

REVIEW

Matrix models for a changeable world: the importance of transient dynamics in population management

Thomas H. G. Ezard^{1*}, James M. Bullock², Harmony J. Dalglish³, Alexandre Millon⁴, Fanie Pelletier^{5,6}, Arpat Ozgul¹ and David N. Koons³

¹Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK; ²Centre for Ecology and Hydrology, Benson Lane, Crowmarsh Gifford, Wallingford, Oxon OX10 8BB, UK; ³Department of Wildland Resources and the Ecology Center, 5230 Old Main Hill, Utah State University, Logan, UT 84322-5230, USA; ⁴Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK; ⁵NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK; and ⁶Canada Research Chair in Evolutionary Demography and Conservation, Département de Biologie, Université de Sherbrooke, 2500 Boul. de l'Université, Sherbrooke, QC J1K 2R1, Canada

Summary

1. Matrix population models are tools for elucidating the association between demographic processes and population dynamics. A large amount of useful theory pivots on the assumption of equilibrium dynamics. The preceding transient is, however, of genuine conservation concern as it encompasses the short-term impact of natural or anthropogenic disturbance on the population.
2. We review recent theoretical advances in deterministic transient analysis of matrix projection models, considering how disturbance can alter population dynamics by provoking a new population trajectory.
3. We illustrate these impacts using plant and vertebrate systems across contiguous and fragmented landscapes.
4. Short-term responses are of fundamental relevance for applied ecology, because the time-scale of transient effects is often similar to the length of many conservation projects. Investigation of the immediate, post-disturbance phase is vital for understanding how population processes respond to widespread disturbance in the short- and into the long term.
5. *Synthesis and applications.* Transient analysis is critical for understanding and predicting the consequences of management activities. By considering short-term population responses to perturbations, especially in long-lived species, managers can develop more informed strategies for species harvesting or controlling of invasive species.

Key-words: asymptotic growth, inertia, Leslie matrix, momentum, stable-age structure, stable-stage structure, transient growth

Introduction

Matrix projection analysis is a flexible tool for incorporating the life history of an organism into a structured population model (Caswell 2001). It has been influential in elucidating how demographic processes impact population dynamics in evolutionary ecology (Lande 1982; van Tienderen 2000) and conservation biology (Morris & Doak 2002). The modelled asymptotic growth λ_1 is an especially important population parameter in matrix projection analysis. In a constant environment, $\lambda_1 > 1$ indicates that the population will eventually

increase whereas $\lambda_1 < 1$ indicates that the population will decline to extinction. The assumption of fixed demographic rates of survival, fertility and dispersal fails in natural populations, provoking development of stochastic alternatives (Tuljapurkar 1990; Lande, Engen & Sæther 2003). However, it is not always necessary for the conservation biologist to use complex and data-intensive stochastic models: no model – no matter how complex – can hope to mirror biological phenomena exactly (Levins 1966). Simple models offer conceptual clarity, and are an increasingly influential tool for rapid diagnosis of the persistence probability of threatened populations and species (Milner-Gulland & Rowcliffe 2007) or managing the spread of re-introduced or non-native species (Bullock, Pywell

*Correspondence author. E-mail: thomas.ezard@imperial.ac.uk

& Coulson-Phillips 2008). Matrix-modelling approaches that address questions like these often assess consider only equilibrium properties, but populations of conservation concern may rarely be in an equilibrium state (Hastings 2004).

We review theoretical advances that focus specifically on the short-term (i.e. transient), rather than equilibrium (i.e. asymptotic), state of the system. The deterministic approaches we consider can provide substantial insight, and have the attraction of moving beyond simplistic equilibrium approaches whilst maintaining the analytical tractability often lost in stochastic modelling. We outline the foundations of asymptotic analysis of population projection matrices (Caswell 2001 describes model construction extensively), and then describe and illustrate the relevance of transient population dynamics in applied ecology.

