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SPECIAL FEATURE: 5TH ANNIVERSARY OF *METHODS IN ECOLOGY AND EVOLUTION*

Perturbation analysis of transient population dynamics using matrix projection models

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Summary

1. Non-stable populations exhibit short-term transient dynamics: size, growth and structure that are unlike predicted long-term asymptotic stable, stationary or equilibrium dynamics. Understanding transient dynamics of non-stable populations is important for designing effective population management strategies, predicting the responses of populations to environmental change or disturbance, and understanding population processes and life-history evolution in variable environments.

2. Transient perturbation analyses are vital tools for achieving these aims. They assess how transient dynamics are affected by changes to vital rates, population structure, or underlying variables that affect these. These changes could be imposed deliberately by population managers, or driven by environmental variables. Methodological approaches to transient perturbation analysis are diverse, and different methods are suited to different applications: choosing a method to use may be challenging.

3. Here, I review existing methods for prospective transient perturbation analysis, and identify a number of key considerations for ecologists when choosing a method. These include the approach taken in calculating the perturbation, the type of model being analysed, the perturbation structure, the population response of interest, nonlinear response to perturbation, standardization for asymptotic dynamics, the initial population structure, and the time frame of interest. I discuss these with reference to the application of transient perturbation analyses in both population management and comparative analysis.

4. The diversity of transient perturbation analyses available means that existing approaches are applicable to a wide range of population management and comparative analysis scenarios. It is important, however, for ecologists using these methods to know exactly what is being measured. Despite a wealth of existing methods, I identify some areas that would benefit from further development.

Key-words: comparative demography, demography, direct perturbation, elasticity, population biology, population management, population viability analysis, sensitivity, transfer function

Introduction

Matrix projection models (MPMs) that project future population dynamics (changes in population structure and growth) are an elementary demographic tool, used often in ecological and evolutionary research. Prospective or ‘forward’ perturbation analyses (Caswell 2000) are almost ubiquitous in studies that use MPMs: these methods assess how future population dynamics are expected to respond to changes in vital rates (survival, reproduction, development, growth, shrinkage), population structure (relative abundances of individuals of different ages, sizes or stages), or other parameters that affect vital rates or population structure (e.g. abiotic environmental variables or biotic interactions). Perturbation analyses are a very

important tool: they identify which individuals or vital rates are most important to population dynamics and thus justify allocation of resources across diverse ecological applications (Heppell, Caswell & Crowder 2000), including management for conservation (Baxter *et al.* 2006), control of pests (Jongejans, Sheppard & Shea 2006), disease (Baines, Eager & Jarosz 2015) and invasive species (Pople & McLeod 2010), and sustainable exploitation of natural populations (Fordham, Georges & Brook 2007). Perturbation analyses of MPMs have also contributed significantly to our understanding of fundamental population processes including density dependence (Grant 1997), cyclic and chaotic dynamics (Costantino *et al.* 1997), influence of environmental variation (Fieberg & Ellner 2001), spread of invasive populations (Neubert & Caswell 2000) and species interactions (Barabás, Meszéná & Ostling 2014). Significant contributions to life-history theory are also based on perturbation analyses of MPMs. Life span, age at maturity and generation time all associate with relative impor-

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tance of different vital rates to stable population growth in plants (Franco & Silvertown 2004). Variation in vital rates is generally assumed to reduce stochastic population growth, and evidence from perturbation analysis suggests that vital rates that are important to stochastic growth may be selected to have lower variance (Pfister 1998; Gaillard *et al.* 2000; Morris & Doak 2004).

MPMs can project both short- and long-term population dynamics, but historically the latter have received far more research attention than the former. Long-term dynamics (stable growth, stable or unstable equilibria and stationary stochastic growth) are independent of population structure: under stable or stationary conditions, a population of any structure eventually exhibits the same dynamics as any other with the same life cycle but different structure (Hastings 2001). Stable and stationary dynamics generally have relatively straightforward analytical solutions that are easily amenable to perturbation analysis: for example, 'asymptotic' (long-term, stable) growth of a linear, time-invariant MPM model is equal to the dominant eigenvalue of the matrix, and sensitivity of that growth to the matrix entries is a simple function of the two dominant eigenvectors (Caswell 1978).

Calculation and perturbation analysis of short-term 'transient dynamics' is less straightforward, however, and transients have only recently started to receive considerable research attention. Transient dynamics are dependent on population structure: even under stable or stationary conditions, a population disturbed or perturbed away from stable or stationary structure will follow short-term dynamics that are unlike, and often dramatically different from, its projected asymptotic dynamics (Hastings 2001; Fig. 1). Understanding transient dynamics could help refine predictions of future population dynamics (Ezard *et al.* 2010), and knowledge of population structure is necessary for accurate projection of transient dynamics. However, estimating structures of natural populations can be difficult, and defining exactly what transient dynamics are is difficult (see section 'Matrix projection models'), so measuring transient dynamics can be challenging (Stott, Townley & Hodgson 2011). As a result, whilst methods for calculating and analysing asymptotic dynamics are well established, the mathematical and computational resources required to calculate transients and conduct transient perturbation analyses have only been developed relatively recently.

It is hotly debated whether or not ignoring transient dynamics is a problem for demographic studies. In animals, population viability analyses based on asymptotic analyses have been shown to be predictive of observed population fate (Brook *et al.* 2000). In plants, asymptotic growth measures intriguingly correlate better with short-term observed population dynamics than simulated transient dynamics do (Crone *et al.* 2013). Conversely, as transient analyses are becoming more widespread, evidence supporting their importance for population management is increasing. For the endemic Puerto Rican orchid *Lepanthes rubripetala*, conservation management decisions based on asymptotic perturbation analyses are likely to be damaging to transient population density (Tremblay, Raventos & Ackerman 2015). In Michigan populations of

