rate from large juveniles to adults, for a population of *Coryphantha robbinsorum* to a perturbation in the transition rate from large juveniles to adults. The bold dashed, dashed-dotted and dotted lines show the sensitivities of the population sizes for small juveniles, $n_1(t)$, large juveniles, $n_2(t)$ and adults, $n_3(t)$, respectively. The equivalent lines in light type show the equivalent sensitivities assuming that the population is initially at equilibrium.

mation is seen in Figs. 2 and 3, which shows a three-fold difference between the approximate and exact sensitivities of the adult population size at $t = 1$.

As time after the perturbation increases the sensitivities of the population size of the other two stages become more important, with the large juvenile stage eventually becoming the most sensitive stage. If the information about the population’s initial structure is ignored (light lines in Fig. 2) then the transient sensitivities are under-predicted. However, as time increases and the sensitivities approach the asymptotic result (Eq. (12)) this discrepancy becomes less. If the rankings of the sensitivities are considered then the initial information makes little difference, because the approximate sensitivities and the exact sensitivities have the same ranking, with all ranks changing at $t \approx 7$. This was found to be approximately the case for the sensitivities of all transitions over a range of initial conditions.

A more complete picture of the model’s near-term sensitivity of the population size to all of the transition rates is shown in Fig. 3 (calculated using Eq. (4) and not time corrected). Each transition has two vectors as-

sociated with it: the vectors in bold are the exact sensitivities, whilst the vectors in normal type are the sensitivities under the assumption that the initial population has a stable stage structure. Each element of the vector indicates the sensitivity of a stage’s population size to changes in a transition rate. Looking at the ‘small to large juvenile’ transition shows that five times steps after a unit change in this transition rate ($t = 5$) leads to an increase of 5.28, 25.9 and 9.45 in the population sizes of the small juveniles, large juveniles and adults, respectively compared to what they would have been if the transition rate had remained constant. As discussed earlier for Fig. 2, the relative rankings of the sensitivities at each demographic transition are the same for the exact and approximate values. However, this is not the case for the rankings of the sensitivities between different demographic transitions. Here the population’s initial departure from equilibrium has an important effect. For example, looking at the results for the adult stage at $t = 1$, the exact and approximate results for the sensitivity to the ‘large juvenile to adult’ transition is 5.00 and 1.24, respectively whilst the sensitivity to the ‘adult to adult’ transition is 2.00