Asymptotic analysis

Despite criticisms concerning its lack of biological reality (e.g. Stephens *et al.* 2002), asymptotic analysis of matrix population models produces a number of informative quantities for applied ecology (Table 1). Asymptotic growth λ_1 can provide an accurate assessment of the best way to control an invasive species (Bullock, Clear Hill & Silvertown 1994), the effect of different herbicide treatments (Crone, Marler & Pearson 2009), whether harvesting of a species is sustainable (Ghimire *et al.* 2008) or if a particular re-introduction approach is the most effective for a declining species (Linares, Coma & Zabala 2008). Such comparisons can be taken further using sensitivities or elasticities (Table 1). Retrospective perturbation analysis, such as a Life Table Response Experiment, suggests how some desired difference among populations can be managed for (Bruna & Oli 2005) or why certain populations are expanding or declining to extinction (Cooch, Rockwell & Brault 2001;

Nicole, Brzosko & Till-Bottraud 2005). A related, but philosophically different approach (Caswell 2000), is prospective perturbation analysis. Prospective analysis does not indicate how the underlying demographic rates respond directly to the environment, revealing simply what the effect on population growth would be if they were changed (Silvertown, Franco & Menges 1996). Prospective analysis can also be used to inform management, for example in determining the least damaging harvesting strategy for an exploited species (Rogers-Bennett & Leaf 2006), how to enhance a particular life stage transition (Norris & McCulloch 2003) or how best to target control of an invasive species (Shea & Kelly 1988).

The limits of asymptotic analysis

Two key assumptions of asymptotic analyses are: (i) linear perturbations in sensitivity or elasticity analysis; and (ii) a stable population structure (Table 1). Any change to a vital rate will have nonlinear consequences for population growth (Hodgson & Townley 2004) and the assumption of linear perturbations infers infinitesimal change, making extrapolations to large increases (say 20%) problematic. Hodgson & Townley's (2004) transfer-function approach assesses the inaccuracy of analysis based on linear perturbations and also of demographic rate independence. ("Integrated sensitivities", [van Tienderen 1995] also correct for dependence among demographic rates, but assume linear perturbations). Although applying nonlinear perturbations can affect model prediction (Carslake, Townley & Hodgson 2009), neglecting a dynamic population structure has been argued to alter conclusions more (Caswell 2001, p. 615).

If the age-specific survival and fecundity rates are constant, the discrepancy between observed and asymptotic population structures declines exponentially over time as the population

Table 1. Summary of the asymptotic properties of matrix models (see Caswell 2001 for full details)

Measure	Symbol	Definition	Biological meaning
Asymptotic growth	λ_1 , or $r = \ln(\lambda_1)$	The dominant (largest) eigenvalue of the population transition matrix A	Eventual population growth rate
Stable distribution	w	The right eigenvector associated with λ_1 , rescaled such that all elements sum to unity	The post-transient proportion in each class (age or stage)
Reproductive value	v	The left eigenvector associated with λ_1 , rescaled such that all elements are relative to the first	Mean number of offspring produced from a post-transient individual in each class
Sensitivity of λ_1 to a matrix element	$\frac{\partial \lambda_1}{\partial a_{ij}}$	Linear approximation of the association between a matrix element a_{ij} and λ_1 . Assumes linearity, hence infinitesimal perturbation and stable population structure. Lower-level sensitivities to the demographic rates constitute matrix elements can be calculated	The influence of a_{ij} on λ_1
Elasticity of λ_1 to a matrix elements	$\frac{\partial \log \lambda_1}{\partial \log a_{ij}}$	As above, except association on a relative scale	The <i>relative</i> influence a_{ij} on λ_1 , enabling direct comparisons of demographic rates between survival (bounded between 0 and 1) and fecundities (bounded below at 0 only)

converges on the stable age distribution. The initial conditions of two populations might be very different, yet if the demographic rates remain the same both will converge on identical population structures (Cohen 1979b). However, population projections for the two populations might change markedly due to transient factors before convergence: there will be different proportions of individuals in each part of the population during this transient than under asymptotic, equilibrium conditions. Asymptotic population structure infers constant cohort size, but populations whose dynamics are influenced by strong cohort effects are widespread (Lindström & Kokko 2002) and the growth rates of such populations can change markedly from one cohort to the next (Gaillard *et al.* 1997). To highlight the effect that consideration of a non-equilibrium population structure has on the influence of demographic rates on λ_1 , Coulson *et al.* (2004) compared elasticities that were weighted by the asymptotic, equilibrium population structure (i.e. the stable age distribution) with elasticities calculated using the observed population structure in a given year. Simply changing one part of the calculation enables the effect of the assumption of equilibrium structure on demographic inference to be determined.