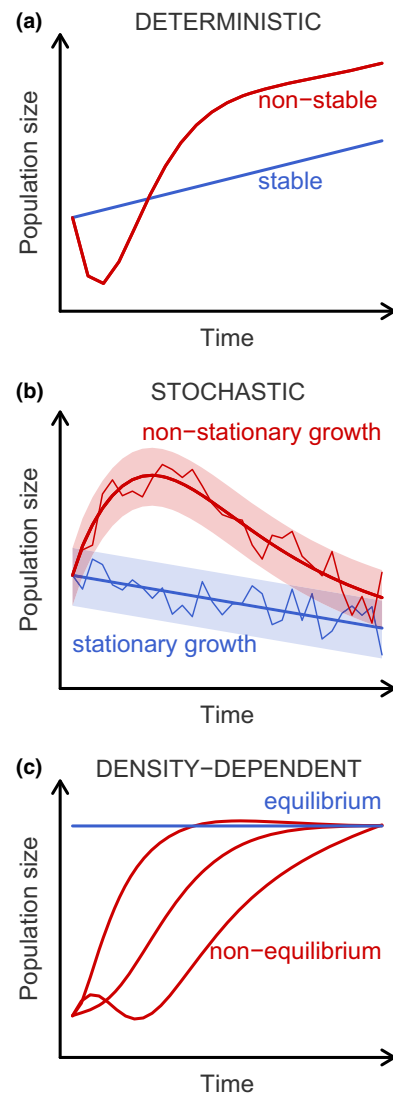


Fig. 1. Illustrations of transient dynamics in different types of model (y-axes on a log scale). (a) Transient dynamics in a 'deterministic' (linear, time-invariant) matrix projection model. Transient growth and structure of a non-stable population are different from those of a population with stable structure. (b) Transient dynamics in a 'stochastic' (time-varying model). Some population structures may result in non-stationary dynamics with mean and/or variance in growth that is not the same as the stationary, long-term stochastic growth of the population. (c) Transient dynamics in a 'density-dependent' (nonlinear) model. Populations not at equilibrium will exhibit different growth rates on their approach to equilibrium, which will depend on their structure.

American chestnut *Castanea dentata* affected by chestnut blight fungus *Cryphonectria parasitica*, perceived recovery following hypoviral infection of the blight may be transient fluctuations masking longer term population declines (Baines, Eager & Jarosz 2015). The Hawaiian vine *Allyxia stellata* is harvested for use in traditional lei (garlands), and management for transient rather than asymptotic population dynamics results in a larger population and more harvestable individuals (Wong & Ticktin 2015). Transient dynamics are also proving important to fundamental population processes. For plants in variable environments, around half of projected stochastic dynamics is attributable to transient responses to fluctuating

population structures (Ellis & Crone 2013; McDonald *et al.* 2016). Simulations also suggest that transient density is as important as asymptotic growth and initial population size to successful seed plant invasions (Iles *et al.* 2015). Relationships between transient dynamics and life history have been found both in plants and animals. In plants, species of early and late successional habitats have transients of larger potential amplitude than those of intermediate habitats (Stott *et al.* 2010). In animals, species with intermediate generation times have transients of larger potential amplitude than those with either short or long generation times (Gamelon *et al.* 2014).

Given the relative intractability of transient dynamics, many diverse methods for their calculation and analysis have been developed. Stott, Townley & Hodgson (2011) reviewed approaches to calculation of transient dynamics *per se* and suggested a framework for their study, but did not consider perturbation analyses of transients. Methods for prospective transient perturbation analysis are probably even more diverse than methods for calculation of transient dynamics *per se*. Here, I review these methods, relate them to the aforementioned framework of study, identify important new considerations when undertaking transient perturbation analysis, and comment on the utility of different methods in the differing contexts of population management and comparative studies.

Matrix projection models

In this section, I describe how MPMs are formulated, and define a number of key terms used throughout.

MODEL REPRESENTATIONS

MPMs may be represented in more than one form. The ‘state-space’ representation, using matrix and vector multiplication, is perhaps the most natural formulation. It is written for ‘deterministic’ (linear, time-invariant) models as

$$\mathbf{n}_t = \mathbf{A}^t \mathbf{n}_0$$

where \mathbf{n}_t is a vector of number or density of individuals at time t , \mathbf{n}_0 is the ‘initial’ or ‘current’ population vector at $t = 0$, and \mathbf{A} represents the projection matrix. In ‘stochastic’ (time-varying) models, the entries of \mathbf{A} vary with t , and in ‘density-dependent’ (nonlinear) models, the entries of \mathbf{A} are functions of \mathbf{n} . For deterministic models, the state-space formula can be rewritten using the ‘characteristic equation’ of the model

$$\mathbf{n}_t = \sum_{i=1}^s (\mathbf{v}_i^* \mathbf{n}_0) \lambda_i^t \mathbf{w}_i$$

where s is the dimension of the matrix, the λ_i are the eigenvalues of \mathbf{A} , the \mathbf{w}_i are the right eigenvectors of \mathbf{A} , the \mathbf{v}_i are the left eigenvectors of \mathbf{A} , and \mathbf{v}_i^* is the complex conjugate transpose of \mathbf{v}_i .

ASYMPTOTIC DYNAMICS

The characteristic equation can help understand the difference between asymptotic and transient dynamics. At its

limit, the characteristic equation reduces to $(\mathbf{v}_1^T \mathbf{n}_0) \lambda_1^t \mathbf{w}_1$ (where \mathbf{v}_1^T denotes the transposition of \mathbf{v}_1 from a column to a row vector and is the equivalent of a complex conjugate transpose for a vector with zero imaginary part). Therefore, after the transient period (at stable state), only the dominant eigendata $(\lambda_1, \mathbf{v}_1, \mathbf{w}_1)$, not the subdominant eigendata (other $\lambda_i, \mathbf{v}_i, \mathbf{w}_i$), dictate asymptotic dynamics. Asymptotic growth is equal to λ_1 and the stable population structure is equal to \mathbf{w}_1 . Thus, asymptotic growth and structure are completely independent of initial structure (\mathbf{n}_0), and only depend on the vital rates of the population (\mathbf{A}). In stochastic models, asymptotic mean and variance in growth are stationary. In density-dependent models, asymptotic dynamics consist of stable abundance, cycles or chaos.

TRANSIENT DYNAMICS

During the ‘transient period’ (before the population reaches stable state), both the subdominant eigendata and the dominant eigendata influence the population projection of deterministic models. The interaction between subdominant eigendata and \mathbf{n}_0 changes transient growth, density and structure around the asymptotic trajectory determined by the dominant eigendata (Fig. 1a). The influence of subdominant eigendata and \mathbf{n}_0 decreases exponentially with increasing t (Cohen 1979). Thus, transient dynamics depend on both initial structure (\mathbf{n}_0) and the vital rates (\mathbf{A}) and the interaction between them. Transient growth and structure of a non-stable population are different from asymptotic dynamics, but transient behaviour diminishes over time to give way to asymptotic dynamics (Fig 1a). In stochastic populations, transient dynamics may cause non-stationary stochastic growth: mean or variance in stochastic growth that is different from steady stochastic growth under stationary conditions (Fig. 1b). In density-dependent populations under non-equilibrium conditions, short-term dynamics of populations may vary during the approach to equilibrium, depending on their initial structure (Fig. 1c).