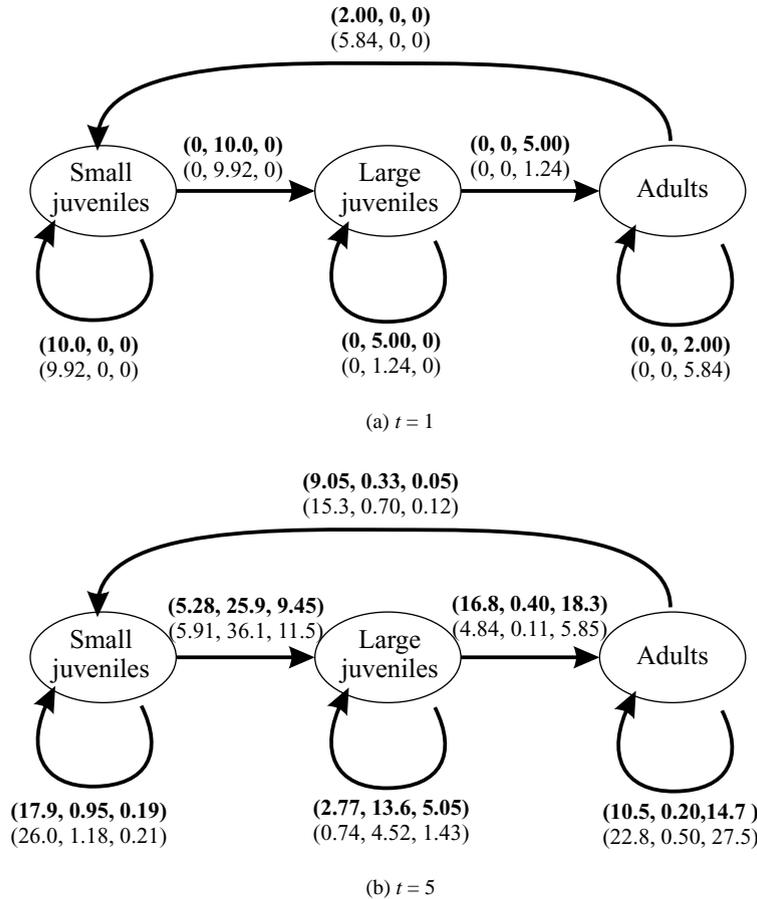


Fig. 3. The sensitivities of the population size, $dn(t)/da_{ij}$, of *Coryphantha robbinsorum* to changes in the transition rates after (a) one time unit ($t = 1$) and (b) five time units ($t = 5$). Figures in bold are the exact sensitivities when the initial population vector is $\mathbf{n}(0) = (10, 5, 2)^T$, whilst figures in normal type are the sensitivities assuming that the initial population was at its asymptotic equilibrium $\mathbf{n}_{eq}(0) \approx (10, 1, 6)^T$.

and 5.84, respectively. So the exact and approximate results predict different rankings for these two sensitivities. Some suggestion of this dependency upon the initial population vector can be gained by comparing $S(t)$ (the contribution to the near-term sensitivity from the stable stage structure) with $\Delta S(t)$ (the contribution to the near-term sensitivity due to the initial departures from the stable stage structure).

4.2. Sensitivities of the population growth rate

First consider the near-term sensitivity of the population growth rates to changes in the transition rate from large juveniles to adults. These are calculated from Eqs. (15) and (16) and are shown in Fig. 4. Com-

pared to the near-term sensitivities of the population size (Fig. 2) the sensitivities of the growth rates quickly approach their asymptotic value. Since this way of displaying the near-term sensitivities is directly comparable with the standard asymptotic analysis, the results from near-term and asymptotic analyses can be compared. The most striking comparison is that the near-term sensitivities are up to four-fold greater than the asymptotic sensitivity, implying that the transient effect of demographic fluctuations is more important than an asymptotic sensitivity analysis would suggest.

Rather than concentrating upon just one transition rate, Fig. 5 shows the sensitivities of $\langle \lambda \rangle$ to all the demographic transitions. The use of an average population growth rate, $\langle \lambda \rangle$, approximately mirrors the