To illustrate how interpretation can change when dynamic structures are considered, we constructed post-breeding population transition matrices using individual-based data collected since 1985 from the population of Soay sheep (*Ovis aries*) living in Village Bay on Hirta in the St. Kilda archipelago, Scotland (57°49', 8°34'; see Clutton-Brock & Pemberton (2004) for comprehensive information on data-collection protocols). Each population transition matrix **A** takes the form given in Ezard *et al.* (2008) and a different **A** was constructed for each year under consideration using observed demographic rates from that year. Population size is defined here as the number of sheep alive on 1 August annually, which is the boundary between each 'sheep year'. We calculated elasticities using the asymptotic and observed population structures for each year and refer to these quantities as equilibrium and non-equilibrium elasticities, respectively (Coulson *et al.* 2004).

The use of asymptotic elasticities does not optimally describe population processes in this case because the population does not appear to be converging on a stable equilibrium due to fluctuations in abundance and age structure (Clutton-Brock & Coulson 2002). The correlation between equilibrium and non-equilibrium elasticities of λ_1 was significant but the variance explained low (Fig. 1; $\beta = 0.401$, $SE = 0.073$, $P < 0.001$, $r^2 = 0.158$, from a GLM with identity link and a squared variance function, the latter selected because the variance around non-equilibrium elasticities increased nonlinearly as elasticities increased). In particular, the contributions of lambs to λ_1 are consistently overestimated when elasticities are calculated using the asymptotic rather than observed population structure, whereas the converse is true for prime-aged individuals, whose relative influence on long-term population growth is consistent across years and population structures (Ezard *et al.* 2008). Thus, in this example, the use of asymptotic elasticities might direct more management and conservation efforts towards lambs compared with efforts driven by an

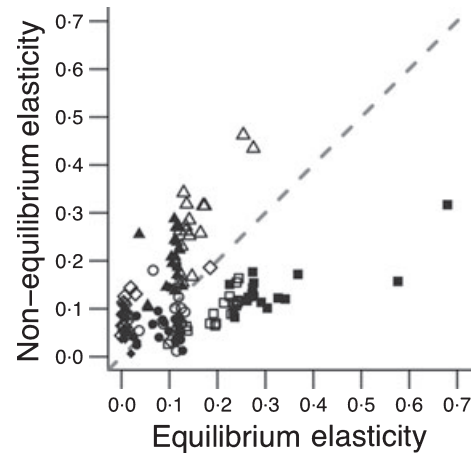


Fig. 1. Equilibrium and non-equilibrium elasticities were only loosely correlated in this Soay sheep population, which emphasizes how assuming an asymptotic population structure can lead to misleading management recommendations. Squares relate to lambs, circles to yearlings, triangles to prime-aged individuals and diamonds to oldest individuals; survival and fecundity are indicated by open and closed symbols, respectively. The dashed line is $y = x$.

analysis that incorporates a dynamic population structure. This sort of insight is arguably highly relevant to the management of ungulates in eco-tourism and hunting industries.

Transient analysis

WHY TRANSIENTS DEMAND ANALYSIS

Analysis of non-equilibrium, transient dynamics has recently been the focus of rapid theoretical developments (Table 2) of particular interest in an applied context because natural disturbances or management actions can disrupt life-history traits in non-uniform ways across the life cycle. Empirical evidence suggests that population structure is perturbed regularly in nature (Bierzychudek 1999; Clutton-Brock & Coulson 2002) and may well occur more frequently than asymptotic dynamics (Fox & Gurevitch 2000; Hastings 2004). Whilst the wavefront of plant invasions consists entirely of dispersing seeds that later progress through the life cycle, animal invasions often begin with the age classes most likely to disperse long distances (Shigesada & Kawasaki 1997). In exploited species, size-selective commercial fishing can exacerbate abundance fluctuations because the remnant population does not contain the largest individuals most likely to reproduce successfully (Anderson *et al.* 2008). Alternatively, the harvesting of young moose (*Alces alces*) freed up resources for older, more productive individuals, causing subsequent increases in population size (Solberg *et al.* 1999).

Unlike asymptotic analogues, transient analysis focuses on perturbations to the population structure rather than just on demographic rates. Following disturbance, a population's dynamics will change in a 'transient' fashion according to fluctuations in that structure until a new equilibrium is achieved. As such, there can be a clear distinction between inference drawn from asymptotic and transient analyses (McMahon &