Transient population dynamics may also be represented using ‘transient indices’, which are functions of the MPM and its properties. For example, population inertia (Koons, Holmes & Grand 2007) is a transient index, which is a function of the dominant eigenvectors of \mathbf{A} and the initial population structure \mathbf{n}_0 :

$$\text{Population inertia} = \frac{\mathbf{v}_1^T \mathbf{n}_0 \|\mathbf{w}_1\|}{\mathbf{v}_1^T \mathbf{w}_1 \|\mathbf{n}_0\|}$$

where $\|\mathbf{x}\|$ denotes the one-norm, equal to the sum, of a vector \mathbf{x} . Transient indices represent a specific property of the MPM: in the case of population inertia, this is a ratio of two abundances: the abundance of a non-stable population as it approaches stable state after experiencing transient dynamics, to the abundance of a stable population of equivalent initial density exhibiting only stable growth and experiencing no transient dynamics (hence inertia is also sometimes called the ‘stable equivalent ratio’: Tuljapurkar & Lee 1997).

PERTURBATION ANALYSES

Perturbation analyses of population dynamics change part of the right-hand side of the equation (the MPM or transient index formula), which elicits a response in the left-hand side of the population equation (the population projection or transient index). Changes to the entries in the projection matrix \mathbf{A} affect both transient and asymptotic dynamics, but changes to the initial population structure \mathbf{n}_0 affect only transient dynamics. Perturbation analyses have commonly been used to find out the most efficient way of achieving management goals, for example, which vital rates and life stages to target to achieve $\lambda_1 = 1$, with the smallest effort or at the cheapest cost.

Methods for transient perturbation analysis

Methods for transient perturbation analysis vary widely in their approach, but distinct parallels and differences can be drawn between them. Broadly, transient perturbation methods can be classified according to whether they evaluate the MPM directly, or evaluate an index of transient dynamics. I have identified eight key points to consider when conducting a transient perturbation analysis. First, what approach is used to calculate the perturbation? Second, what type of model is being analysed? Third, what does the perturbation act on? Fourth, what is the response being measured? Fifth, does the method model perturbation nonlinearity? These points add to the following three important considerations identified by Stott, Townley & Hodgson (2011) when studying transient dynamics in deterministic linear, time-invariant MPMs, which are equally as relevant for transient perturbation analyses of these models. Sixth, does the method separate dynamics dependent on, and independent of, population structure? Seventh, what population structure is used to calculate the perturbation? Eighth, at what time in the projection is the perturbation measured? The eight points are discussed in turn, in reference to published methods for transient perturbation analysis of MPMs (Table 1).

WHAT APPROACH IS USED TO CALCULATE THE PERTURBATION?

The primary difference between methods for transient perturbation analysis is how they are calculated. There are three main approaches: *differentiation*, either of the MPM itself or of transient indices, using either characteristic algebraic formulae or matrix calculus; *transfer function analyses*, which were brought to ecology from engineering systems control; and *direct perturbation analyses*, which take a simulation approach. In this section, I introduce these three approaches and summarize their general strengths and weaknesses with reference to subsequent sections, which contain further detail.

As a perturbation analysis involves evaluating change in one parameter with respect to another parameter, an intuitive and common approach is *differentiation* of the MPM or transient index. This measures the linear response of population dynamics to perturbations of a very small magnitude. Differ-

entiation methods are usually referred to as 'sensitivity', which measures population response to absolute changes in vital rates or structure, and 'elasticity', which measures population response to proportional changes in vital rates or structure (Caswell 1978). Established sensitivity and elasticity analyses of asymptotic growth in deterministic models are formulated as differentials of the characteristic equation at its limit, which consists of a simple solution involving only the dominant eigenvectors (Caswell 1978). The earliest transient perturbation analyses extended this traditional approach by differentiating the entire characteristic equation, including *all* the eigenvalues and eigenvectors (Fox & Gurevitch 2000). This can be decomposed into contributions dependent on, and independent of, population structure (Yearsley 2004). Use of the characteristic equation has significant drawbacks, however. First, the characteristic equation cannot represent time-varying or nonlinear models (Caswell 2007; section 'What type of model is being analysed?'). Second, calculations involving all the eigenvalues and eigenvectors quickly become unwieldy, especially for matrices of large dimension. Differentiation of the state-space model overcomes these problems, so the introduction of matrix calculus by Caswell (2007) is what makes his method adaptable to so many model classes (section 'What type of model is being analysed?'), perturbation structures (section 'What does the perturbation act on?') and population responses (section 'What response is being measured?'). On the other hand, it is not as easy to decompose a state-space model into contributions independent of, and dependent on, population structure, and differences among MPMs mean that other methods that standardize for asymptotic growth (section 'Does the method separate dynamics dependent on, and independent of, population structure?') are perhaps more useful when comparing among models. Whether the state-space or characteristic formulation is used, no differentiation of the MPM is able to describe nonlinearity in the response of population parameters to perturbation (section 'Does the method model perturbation nonlinearity?'). Indices of transient population dynamics may also be directly differentiated to ascertain their sensitivity and elasticity. Most indices of transient dynamics have methods for their perturbation analysis (Table 1), and the best index to use will depend on the ecological application (as discussed in Stott, Townley & Hodgson 2011). When the equation for calculation of an index involves eigenvectors, then matrix calculus may be used (e.g. Verdy & Caswell 2008), but the relatively recent introduction of matrix calculus to ecology means that this is usually not the case for published indices. Transient indices have the advantage of being more comparable between different MPMs, as they can standardize for asymptotic growth of the MPM (section 'Does the method separate dynamics dependent on, and independent of, population structure?') and be insensitive to differences in the length of the transient period (section 'At what time in the projection is the perturbation measured?'), but are perhaps less informative for population management than evaluation of the MPM projection directly, as they are often less tractable than direct measures of population size or growth. Differentiation of transient indices is also

Table 1. Published methods for perturbation analysis of transient population dynamics