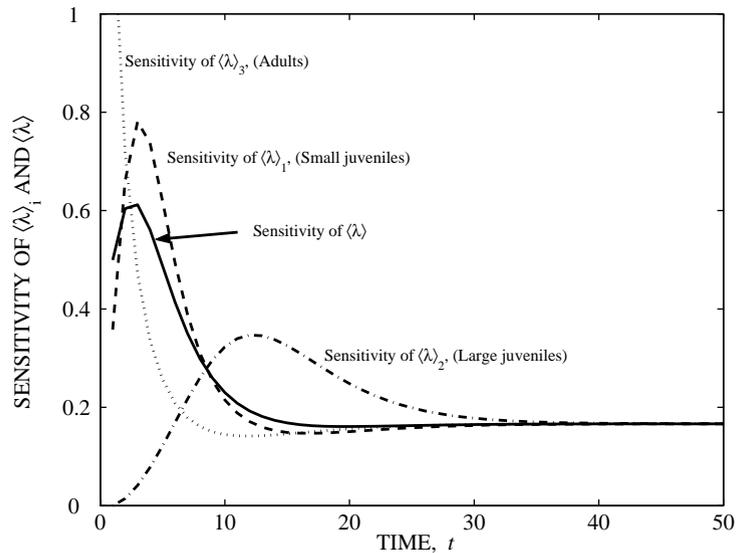


Fig. 4. The sensitivity of the population growth rates (Eqs. (15) and (16)) as a function of the time after a perturbation in the transition rate from large juveniles to adults, for a population of *Coryphantha robbinsorum* to a perturbation in the transition rate from large juveniles to adults. The solid line shows the sensitivity of the average population growth rate $\langle \lambda \rangle$ (Eq. (14)), whilst the dashed, dashed-dotted and dotted lines show the sensitivities of the growth rates for small juveniles, large juveniles and adults, respectively (Eq. (13)). All sensitivities approach the same asymptotic sensitivity, $d\lambda_1/da_{32} = 0.17$.

sensitivities of the individual stages, and allows the transient effect of a perturbation to be clearly and simply displayed, albeit with some loss of information. In all but a couple of exceptions the near-term sensitivities (Fig. 5) are greater than the asymptotic sensitivities (Fig. 1). Fig. 5 shows that the average population growth rate is initially highly sensitive to perturbations in the transition rates of both ‘small to large juveniles’, and ‘large juveniles to adults’. These sensitivities can be compared with the asymptotic result (Fig. 1(b)), showing how the pattern in the sensitivities changes with time after a perturbation in each transition rate. At $t = 1$ the population growth rate is particularly sensitive to the ‘large juvenile to adult’ transition rate compare to the asymptotic result. The ‘small juvenile to small juvenile’ transition rate (a_{11} matrix element) also shows a high near-term sensitivity compared to the asymptotic result. On the basis of an asymptotic sensitivity analysis, perturbations in the a_{11} and a_{32} transition rates may be thought of as relatively unimportant, but the short-term effect of perturbations in these transition rates will be highly significant.

Fig. 5 further emphasises the importance of the initial population structure in determining the transient

behaviour in this example. The rankings of the sensitivities are distorted by ignoring the initial population structure, especially for important transition rates such as a_{32} . Furthermore, the approximate sensitivities are generally closer to the asymptotic values, so that ignoring the initial population structure underestimates the transient effect of a perturbation. On the other hand, the approximate results give a fair representation of the sign and order of magnitude of the near-term sensitivities.

5. Discussion

This paper has considered the analysis of transient demographic effects in matrix population models and the necessity of gathering additional data to parameterise the transient sensitivity analysis. Although there is an extensive literature on the analysis and application of matrix population model (Caswell, 2001 and references therein), the overwhelming majority consider long-term, asymptotic population dynamics. The results of this paper differ from the majority of the literature because they address the analysis of short-