Table 2. Summary of transient properties of matrix models

Measure	Definition	Biological meaning	References
Transient growth	$\lambda_t = \frac{1}{m} \ln \left(\frac{n_m}{n_0} \right)$. n_m is the population structure after m years	Transient population growth for a short interval	Koons <i>et al.</i> 2005
Damping ratio	$\rho = \lambda_1 / \lambda_2 $. λ_2 is the second-most dominant eigenvalue and $ \cdot $ magnitude	The speed of convergence to the stable-age distribution. Proportional to generation time	Caswell 2001, p. 95
Inertia	$M = (\mathbf{e}^T (\mathbf{v}_1^* \mathbf{n}_0) \mathbf{w}_1) / (\mathbf{e}^T \mathbf{n}_0)$. \mathbf{w}_m and \mathbf{v}_m denote the right and left eigenvectors of eigenvalue λ_m and $*$ denotes the complex conjugate transpose	The eventual abundance of a population with any historical structure relative to the asymptotic expectation	Koons <i>et al.</i> 2007
Momentum		A specific case of momentum for populations with stationary long-term trajectories	Koons <i>et al.</i> 2006b
Reactivity	Maximal transient rate at which a population could grow or decline.		Caswell & Neubert 2005
Amplitude	Maximum amplification in abundance (A_{\max}), and the time at which A_{\max} occurs		

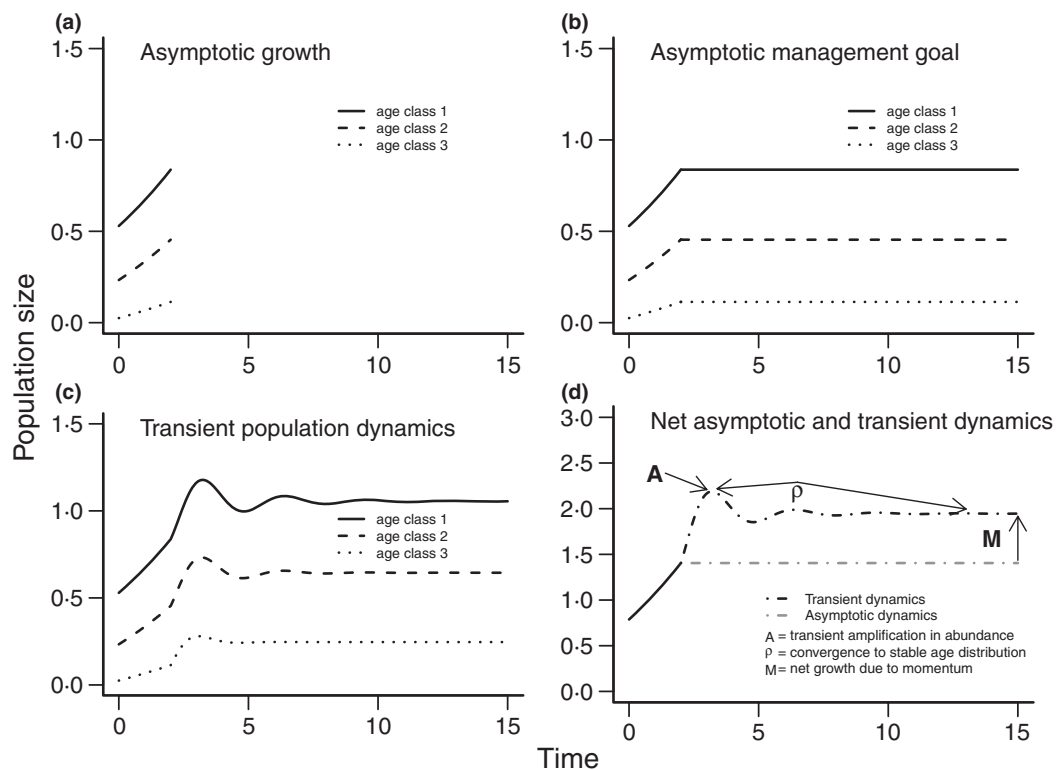


Fig. 2. Consider a population growing asymptotically until the probability of survival is changed to produce stationary asymptotic growth – $\lambda_1 = 1$ (a), which can only happen if the population somehow transitions immediately to the new stable population structure (b). The oscillating transient dynamics in (c) would only occur if the survival probability is changed but the population structure is not; (d) depicts the projected net population size for the two scenarios in (b) and (c). Note how the population’s initial reaction to the changed survival probability produces a large amplification (A) in abundance, an eventual net increase in abundance caused by population momentum (M) and non-negligible oscillations during convergence to the new stable structure determined by the damping ratio, ρ .

Metcalf 2008); focusing solely on asymptotic dynamics can lead to misleading results that affect management recommendations.