Reference	Perturbation approach	Model type	Model formulation	Perturbation structure	Response	Nonlinear?	Standardizes for long-term growth?	Measured at what time?	Notes
Fox & Gurevitch (2000)	Differentiation	Deterministic	Characteristic equation	Vital rates, population structure	Population size/density, structure	No	No	Any $t \geq 0$	Decomposes into contributions dependent on, and independent of, t_0 . Koons, Rockwell & Grand (2006) derive a simpler solution to the transient growth rate of the whole population. Software available for MATLAB in article supplementary materials
Yearsley (2004)	Differentiation	Deterministic	Characteristic equation	Vital rates	Population size/density, structure, growth	No	No	Any $t \geq 0$	
Mertens <i>et al.</i> (2006)	Differentiation	Deterministic (periodic)	Characteristic equation	Vital rates	Population size/density, structure	No	No	Any $t \geq 0$	Software available for MATLAB in article supplementary materials
Taverner <i>et al.</i> (2011)	Differentiation	Density-dependent	General nonlinear function	Vital rates, population structure	Population size/density, structure, growth, functions of these	No	N/A	Any $t \geq 0$	Software available for MATLAB/Maple in article supplementary materials
Haridas & Tuljapurkar (2007)	Direct perturbation	Deterministic	Modified state-space MPM	Vital rates	Population growth	No	Yes, but see notes	Any $t \geq 0$	Decomposes into components 1) perturbation acting on unperturbed population, 2) unperturbed dynamics acting on perturbed population. Standardizes for long-term growth of unperturbed model
Haridas, Tuljapurkar & Coulson (2009)	Direct perturbation	Stochastic	Modified state-space MPM	Vital rates	Population growth	No	No	Any $t \geq 0$	Decomposes into components 1) perturbation acting on unperturbed population, 2) unperturbed dynamics acting on perturbed population. Considers perturbation to both mean and variance in vital rates. Software available for MATLAB in article supplementary materials

Table 1. (continued)

Reference	Perturbation approach	Model type	Model formulation	Perturbation structure	Response	Nonlinear?	Standardizes for long-term growth?	Measured at what time?	Notes
Caswell (2007)	Differentiation (matrix calculus)	Deterministic, stochastic, density-dependent	State-space MPM	Vital rates, population structure	Population size/density, structure, growth, functions of these	No	No	Any $t \geq 0$	Software available for MATLAB in article supplementary materials
Caswell (2012)	Differentiation (matrix calculus)	Deterministic (age + stage), but see notes	State-space MPM	Vital rates, population structure	Population size/density, structure, growth, functions of these	No	No	Any $t \geq 0$	Article gives examples of deterministic models and long-term dynamics, but applying logic of Caswell (2007) extends to other model types and transient dynamics
Verdy & Caswell (2008)	Differentiation (matrix calculus)	Deterministic	Transient index	Vital rates, population structure	Reactivity, amplification envelope bounds	No	Yes, but see notes	$t = 1$ (reactivity), time of maximum amplification	Indices calculated using the 2-norm. Assumes $\lambda_1 < 1$. Matrix calculus version of Neubert & Caswell (1997) with extension to discrete-time population models
Townley <i>et al.</i> (2007)	Direct perturbation	Deterministic	Transient index	Vital rates	Maximum amplification and its bounds	Yes	Yes, but see notes	Time of maximum amplification	Indices calculated using the 1-norm. Standardizes for long-term growth of unperturbed model. Extension of Neubert & Caswell (1997) to discrete-time population models
Koons, Holmes & Grand (2007)	Differentiation	Deterministic	Transient index	Vital rates, population structure	Population inertia	No	Yes	$t \rightarrow \infty$	Software available for MATLAB in article supplementary materials
Stott, Hodgson & Townley (2012a)	Transfer function	Deterministic	Transient index	Vital rates	Population inertia	Yes	Yes	$t \rightarrow \infty$	Software available in R package popdemo (Stott, Hodgson & Townley 2012b)

limited in not being able to describe nonlinearity in the response of population parameters to perturbation (section ‘Does the method model perturbation nonlinearity?’).

Transfer function methods, translated to ecology from engineering systems control theory, are able to describe the exact relationship between perturbations to an MPM and expected population dynamic response over all possible perturbation magnitudes (Hodgson & Townley 2004). The transfer function of population inertia applies this methodology to transient perturbation analysis (Stott, Hodgson & Townley 2012a), although, in theory, the transfer function methodology could be applied to other measures of transient dynamics. The transfer function method has some significant advantages: it captures nonlinearity in perturbations (section ‘Does the method model perturbation nonlinearity?’), can easily model combined management approaches (section ‘What does the perturbation act on?’) and it is possible to calculate linear sensitivity or elasticity at non-zero perturbation magnitudes by differentiating the transfer function. However, it is hampered by certain restrictions on perturbation structures (section ‘What does the perturbation act on?’) and population responses (section ‘What response is being measured?’) it can evaluate. Population inertia is a standardized index that is comparable among models due to its standardization for asymptotic growth (section ‘Does the method separate dynamics dependent on, and independent of, population structure?’), insensitivity to length of the transient period (section ‘At what time in the projection is the perturbation measured?’), and existence of formulation on both its upper and lower bounds (Townley & Hodgson 2008; section ‘What population structure is used to calculate the perturbation?’). These attributes make population inertia a particularly useful measure for comparative analysis, but of more limited use in management of individual populations (although see Koons, Rockwell & Grand 2006).

Finally, perhaps the most flexible transient perturbation approach is *direct perturbation analysis*. This uses simulation: change the MPM and calculate the difference in dynamics compared to the original MPM, for whatever perturbation structure and perturbation magnitude desired. Direct perturbation analysis has been described for MPMs *per se* (Haridas & Tuljapurkar 2007; Haridas, Tuljapurkar & Coulson 2009), and is used implicitly in perturbation analysis of many transient indices (Townley *et al.* 2007). Direct perturbation analyses have the advantage of being able to model completely flexible perturbation structures (section ‘What does the perturbation act on?’), measure any desired response parameters (section ‘What response is being measured?’), and evaluate over any time frame (section ‘At what time in the projection is the perturbation measured?’). However, the simulation-based approach means comparing different structures and magnitudes becomes a heavy computational exercise and unwieldy for designing population management strategies. Evaluating the MPM directly does not standardize for differences in asymptotic growth and length of the transient period among models, and although direct perturbation methods for standardized transient indices exist, caution should be exercised when using these: they may not standardize properly (section

‘Does the method separate dynamics dependent on, and independent of, population structure?’). Direct perturbation analysis inherently incorporates nonlinearity in perturbation response, but methods using this approach may still erroneously assume linear response (section ‘Does the method model perturbation nonlinearity?’).