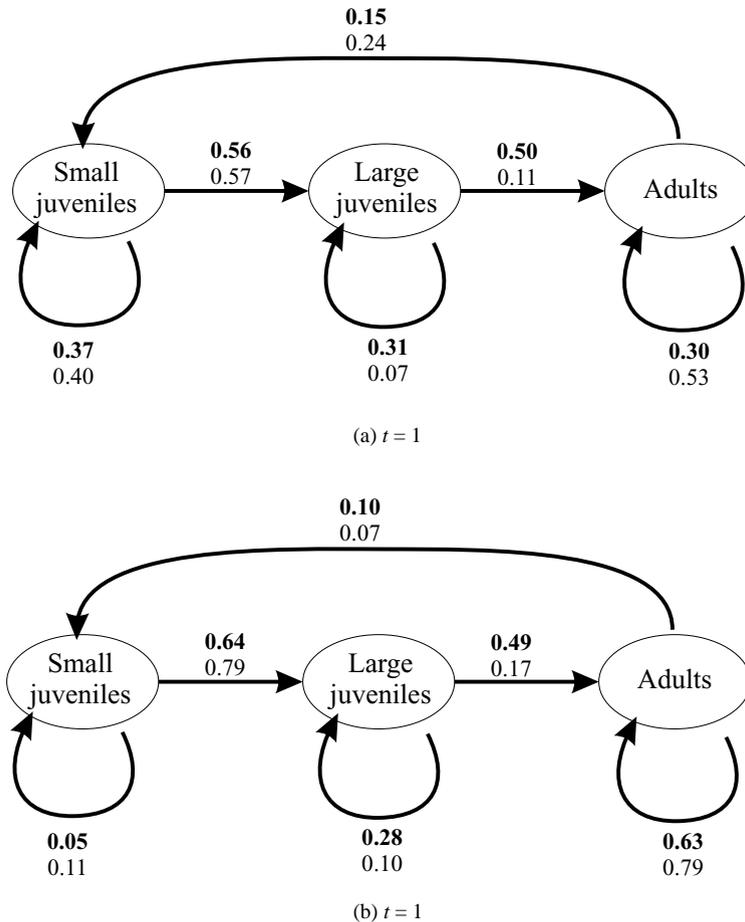


Fig. 5. The sensitivities of the population growth rate, $d(\lambda)/da_{kl}$ (Eq. (16)), of *Coryphantha robbinsorum* to changes in the transition rates after (a) one time unit ($t = 1$) and (b) five time units ($t = 5$). Figures in bold are the exact sensitivities when the initial population vector is $\mathbf{n}(0) = (10, 5, 2)^T$, whilst figures in normal type are the sensitivities assuming that the initial population was in at its asymptotic equilibrium $\mathbf{n}_{eq}(0) \approx (10, 1, 6)^T$. All values are accurate to two decimal places.

term, transient population dynamics, which despite its importance is a topic which has received little attention (Fox and Gurevitch, 2000; Wilder, 2001). The analysis of transient dynamics (e.g. Fox and Gurevitch, 2000; Wilder, 2001; Satterthwaite et al., 2002) allows the *immediate* response of a population to an environmental or demographic perturbation to be studied, whereas a long-term, asymptotic analysis is restricted to looking at the response of a population *long after* an initial perturbation. Short- and long-term analyses are therefore complementary, giving valuable information to population conservation and management.

The results of this paper build upon the near-term demographic analysis of Fox and Gurevitch (2000) in

two respects. Firstly, the near-term sensitivity of the population size has been extended to consider the near-term sensitivity of the population's growth rate. This allows the output from the near-term sensitivity analysis to be simplified and directly compared with the standard asymptotic sensitivity analysis. Secondly the near-term sensitivity analysis has been decomposed into two components (Eq. (4)); the first being independent of a population's initial stage structure, whilst the second component gives the corrections necessary to take the initial stage structure into account. This decomposition gives an analytical formula which allows insights into the practical data requirements of a near-term sensitivity analysis. Our results from the

example show that this decomposition can be used to predict the importance of the population's structure for a near term analysis. The example showed that the population's initial structure was important when ranking the sensitivities of the different demographic transitions, but was less important when ranking the sensitivities of the population stages to the same demographic transition. MATLAB scripts for calculating all the important quantities described in this paper are available from the author.

Several scenarios can be envisaged where near-term demographic analysis is likely to give important additional information over an asymptotic analysis (the issue is often whether such information is worth the effort to obtain). Examples are: when the immediate impact of a management strategy upon a population is of interest, when a population undergoes frequent perturbations, or when a population is thought to be critically endangered and extinction could occur due to the transient population dynamics. Near-term sensitivity analysis provides a full description of the effect of a perturbation, so even if the asymptotic behaviour is of ultimate interest, it gives guidance on the behaviour to be expected before the asymptotic behaviour is reached. It may also provide evidence for the robustness of an asymptotic analysis. If the population is likely to be perturbed before reaching an asymptotic behaviour (e.g. yearly management intervention, or seasonal changes in the environment), then near-term sensitivities provide an additional tool to the analysis of matrix models in periodic and aperiodic environments (Caswell, 2001; Lesnoff et al., 2003). Finally, if a population stage is close to a critical threshold size, near-term sensitivities are required in order to predict whether the transient dynamics will tend to push the population below the threshold. This is not intended to be an exhaustive list, and other applications no doubt exist.