PROPERTIES OF TRANSIENT DYNAMICS

Consider a population with three age classes in its stable structure that is growing rapidly (Fig. 2a). Such rapid growth could

pose a threat to habitat conditions, community interactions and ecosystem functioning (Jefferies, Jano & Abraham 2006; Sinclair *et al.* 2007). Thus, a manager might act to halt population growth, i.e. induce stationary growth (Fig. 2b), by reducing reproduction or survival. When any management action such as harvesting occurs, the once stable structure will not match the new stable structure, inducing transient instability (Fig. 2c). Sudden instability in population structure can pro-

duce a large transient response in total abundance known as amplification (A in Fig. 2d). Although amplification suggests that transients increase population trajectories, they can suppress population growth as well (when the transient generates decreased trajectories compared to the asymptotic model, it is referred to as 'attenuation' in Townley *et al.* 2007; Townley & Hodgson 2008). The population structure will eventually converge to the new stable structure assuming no subsequent changes in underlying demographic rates (Fig. 2d). Before convergence, however, abundance and population growth will undergo transient fluctuations that have long-term effects on net abundance via a phenomenon that Keyfitz (1971) called 'population momentum' (M in Fig. 2d, Table 2). Consider a large ship attempting to turn east at a fixed point from a northerly course. By the time the ship achieves a perfect easterly bearing, it will have drifted north of the intended turning point as a result of the ship's physical momentum. In a population context, momentum could help or hinder a manager's ability to achieve immediate population goals (Koons, Rockwell & Grand 2006b).

The initial transient response of a population to perturbation (Fig. 2d), or of a newly established population, is sometimes examined using 'maximal' measures of dynamics that could result from very large departures away from a stable population structure. These include 'reactivity' (the maximal transient rate at which a population could grow or decline), the maximum amplification or attenuation in abundance (A_{\max}), and the time at which A_{\max} occurs; collectively known as the 'amplification envelope' (Neubert & Caswell 1997; Caswell & Neubert 2005). The Kreiss bound provides a lower bound for maximal amplification (Townley *et al.* 2007; Townley & Hodgson 2008).

PERTURBATION ANALYSIS FOR TRANSIENT DYNAMICS

Analysis of transient dynamics need not be limited to the early response of a population to unstable population structure. Several methods now exist for examining the response of short-term population abundance and growth at any time step (or time horizon) to a variety of realistic perturbations (Fox & Gurevitch 2000; Yearsley 2004; Koons *et al.* 2005; Mertens *et al.* 2006; Caswell 2007; Haridas & Tuljapurkar 2007). Caswell's (2007) matrix-calculus method serves as the most comprehensive approach for examining the transient effects of perturbations of linear, nonlinear, time-varying, stochastic and subsidized systems.

All else being equal, the time to reach asymptotic conditions is dictated by the initial population structure and damping ratio ρ , an inherent property of an organism's life cycle (Fig. 2d, Table 2), which can be affected by model construction (e.g. choice of stage numbers; Tenhumberg, Tyre & Rebarber 2009). Large values of ρ correspond to rapid approaches to asymptotic conditions, and *vice versa*. As perturbations can change the demographic rates comprising a species' life cycle, they can change the damping ratio and time spent in transient conditions as well (Caswell 2001, p. 244). Perturbation analysis is thus a powerful tool for gaining insight

into the impacts that alternative policy and management actions might have. The magnitude and duration of transient dynamics created by an unstable population structure will affect the asymptotic trajectory of abundance; a useful hypothetical comparison is how the trajectory of abundance differs relative to that of an otherwise identical population that always resides in a stable population structure. The general rationale is that a desired change has a lag before it becomes effective, during which the population trajectory 'drifts' depending on the historical population structure. Large magnitudes of such 'population momentum', i.e. M substantially below or above 1, respectively, signify populations whose long-term abundance is greatly affected by historical population structure (Koons, Holmes & Grand 2007). A negative elasticity value indicates that increasing the demographic rate decreases M or ρ , further reducing population size relative to an otherwise equivalent population in its stable structure (M) or increasing the time required to reach asymptotic conditions (ρ). In both cases, decreasing the parameter produces the opposite effect. Note that both the damping ratio and momentum elasticities to matrix elements sum to zero, but not those to lower-level parameters.

Taken in concert, analysis of these four measures (asymptotic growth, transient growth, damping ratio and population momentum) can yield a thorough understanding of the critical population processes in the short- and into the long term.

INVASIVE PLANT EXAMPLE

This section illustrates how one might investigate the importance of demographic rates using various measures, based on a model of the perennial monocarpic thistle *Carduus nutans*. Neglecting the transient and focusing only on the eventual, equilibrium state can ignore demographic rates that impact key population processes in the immediate, post-disturbance phase.