WHAT TYPE OF MODEL IS BEING ANALYSED?

Matrix projection models include many different classes of model, including ‘deterministic’ (linear, time-invariant) models, which do not model density dependence or stochasticity, ‘density-dependent’ (nonlinear) models (Costantino *et al.* 1997), ‘stochastic’ (time-varying) models (Fieberg & Ellner 2001), and nonlinear, time-varying models, which model both stochasticity and density dependence (Grant & Benton 2000). Methods for transient perturbation analysis exist for most model classes and also for specific model subclasses (Mertens *et al.* 2006; Caswell 2012), and so the most suitable method to use may depend largely on the type of model being analysed. The most comprehensive of existing methods is undoubtedly Caswell (2007), which owes its flexibility to the use of matrix calculus. It is applicable to linear, nonlinear, time-invariant and time-varying models, and the article includes worked-through examples for many varied MPM examples. All other existing methods for transient perturbation analysis focus on a specific class of model, as summarized in Table 1.

WHAT DOES THE PERTURBATION ACT ON?

There are two major components to an MPM: the matrix, and the population vector. Asymptotic dynamics are only sensitive to changes in the matrix, but transient dynamics are sensitive to changes in both the matrix and the population vector.

Minimally, methods for transient perturbation analysis usually include calculations for perturbations to individual matrix elements. For methods that use differentiation, summing the sensitivities or elasticities of multiple elements can inform on the impact of perturbations that affect multiple uncorrelated vital rates, even if they impact more than one life stage. Transfer function analysis offers a more flexible solution for complicated management strategies, as it offers the option of modelling simultaneous management affecting many matrix elements (including correlated vital rates). Stott, Hodgson & Townley (2012a) illustrate, for example, how transfer function methods can model the effect on transient dynamics of combined management of survival and fertility of a population of Koalas, *Phascolarctos cinereus*, on Snake Island, Victoria, Australia (Baxter *et al.* 2006). The perturbation structures that can be modelled by existing transfer function methods are not completely flexible, however: to model certain perturbation structures, it is necessary to use multi-rank, multi-parameter perturbation structures (see Hodgson & Townley 2004), but transfer function analysis of transient population dynamics is thus far limited to single-rank, single-parameter perturbation structures.

Matrix elements are usually functions of lower level vital rates: for example, fecundity may be a function of many parameters including probability of breeding, breeding success, seed production and germination probability in plants, clutch or litter size in vertebrates, parental survival in organisms with parental care, hatchling survival in precocious organisms, and many more organism- or system-specific parameters besides. Although not always explicitly stated, for differentiation methods, the sensitivity or elasticity of population dynamics to these lower level vital rates can be found by simply using the chain rule: multiplying the sensitivity of the matrix elements to the vital rate by the sensitivity of the population response to the matrix elements (Caswell 1989). Direct perturbation analyses are also able to model perturbation of lower level vital rates directly: the effect of perturbation to a lower level vital rate is found by making the direct perturbation a function of the lower level parameter. In theory, this can also be done for transfer functions, although they are currently more limited, due to their inability to model multi-rank and multi-parameter perturbations. Where circumstances allow, they may be able to model perturbations to lower level vital rates, but in other cases they may not.

Although transient dynamics are sensitive to changes in population structure, not all transient perturbation methods include calculations to facilitate this (Table 1). A perturbation to the matrix models sustained changes to vital rates, whilst perturbations to the population structure model instantaneous and non-sustained changes to the population structure. Analysing perturbations to population structure could be important in understanding the impacts on transient dynamics of unique exogenous disturbances such as fire, extreme weather, natural disasters, disease epidemics or migration. This information could be crucial to successful management of populations frequently exposed to such events. The ability to measure perturbation to population structure as well as vital rates may also be useful in informing whether sustained or one-off management actions are more effective at achieving population goals. As an example, population culls may be conducted with intense effort over a short time period, which could be modelled using perturbation to the population structure, or with moderate effort over a longer time period, which could be modelled using a perturbation to the vital rates. For some methods that do not standardize for population size, perturbations to the population structure may include addition of individuals as well as removal: for an example of transient sensitivity in subsidized populations, see Caswell (2007). Whilst many differentiation and direct perturbation methods include perturbation to population structure as well as vital rates, there are no existing transient perturbation analyses that measure nonlinear responses to changes in the population structure: the transfer function of inertia includes only formulae for vital rates (Stott, Hodgson & Townley 2012a).

WHAT RESPONSE IS BEING MEASURED?

Population dynamics may be expressed using abundance/density, or as growth, which is change in abundance or density

over time. Perturbation analyses of long-term dynamics usually focus on whichever of these is steady under stable or stationary conditions: growth in linear, time-invariant models, mean and variance in growth in time-varying models, and density in nonlinear models (although note that the ‘steady’ state of a nonlinear model may include unstable equilibria). Neither growth nor density is stable under transient dynamics, and so methods vary in whether they describe the population response to perturbation using density or growth, and some facilitate measurement of both (Table 1). Whether density or growth is a more pertinent measure to use depends largely on the application. For population management, the goal of intervention will probably matter: perhaps this is reduction of a pest to a certain density level; increase of growth of a threatened population to above a certain level; or maintaining a population at a certain density, and simultaneously retaining non-zero or positive population growth, whilst maximizing harvest from that population. For comparative analysis, the research question will dictate whether density or growth is more relevant.

Certain functions or components of population density and growth may also be of interest: again, the approach taken by Caswell (2007) is the most flexible in this regard and he explicitly recognizes that ‘sensitivity of other dependent variables may be more interesting than that of $n(t)$ ’. He gives examples that include averages, variances, maxima and minima of density, cumulative density, relative density of different stages, and more. This may be theoretically possible for other methods, but Caswell is forthcoming in stating the flexibilities of matrix calculus. Again, the best measure to use will depend on the managerial or comparative context in which it is being applied.

DOES THE METHOD MODEL PERTURBATION NONLINEARITY?