In terms of the effort required to perform a near-term analysis, the most dramatic saving in effort is obtained when the initial population can be assumed to have reached a stable stage structure. In this case, near-term sensitivities still give valuable information and can be calculated with only a knowledge of the Leslie matrix. Such scenarios would correspond to populations where perturbations are relatively infrequent but the short-term response after a perturbation is of interest. In general however, a population can-

not be assumed to have a stable stage structure. Often there is little data available about the population structure, and limited resources or time to collect such information. Similar issues have already been raised in relation to the standard asymptotic analysis, and methods have been suggested to reduce the data collection effort (Heppell et al., 2000). For a near-term sensitivity analysis, comparing the two quantities $S(t)$ and $\Delta S(t)$, derived in this paper, gives an indication of the importance in gathering population structure data for an accurate analysis. This allows the possibility of using near-term demographic analysis in applications which would have been thought infeasible given the earlier published results (Fox and Gurevitch, 2000). The interpretation of near-term demographic analysis can also be simplified by considering the sensitivity of the average population growth rate, which summarises the results of the analysis into one number, albeit with the loss of some information.

Stochasticity and density-dependence are increasingly being recognised as important considerations for a population's dynamics. In response to this, demographic analysis methods which incorporate stochasticity (e.g. Tuljapurkar, 1992; Fieberg and Ellner, 2001; Buckland et al., 2003) and density-dependence (e.g. Grant, 1997; Grant and Benton, 2000; Yearsley et al., 2003) are becoming increasingly available. The current formulation of near-term demographic analysis includes neither stochasticity nor density-dependence. However, on the short-term the effects of density-dependence and stochasticity are weak compared to their effect on the asymptotic behaviour of a population. Immediately after a perturbation density-dependence can be ignored because it has had no time to act, and the stochasticity can often be incorporated into the perturbation itself. So near-term demographic analysis may provide an interesting angle from which to look at the effects of stochasticity and density-dependence upon a population's dynamics, because their effect will initially be weak. The incorporation of stochastic effects into near-term analysis should provide another tool for estimating extinction risk, whose results could be compared with the population viability analyses used at present (Boyce, 1992; Bessinger and Westphal, 1998). This raises the question of how best to use the near-term sensitivities to guide population management efforts? Is the best approach to incorporate the analysis into a broader framework

which incorporates a population viability analysis, or are the near-term sensitivities of practical use as they stand? Future work will need to concentrate upon the application of these methods if they are to be of practical use in conservation and population management.

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Appendix A. Conventions

This paper follows the matrix convention used by Caswell (2001). A summary of the symbols used in the paper and their meaning is given in Table 1. For a Leslie matrix, \mathbf{A} , the i th eigenvalue, λ_i , and right-eigenvector, $\mathbf{w}^{(i)}$, are defined as the solution of

$$\mathbf{A}\mathbf{w}^{(i)} = \lambda_i \mathbf{w}^{(i)} \tag{A.1}$$

The corresponding left-eigenvector, $\mathbf{v}^{(i)}$, is the solution of

$$\mathbf{v}^{(i)*} \mathbf{A} = \lambda_i \mathbf{v}^{(i)*} \tag{A.2}$$

The eigenvalues are ordered so that $\lambda_1 > \lambda_2 > \dots$, making λ_1 the dominant eigenvalue. If \mathbf{V} is the matrix whose columns are the left-eigenvectors, and \mathbf{W} is a similar matrix of right-eigenvectors, then the left-eigenvectors can also be calculated from