Carduus nutans has a life cycle that consists of seeds in the seed bank (SB; n_1), small rosettes (S; n_2), medium rosettes (M; n_3) and large rosettes (L; n_4). All rosettes have a chance of flowering and reproducing in a year's time, but larger rosettes do so with greater success (see Shea & Kelly 1988). Jongejans *et al.* (2008) formulated a stage-structured matrix model for *C. nutans* (Appendix S1, Supporting Information). Self-contained MATLAB and R (R Development Core Team 2009) code for this analysis is supplied as Appendices S2 and S3 (Supporting information).

This population has an asymptotic population growth rate of $\lambda_1 = 1.75$, stable population structure = [0.872 0.093 0.031 0.004] and reproductive value = [1 32 143 1084]. Thus, in the long term, the population should grow rapidly (increasing annually by 75%). Population control efforts based on asymptotic elasticities would suggest that managers should focus, in order of importance, on decreasing the chance of seeds escaping from floral herbivory, the establishment of new seeds from seedlings and survival of medium-sized individuals (Fig. 3a).

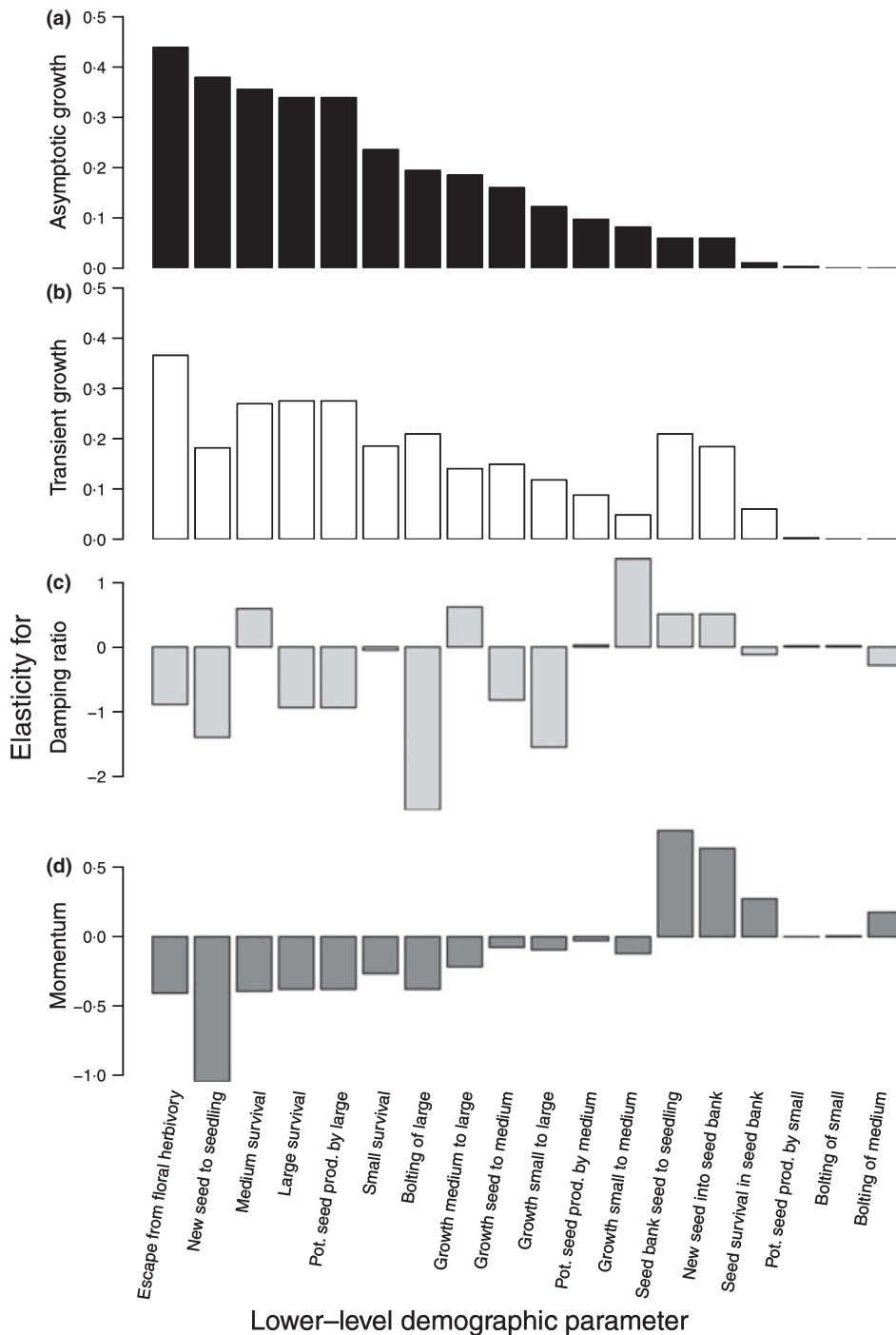


Fig. 3. Elasticities for (a) asymptotic population growth (λ_1); (b) average rate of transient growth during the 5 years after invasion $\frac{1}{5} \ln \left(\frac{n_5}{n_0} \right)$, where n_m is the population structure after m years; (c) the damping ratio (ρ); and (d) population momentum (M) for the *Carduus nutans* case study. Neglecting the transient and focusing only on the eventual, equilibrium state can ignore demographic rates that impact population processes in the short-term: here, seedbank-related variables impact the transient substantially whilst being relatively unimportant asymptotically.

Yet, given that *C. nutans* is an invasive weed outside its endemic range, analysis of the transient dynamics following invasion might be more applicable for management (Caswell 2007). The few large rosettes (<0.5%) in the final life-history stage of a stable population have nearly all (>85%) of the reproductive value. Subtle perturbations to population structure could therefore have substantial impacts on population performance. Invasion is, by definition, a process that

evolves from originally unstable conditions in plants, where only the offspring can disperse naturally. For the sake of example, consider an initial invasion of one dormant seed (population structure = [1 0 0 0]). The average rate of transient growth during the 5 years after invasion is 1.06, much lower than λ_1 . There are furthermore notable differences in rank order of demographic rates: seedling establishment from new seeds has the second highest influence on λ_1 but only the eighth

highest influence on transient growth over the five post-invasion years. Rates associated with the seed bank influence transient growth much more than they do asymptotic growth (Fig. 3a, b). Immediate control efforts might therefore be directed at different demographic rates than those indicated by an asymptotic analysis.