The response of population dynamics to a change in vital rates or population structure might not be linear (Fig. 2; Hodgson

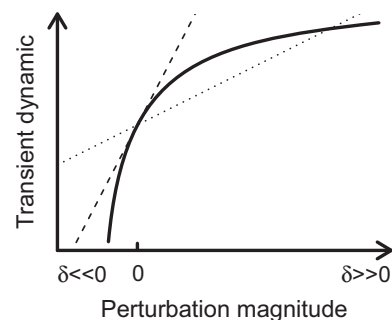


Fig. 2. Illustration of nonlinearity in transient response of a population to perturbation. A perturbation to vital rates or population structure (δ , x-axis) elicits a response in transient dynamics (transient population size or growth, y-axis). The exact relationship between the perturbation and the transient response may be nonlinear (solid line). Differentiation methods describe the tangent to this curve where the perturbation equals zero (dashed line), which may over- or underestimate the transient response to perturbation. Direct perturbation methods calculate the exact response for some perturbation value (in this case, $\delta \gg 0$), but may assume that this is linear over the entire perturbation range (dotted line).

& Townley 2004), but nearly all perturbation analyses assume that it is. Evidence suggests that the response of transient dynamics to perturbation may be extremely nonlinear (Stott, Hodgson & Townley 2012a; Tremblay, Raventos & Ackerman 2015). Whilst the response of long-term growth to increases in vital rates is always positive, the response of transient dynamics may be positive or negative. This means that, counterintuitively, increasing survival or fecundity of some stages may in fact decrease population growth in the short term. Ignoring nonlinearity may be a significant drawback of traditional sensitivity and elasticity analyses, although the importance of nonlinearity in comparison to other factors such as dynamic population structure has been questioned (Caswell 2001, p. 615).

Differentiation methods do not capture perturbation nonlinearity, as they evaluate the linear response of the population when the perturbation (δ) is infinitesimally close to zero ($\delta \approx 0$). This is equal to the tangent of the real relationship between δ and transient dynamics (dashed line in Fig. 2). This is a problem, because if population management involves perturbations that are not close to zero ($\delta \gg 0$ or $\delta \ll 0$), the population response may not at all be what is predicted by the linear perturbation analysis: it could be more extreme, less extreme or even the opposite of what linear sensitivity and elasticity analyses predict.

Transfer functions, on the other hand, measure the exact nonlinearity in expected population response to perturbation (solid line in Fig. 2). Management plans based on transfer function analyses could therefore be completely different from management plans based on linear perturbation analyses (Stott, Hodgson & Townley 2012a). However, transfer functions are unwieldy when comparing among different management possibilities for a population, or comparing among populations, as they are entire functions rather than single-number measures.

Direct perturbation analysis implicitly includes nonlinear responses. However, it is worth noting that some methods may use direct perturbation analysis but still assume linear response of the population to perturbation. For example, Haridas & Tuljapurkar (2007) use direct perturbation to measure elasticity in the population by making the perturbation magnitude equal to the size of the vital rate in the matrix ($\delta = a_{ij}$). Although this describes the population response to perturbation at that particular magnitude, their method assumes linearity across all perturbation magnitudes. If the real transient response is nonlinear, this means the measure does not capture the tangent to the curve for close-to-zero perturbations, but the chord of the curve that joins $\delta = 0$ and $\delta = a_{ij}$ (dotted line in Fig. 2, where $\delta = a_{ij} \gg 0$).

DOES THE METHOD SEPARATE DYNAMICS DEPENDENT ON, AND INDEPENDENT OF, POPULATION STRUCTURE?

Stott, Townley & Hodgson (2011) placed emphasis on the importance of separating population dynamics that are dependent on population structure from those that are not. Non-stable population structure interacts with subdominant matrix

eigendata to alter transient population dynamics around the asymptotic trajectory described by dominant matrix eigendata (Fig. 1c, section 'Transient dynamics'), so transient dynamics consist of a component that is dependent on population structure, and a component that is not. Separating dynamics dependent on, and independent of, population structure is perhaps less an issue for transient perturbation analyses of single populations for management: in this case, a manager may not care how much of the dynamic depends on the structure, only what the transient density or growth in response to perturbation is. However, when comparing among populations that have different asymptotic dynamics, especially in comparative studies, standardization against asymptotic growth may be important, as different MPMs have different asymptotic growth rates.

Separating out components dependent on, and independent of, population structure is more difficult in transient perturbation analyses than when calculating transient dynamics *per se*. Any perturbation to vital rates has an influence on asymptotic growth as well as the transient dynamics (Fig. 3b). Perturbations to population structure do not affect asymptotic growth or structure, but will affect the relative contribution of non-stable population structure during the transient period. Therefore, in a transient perturbation analysis that controls for asymptotic dynamics, it is necessary to dissociate both the

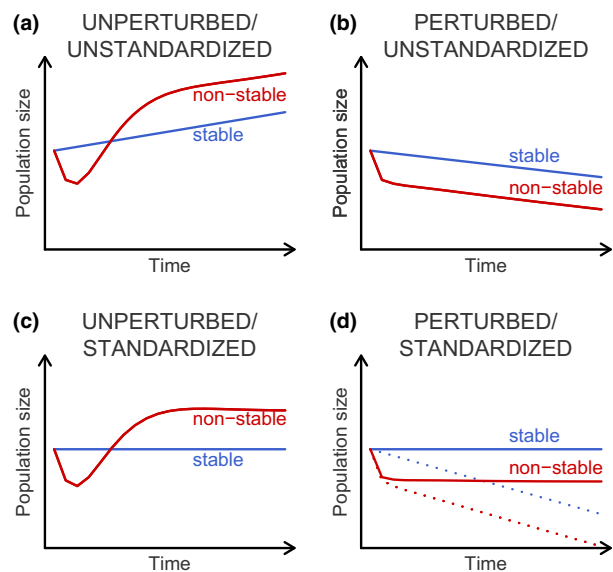


Fig. 3. Illustration of standardization of transient dynamics (y-axes on a log scale). (a) A population projection showing dynamics of a stable population vs. a non-stable population. (b) A perturbation to the same MPM results in a population projection with different asymptotic growth and different transient dynamics. (c) If the population dynamics in panel a are standardized, then density and growth of the non-stable population are measured relative to the stable population (the ratio of the red line to the blue line in panel a). (d) Because perturbations change both transient and asymptotic dynamics, transient perturbation analyses that standardize for asymptotic growth should measure the ratio of the non-stable perturbed population to the stable perturbed population (solid lines; the ratio of the red line to the blue line in panel b). Standardization of the MPM before perturbation does not account for the effect of the perturbation on asymptotic dynamics (dashed lines).

influence of long-term growth during the transient period in the unperturbed model, and the influence of the perturbation on long-term growth (solid lines in Fig. 3d). This is simple to achieve for unperturbed transient dynamics, by scaling the matrix \mathbf{A} by asymptotic growth λ_1 (Fig. 3c; Haridas & Tuljapurkar 2007; Townley *et al.* 2007). This does not work for transient perturbation analysis, however: scaling the matrix by λ_1 and then applying a perturbation still affects both transient and asymptotic dynamics of the standardized matrix (dotted lines in Fig. 3d), and so controls for the asymptotic growth of the unperturbed population, but not the effect of perturbation on asymptotic growth.