$$\mathbf{V}^* = \mathbf{W}^{-1} \tag{A.3}$$

Finally, the scalar product of left and right-eigenvectors obey,

$$\langle \mathbf{v}^{(i)}, \mathbf{w}^{(j)} \rangle = \sum_k \bar{v}_k^{(i)} w_k^{(j)} = 0, \quad \text{if } i \neq j \tag{A.4}$$

where $\bar{v}^{(i)}$ denotes the complex conjugate $\mathbf{v}^{(i)}$, and $\langle \mathbf{a}, \mathbf{b} \rangle$ denotes the scalar product of vectors \mathbf{a} and \mathbf{b} . We will assume that the eigenvectors have been normalised so that $\langle \mathbf{v}^{(i)}, \mathbf{w}^{(i)} \rangle = 1$.

A population at time t can be decomposed into components of the right-eigenvectors,

$$\mathbf{n}(t) = \mathbf{A}^t \mathbf{n}(0) \tag{A.5a}$$

$$\mathbf{n}(t) = \sum_i \mathbf{n}^{(i)}(t) \tag{A.5b}$$

$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{w}^{(i)} \tag{A.5c}$$

where $\mathbf{n}(0)$ is the initial population vector at time $t = 0$, c_i is a scalar quantity giving the proportion of the initial population which lies along $\mathbf{w}^{(i)}$. The scalar c_i can be written as,

$$c_i = \langle \mathbf{v}^{(i)}, \mathbf{n}(0) \rangle \tag{A.6}$$

and its derivative with respect to a_{kl} , which is used in the near-term demographic analysis, is

$$\frac{\partial c_i}{\partial a_{kl}} = \left\langle \frac{\partial \mathbf{v}^{(i)}}{\partial a_{kl}}, \mathbf{n}(0) \right\rangle = \sum_j \frac{\partial \bar{v}_j^{(i)}}{\partial a_{kl}} n_j(0) \tag{A.7}$$

In summary, the notations for the population vectors are related as follows,

$$n_j^{(i)}(t) = \lambda_i^t c_i w_j^{(i)} \tag{A.8}$$

$$n_j(t) = \sum_i n_j^{(i)}(t) \tag{A.9}$$

$$\mathbf{n}^{(i)}(t) = \lambda_i^t c_i \mathbf{w}^{(i)} \tag{A.10}$$

$$\mathbf{n}(t) = \sum_i \mathbf{n}^{(i)}(t) \tag{A.11}$$

All results use the notation that $\mathbf{n}^{(i)}(t)$ represents the component of the population that lies along the i th right-eigenvector at time t and $n_j^{(i)}(t)$ represents the j th element of this component.

Appendix B. Asymptotic sensitivity analysis

The standard demographic analysis calculates the sensitivity of λ_i with respect to a change in the element a_{kl} of the Leslie matrix as,

$$\frac{\partial \lambda_i}{\partial a_{kl}} = \bar{v}_k^{(i)} w_l^{(i)} \tag{B.1}$$

and the sensitivity of the left- and right-eigenvectors as,

$$\frac{\partial \mathbf{w}^{(i)}}{\partial a_{kl}} = w_l^{(i)} \sum_{m \neq i} \frac{\bar{v}_k^{(m)}}{\lambda_i - \lambda_m} \mathbf{w}^{(m)} \tag{B.2}$$

$$\frac{\partial \mathbf{v}^{(i)}}{\partial a_{kl}} = v_k^{(i)} \sum_{m \neq i} \frac{\bar{w}_l^{(m)}}{\bar{\lambda}_i - \bar{\lambda}_m} \mathbf{v}^{(m)} \tag{B.3}$$

assuming that the eigenvectors are normalised such that $\langle \mathbf{v}^{(i)}, \mathbf{w}^{(i)} \rangle = 1$. These results can be rewritten in terms of sensitivity matrices as,