Management actions that change demographic rates will also affect the duration of the transient before asymptotic conditions are reached (ρ ; Fig. 3c). For *C. nutans*, $\rho = 2.64$, and is most sensitive to proportional changes in bolting of large individuals and growth from small to large plants (Fig. 3d), both of which are negative suggesting that increases to these rates would increase the duration of the transient dynamics. An invasion of seeds produces $M = 0.08$, i.e. the eventual population size is 92% smaller than a hypothetical population that always resided at the stable structure. Population momentum is most sensitive to proportional changes in the establishment of seedlings from new seeds and the seedbank as well as new seeds entering the seedbank (Fig. 3d). Whilst an increase in establishment of seedlings from new seeds further reduces the eventual size of the perturbed population relative to the hypothetical comparison, an increase in storage of seeds in the seed bank would increase the perturbed population's eventual abundance.

By considering a variety of measures, the consequences of any planned action are more fully understood.

POPULATION TRANSIENTS IN FRAGMENTED LANDSCAPES

Many species of conservation concern live in fragmented landscapes, due to natural and/or anthropogenic pressures. Understanding the dynamics and persistence of small, isolated populations requires explicit consideration of spatial heterogeneity (Akçakaya & Sjørgen-Gulve 2000; Hanski & Gaggiotti 2004). Empirical tests of the theory and its application to wildlife conservation have mostly been limited to approaches that do not explicitly consider local demographic processes (e.g. patch occupancy models, Lopez & Pfister 2001). Spatial structure can, however, be incorporated in matrix models using demographically structured metapopulation models (Akçakaya & Sjørgen-Gulve 2000; Hunter & Caswell 2005), sometimes referred to as the megamatrix (Pascarella & Horvitz 1998; Stephens *et al.* 2002). Hunter & Caswell's (2005) vec-permutation matrix approach allows the construction of a matrix-based metapopulation model using demographic data from several local populations. Quantifying the contribution of populations to the metapopulation is achieved by decomposing the metapopulation projection matrix into components that model local demography and between-patch dispersal in the asymptotic (Caswell 2001) or transient case (Caswell 2007). The inclusion of dispersal into matrix models permits projection of population spread (Neubert & Caswell 2000; Caswell, Lensink & Neubert 2003). Although asymptotic methods can yield high predictive ability (Bullock *et al.* 2008), patch importance can fluctuate markedly in the short-term, which impacts metapopulation

connectivity and therefore metapopulation dynamics. The relative importance of sites can differ between long- and short-term dynamics even when the demography remains constant (Ozgul *et al.* 2009). As in contiguous landscapes, analysis of short-term consequences increases understanding of the population dynamics.