One approach to overcoming this problem when evaluating the MPM directly is to decompose the perturbation analysis into components dependent on, and independent of, the population structure (Yearsley 2004; Haridas & Tuljapurkar 2007), although a more precise interpretation is somewhat confusing: components that describe first, the action of the perturbation on the original population trajectory and second, the action of the original vital rates on the difference in population trajectory imposed by the perturbation (Haridas & Tuljapurkar 2007). However, if the component that does depend on population structure is large, this goes only partway to solving the problem.

Stott, Townley & Hodgson (2011) promoted the use of population inertia (defined in section 'Transient dynamics'). Population inertia inherently standardizes for asymptotic dynamics in both unperturbed and perturbed models, as it measures the density of a non-stable population at its limit to the density of an equivalent stable population at its limit, irrespective of the stable asymptotic growth rate. For this reason, sensitivity and transfer function analyses of population inertia (Koons, Holmes & Grand 2007; Stott, Hodgson & Townley 2012a) are good methods to use when comparing perturbation analyses among models where standardization for asymptotic growth is important, as may be the case for many comparative analyses addressing research questions concerning transient population dynamics.

WHAT POPULATION STRUCTURE IS USED TO CALCULATE THE PERTURBATION?

Transient dynamics are dependent on population structure, but it is not always possible to know the structure of a natural population. Such information requires a census, or detailed and unbiased sampling of individuals at all life stages. This is difficult to achieve in natural populations, where detection of individuals is likely to depend on life-cycle stage: for example, seedlings are far more difficult to find and to identify than adult plants (Forbis & Doak 2004), and in motile organisms, certain life stages are far more likely to move or migrate than others (Tidemann *et al.* 2000).

If population structure is known to some degree but uncertain, transient perturbation methods that decompose the formula into components variously dependent on, and independent of, population structure (Yearsley 2004; Haridas & Tuljapurkar 2007) are useful. These methods can inform on

whether the component of sensitivity or elasticity dependent on population structure is small or large, but if this component is large, then uncertainty in the population structure is still an issue.

When knowledge of the population structure is missing, it is possible to calculate bounds on transient dynamics. These are the most extreme transient dynamics a population may exhibit (Verdy & Caswell 2008), and transient dynamics of any possible population structure will lie within these bounds (see Stott, Townley & Hodgson 2011 for detailed information). Bounds are better defined for deterministic models (Townley & Hodgson 2008), although certain stochastic parameterizations also exist (Eager *et al.* 2014). They are of some use in population management, as they describe the best- and worse-case scenarios of population fate, although some evidence suggests that real populations do not usually reach such extreme magnitudes of transient dynamics (Ellis 2013). Bounds have been used in comparative studies, in describing the overall transient properties of a population (Stott *et al.* 2010; Gamelon *et al.* 2014). The population structures that achieve bounds on dynamics can, in theory, be applied using any transient perturbation analysis, but it is worth bearing certain caveats in mind. When the model is perturbed, the population structure that achieves the transient bound in the perturbed model may be different from that which achieves it in the unperturbed model if perturbation magnitude is much greater or lesser than zero (Stott, Hodgson & Townley 2012a). Transient bounds may respond differently to perturbations in vital rates or population structure than real-world population structures, and thus be limited in their ability to describe how a real population responds to perturbation. Last, bounds are better defined for certain transient indices such as population inertia (Koons, Holmes & Grand 2007) or maximum amplification (Townley & Hodgson 2008) than for other time points in the population projection.

AT WHAT TIME IN THE PROJECTION IS THE PERTURBATION MEASURED?

The transient period can last for variable times for different models. Transient dynamics at $t = 5$ would have very different interpretations for two models, where one reaches stability within five timesteps and the other takes many thousands of timesteps to do so. When conducting transient perturbation analyses, choosing a point in time or time interval to evaluate is a non-trivial problem (Stott, Townley & Hodgson 2011).

Transient perturbation methods that evaluate the MPM directly can evaluate transient dynamics at any time point in the projection, or over any interval of time in the projection. This is useful for population management: it is possible to evaluate management schemes over timescales that are relevant, evaluate how timing of management interventions may detrimentally or advantageously affect population dynamics, and predict population density or growth at precise points in the future.

However, when comparing between models, it may be important to ensure parity between dynamics, which evaluating at arbitrary time points does not afford. One solution is to

evaluate dynamics at $t = 1$, as this always describes the first-timestep transient response of the population. Alternatively, population inertia is a measure independent of the length of the transient period, but correlates strongly with other measures of transient dynamics (Stott, Townley & Hodgson 2011), and thus offers a pleasing solution to controlling for length of the transient period.

Discussion

The wealth of available methods for transient perturbation analysis means that suitable methods are already available for a diverse range of ecological applications. In this section, I summarize the utility of existing methods for population management and comparative studies, and identify a number of future directions for method development.

TRANSIENT PERTURBATION ANALYSIS FOR POPULATION MANAGEMENT

When using transient perturbation analyses for population management, it may be important to measure the actual response of a population in terms of real size or structure, over exact time frames. This will be relevant to management goals, which may aim to achieve certain densities or growth rates, within the period of policy-relevant or funding-restricted timescales. In such situations, using methods that evaluate the MPM directly, whether in a state-space or characteristic equation form, is a good approach. Depending on the method used, it may not always be possible to differentiate transient from asymptotic drivers of population growth, but this may not matter. Which method is preferable will depend on the model and personal preferences (e.g. familiarity with matrix calculus). More limited choices are available to those working with stochastic (Caswell 2007; Haridas, Tuljapurkar & Coulson 2009) and density-dependent (Caswell 2001; Tavecner *et al.* 2011) models. When working with deterministic models, the methods of Fox & Gurevitch (2000) or Yearsley (2004) offer an alternative solution to Caswell (2007) for anyone not comfortable with matrix calculus, although these methods may be relatively computationally intensive for MPMs of large dimension. The method of Haridas & Tuljapurkar (2007) uses direct perturbation and so can model more flexible perturbation structures than the above, if required. It is important to note that no methods are currently available that evaluate the MPM directly and that capture nonlinearity in transient response to perturbation: without simulation, it is not possible to evaluate nonlinearity in the impact of management on actual transient growth, density and structure over specific time periods. Any perturbation analysis that directly evaluates an MPM is inherently going to be very specific to that MPM, making it difficult to extrapolate results from one population to another one with different asymptotic dynamics, a different population structure, and a transient period of different length.