$$\frac{\partial \lambda_i}{\partial \mathbf{A}} = \bar{\mathbf{v}}^{(i)} \otimes \mathbf{w}^{(i)\text{T}} \tag{B.4}$$

$$\frac{\partial \mathbf{w}_k^{(i)}}{\partial \mathbf{A}} = \sum_{m \neq i} \frac{\mathbf{v}^{(m)} \otimes \mathbf{w}^{(i)\text{T}}}{\lambda_i - \lambda_m} \mathbf{w}_k^{(m)} \tag{B.5}$$

$$\frac{\partial v_k^{(i)}}{\partial \mathbf{A}} = \sum_{m \neq i} \frac{\bar{v}^{(i)} \otimes \mathbf{w}^{(m)*}}{\bar{\lambda}_i - \bar{\lambda}_m} v_k^{(m)} \tag{B.6}$$

The asymptotic analysis concentrates upon the dominant eigenvalue, λ_1 , and its associated eigenvectors, because this eigenvalue can be associated with the asymptotic growth rate of the population (Caswell, 2001, pp. 210, 250).

Appendix C. Decomposition of near-term analysis

In order to derive the decomposition of the near-term analysis presented in Eq. (4) the original equation (Eq. (2)) is rewritten as a Taylor expansion about $\mathbf{n}(0) = c_1 \mathbf{w}^{(1)}$,

$$\begin{aligned} \frac{\partial \mathbf{n}(t)}{\partial a_{kl}} &= \left. \frac{\partial \mathbf{n}(t)}{\partial a_{kl}} \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} \\ &+ \left. \frac{\partial}{\partial \mathbf{n}^{\text{T}}(0)} \left(\frac{\partial \mathbf{n}(t)}{\partial a_{kl}} \right) \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} \Delta \mathbf{n} \\ &+ \left. \frac{\partial^2}{\partial \mathbf{n}^{\text{T}}(0)^2} \left(\frac{\partial \mathbf{n}(t)}{\partial a_{kl}} \right) \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} \Delta \mathbf{n}^2 \\ &+ O(\Delta \mathbf{n}^3) \end{aligned} \tag{C.1}$$

where $\Delta \mathbf{n}$ is the deviation of the initial population structure away from a stable stage structure (Eq. (5)). Since Eq. (2) is a linear function of $\mathbf{n}(0)$ all terms of order $\Delta \mathbf{n}^2$ and higher are zero, leaving only the first two terms as non-zero in the Taylor expansion of Eq. (C.1). Rewriting these two remaining terms as

$$S_i(t) \frac{n(0)}{\|\mathbf{w}^{(1)}\|} = \left. \frac{\partial n_i(t)}{\partial a_{kl}} \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} \tag{C.2}$$

$$\Delta S_{ij}(t) = \left. \frac{\partial}{\partial n_j(0)} \left(\frac{\partial n_i(t)}{\partial a_{kl}} \right) \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} \tag{C.3}$$

gives Eq. (4). The expressions for $S(t)$ and $\Delta S(t)$ which appear in Eq. (4) must now be derived.

Firstly, $S(t)$ is calculated by evaluating Eq. (2) when $\mathbf{n}(0) = c_1 \mathbf{w}^{(1)}$. When this is the case $\mathbf{n}(0)$ is proportional to $\mathbf{w}^{(1)}$, implying that $c_1 = n(0)/\|\mathbf{w}^{(1)}\|$, whilst $c_m = 0$ for $m > 1$. The differential of c_m with respect to a_{kl} can then be calculated from Eqs. (A.6) and (B.3) to be

$$\frac{\partial c_1}{\partial a_{kl}} = 0 \tag{C.4}$$

$$\frac{\partial c_m}{\partial a_{kl}} = \frac{v_k^{(m)} w_l^{(1)}}{\lambda_m - \lambda_1} c_1 \quad \forall m > 1 \tag{C.5}$$