Evaluation of transient indices can overcome problems of decoupling transient and asymptotic dynamics, choosing a time point for analysis and capturing nonlinearity in population response to perturbation, whilst still being informative for achieving population management targets, especially when combined with evaluation of asymptotic dynamics. Indices that control for differences in asymptotic growth rate and are independent of the length of the transient period have greater parity among different models. Population inertia (Koons, Holmes & Grand 2007) is one such index, and correlates strongly with other indices of transient dynamics (Stott, Townley & Hodgson 2011). Nonlinear perturbation analyses for population inertia exist (Stott, Hodgson & Townley 2012a), which may provide more accurate descriptions of population response to perturbation than linear sensitivities or elasticities. However, the use of transient indices has downsides. They may be hampered by restrictions on the perturbation structure: for example, the transfer function of inertia cannot currently assess perturbations to population structure, and although is able to model combined management approaches, is restricted in the structures of perturbations to vital rates that it is able to model. Because indices represent specific functions of transient dynamics, choice of index will affect the response that can be measured: usually either population size, or growth, and often not structure.

TRANSIENT PERTURBATION ANALYSIS FOR COMPARATIVE STUDIES

The properties of transient indices that make them less useful for population management applications often make them more useful for comparative studies. Correcting for differences in asymptotic growth and length of the transient period are essential for making sure it is truly the transient population dynamics that are being compared (Stott *et al.* 2010; Stott, Townley & Hodgson 2011; Gamelon *et al.* 2014). This is particularly important for perturbation analyses, as any perturbation to vital rates will change both transient and asymptotic dynamics; thus, in perturbed models, asymptotic growth and the transient period are changed. For complete parity among models in comparative analyses, methods should correct both for the asymptotic dynamics of the unperturbed population, and the effect of the perturbation on asymptotic dynamics. As for population management, choice of index may restrict the perturbation structures that can be modelled and population responses that can be measured. Whilst nonlinear perturbation analyses might be relevant to comparative analysis, current methods are unwieldy: as they describe nonlinearity as an entire function, they are not easily amenable to statistical analysis.

Methods that evaluate the MPM directly may also be relevant to comparative analysis. This will depend on the nature of the question in hand: if the quantity of interest is the actual transient density or growth of different populations in response to perturbation, over a specific timescale, then these methods are equally as relevant. In any case, it is important to be aware

of what exactly is being measured, and whether the research question requires proper standardization of the transient dynamics or not.

FURTHER DIRECTIONS

Clear gaps in methodology exist, which would allow greater flexibility in the types of transient perturbation analysis that can be performed, and expand the specific applications that these tools can be extended to.

Basic extensions of asymptotic perturbation analysis have not yet been described for transient dynamics. Many of these would be of direct relevance to population management, and greatly aid design of management strategies. In particular, economic perturbation analyses evaluate not just the ecological efficiency of management, but its economic feasibility (Baxter *et al.* 2006). There is also greater scope for transient perturbation analyses that explicitly include the influence of spatial and temporal trends in environmental variables. For the most part, such extensions may involve some application of the chain rule (Brault & Caswell 1993), or its equivalent for nonlinear functions, and so should be simple to achieve.

There is a clear need for greater consideration of nonlinearity in transient perturbation analyses. Only one method for nonlinear transient perturbation analysis currently exists (Stott, Hodgson & Townley 2012a), and this is restricted in the perturbation structures and population responses it can describe. Extension of the transfer function method to other measures of transient population size, growth and structure would be welcome, and implementation of multi-rank, multi-parameter perturbations (Hodgson & Townley 2004) would make these methods more flexible. Alternatively, there is scope for introducing other methods that model nonlinear perturbations (Tavener *et al.* 2011), but that have not yet been applied to transient perturbation analysis. Existing nonlinear perturbation analyses are unwieldy, as they are described by entire functions rather than the single numbers of differentials. Second derivatives of population dynamics are a less unwieldy alternative, which measure the rate of change of the nonlinear perturbation curve with respect to the magnitude of the perturbation at $\delta \approx 0$, and are found by taking the differential of the differential of population dynamics. Many methods for their calculation for long-term growth and other population parameters exist (Caswell 1996; McCarthy, Townley & Hodgson 2008; Shyu & Caswell 2014); however, none currently exist for transient dynamics. Second derivatives are advantageous in that they can inform whether the response to perturbation is significantly nonlinear using a single number, rather than the whole function output of transfer function analyses. However, they are hampered by the same drawbacks as first-derivative sensitivity and elasticity in that rate of change of the curve may be a certain value at $\delta \approx 0$, but a very different value at $\delta \gg 0$ or $\delta \ll 0$. In any case, second-derivative approaches to transient perturbation analysis would be a welcome development.

The extension of transient perturbation analyses to other classes of matrix model would also be welcome. Although uncommon, nonlinear time-varying models that model both

density dependence and stochasticity (Grant & Benton 2000) are not covered explicitly by any existing methods. Other specific classes of matrix model such as coupled matrix models (Barabás, Meszéna & Ostling 2014) benefit from perturbation analyses for asymptotic, but not transient, dynamics. Integral projection models (Easterling, Ellner & Dixon 2000) are gaining fast popularity in population ecology, and calculations and perturbation analyses of transient dynamics are something that are very obviously missing for these.

Prospective ‘forward’ perturbation analyses are useful in assessing the response of projected population dynamics to potential changes in vital rates and population structure, but retrospective ‘backward’ perturbation analyses (e.g. life-table response experiments; Caswell 2000, 2010) are able to assess how recorded time series of population size and structure describe real population dynamic response to real variation in vital rates and population structure. Transient life table response experiments would be a welcome addition to the toolkit of population ecology.

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Data accessibility

This manuscript does not use any data.

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