Substituting these results into Eq. (2), and using Eq. (A.5b) and (B.2) gives

$$\begin{aligned} \left. \frac{\partial \mathbf{n}^{(1)}(t)}{\partial a_{kl}} \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} &= \left[t \lambda_1^{t-1} \frac{\partial \lambda_1}{\partial a_{kl}} \mathbf{w}^{(1)} + \lambda_1^t \sum_{m>1} \frac{\bar{v}_k^{(m)} w_l^{(1)}}{\lambda_1 - \lambda_m} \mathbf{w}^{(m)} \right] \frac{n(0)}{\|\mathbf{w}^{(1)}\|} \end{aligned} \tag{C.6}$$

$$\begin{aligned} \left. \frac{\partial \mathbf{n}^{(m)}(t)}{\partial a_{kl}} \right|_{\mathbf{n}(0)=c_1 \mathbf{w}^{(1)}} &= - \left[\lambda_m^t \frac{\bar{v}_k^{(m)} w_l^{(1)}}{\lambda_1 - \lambda_m} \mathbf{w}^{(m)} \right] \frac{n(0)}{\|\mathbf{w}^{(1)}\|} \quad \forall m > 1 \end{aligned} \tag{C.7}$$

from which the expression for $S(t)$ in Eq. (6) and $S^{(i)}(t)$ in Eq. (9) can be obtained.

Secondly, $\Delta S(t)$ is derived by the calculating derivatives in Eq. (C.3). The simplest approach is first to differentiate Eq. (A.5c) with respect to a component of $\mathbf{n}(0)$ giving,

$$\frac{\partial \mathbf{n}(t)}{\partial n_j(0)} = \sum_m \bar{v}_j^{(m)} \lambda_m^t \mathbf{w}^{(m)} \tag{C.8}$$

which is independent of $\mathbf{n}(0)$, making all higher derivatives zero. It now remains to differentiate Eq. (C.8) with respect to a_{kl} . Using Eqs. (B.2) and (B.3),

this gives

$$\begin{aligned} \frac{\partial}{\partial a_{kl}} \frac{\partial n_i(t)}{\partial n_j(0)} &= \sum_m t \lambda_m^{t-1} \frac{\partial \lambda_m}{\partial a_{kl}} w_i^{(m)} \bar{v}_j^{(m)} \\ &+ \sum_{n \neq m} \frac{\lambda_m^t}{\lambda_m - \lambda_n} [\bar{v}_k^{(m)} w_l^{(n)} w_i^{(m)} \bar{v}_j^{(n)} \\ &+ \bar{v}_k^{(n)} w_l^{(m)} w_i^{(n)} \bar{v}_j^{(m)}] \end{aligned} \quad (\text{C.9})$$

which is used to give the expression for $\Delta S^{(i)}(t)$ of Eq. (10). By permuting the indices, Eq. (C.9) can be simplified to

$$\begin{aligned} \frac{\partial}{\partial a_{kl}} \frac{\partial n_i(t)}{\partial n_j(0)} &= \sum_m t \lambda_m^{t-1} \frac{\partial \lambda_m}{\partial a_{kl}} w_i^{(m)} \bar{v}_j^{(m)} \\ &+ \sum_{n \neq m} \frac{\lambda_m^t - \lambda_n^t}{\lambda_m - \lambda_n} \bar{v}_k^{(m)} w_l^{(n)} w_i^{(m)} \bar{v}_j^{(n)} \end{aligned} \quad (\text{C.10})$$

which gives the expression for the matrix $\Delta S(t)$ given in Eq. (7).

The expression for $\Delta S(t)$ can be simplified when $t = 1$. Differentiating Eq. (A.5) with respect to $\mathbf{n}(0)$ and a_{kl} gives the result that

$$\Delta S_{ij}(1) = \begin{cases} 1, & \text{if } i = k \text{ and } j = l \\ 0, & \text{otherwise} \end{cases} \quad (\text{C.11})$$

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