Models as part of the applied ecologist's toolbox

Management recommendations from mathematical models and achievable field protocols are rarely concordant. The power of models often lies in their ability to determine the population consequences, as assumed by a model, of management actions. Rather than a start- or end-point, population modelling ideally forms part of an integrated approach to applied ecology (Milner-Gulland & Rowcliffe 2007). Appropriate perturbation analysis might identify a key demographic rate, which in turn might become the focus of data collection efforts, which in turn might identify model limitations or flawed assumptions. Exceedingly complex models (e.g. stochastic, spatially-explicit, individual-based models) are often used in conservation, but may not always be necessary: simpler models can often provide sufficient detail and accuracy (Bullock *et al.* 2008). A rebuttal to the critique of a lack of biological realism in asymptotic analysis (e.g. Stephens *et al.* 2002) often lies in the flexibility of matrix modelling, which can eschew asymptotic analysis whilst retaining the analytical tractability of deterministic approaches. Examples include incorporation of interactions between harvesting and density dependence (Barbraud *et al.* 2008), functional relationships between predator demographic rates and prey abundance (Henden *et al.* 2008) or achievable change per unit cost (Baxter *et al.* 2006).

Transient analysis of matrix models can be used to estimate relevant elasticities amidst density dependence, environmental stochasticity and many other conservation-relevant scenarios (Caswell 2007). Analysis of transient dynamics forms a crucial part of the applied ecologist's toolbox, potentially elucidating why asymptotic analysis can fail to approximate satisfactorily the short-term, on-the-ground reality of conservation and management. The differences between transient and asymptotic analysis reduce as the short-term blends into the medium- and long term (Cohen 1979a,b). The boundaries between these time frames depend, in part, upon the life history of the organism. Theoretical studies suggest that organisms with long generation times are more apt to experience: (i) longer durations of transient dynamics (Koons *et al.* 2005); (ii) larger departures in transient abundance and growth rates away from asymptotic conditions (Koons *et al.* 2005; Haridas & Tuljapurkar 2007); and (iii) larger magnitudes of population momentum relative to those with short generation times (Koons, Grand & Arnold 2006a; Koons *et al.* 2006b).

When considering mathematical models, 'it is important to match the time-scale of observation with the analysis' (Hastings 2004, p. 40). In applied ecology, the period described by the transient dynamics is likely to be the fundamental period of interest because it considers explicitly the ramifications

of disturbance originating from abiotic, biotic and/or anthropogenic processes. Despite this, transients are not the be-all and end-all: both asymptotic and transient analyses assume a single perturbation to the system over the timeframe under consideration. This may be no more likely over 5 years than 50 or 500. Stochastic transient analysis has a role to play in systems characterized by numerous and repetitive disturbance, but may be less than informative in non-data rich systems when reliant on uninformed assumptions.

Conclusion

Analysis of transient dynamics is of particular relevance for the management of species (i) in exploited populations; (ii) with long generation times; and/or (iii) subject to or part of a biological invasion. Analysis in a deterministic framework retains analytical tractability. By investigating population processes in the short- and long term, the tools reviewed here should help provide more accurate answers to questions about population management and conservation. For example, will reducing exploitation of a particular life stage only have a lagged effect on population growth? If individuals of a certain stage are introduced to a population, will this stop the decline in population size? Would individuals of a different stage provoke a more rapid response?

Acknowledgements

This manuscript was a result of discussions held at the 2008 Populations under Pressure symposium; we gratefully acknowledge the financial and logistical support given by the NERC Centre for Population Biology. Additionally, we would like to thank Luca Börger, Nils Bunnefeld, Maria Dickinson, Martina Di Fonzo, Jean-Michel Gaillard, E.J. Milner-Gulland, Andy Purvis and three anonymous reviewers for excellent comments that improved earlier versions of this manuscript. We would also like to thank Tim Clutton-Brock and Josephine Pemberton for allowing us access to the soay sheep data, and everyone involved in the project for helping collect it. T.H.G.E. was supported by NERC (grant NE/E015956/1 to Andy Purvis & Paul Pearson) and J.M.B. by CEH project C03513.

References

Akçakaya, H.R. & Sjørgen-Gulve, P. (2000) Population viability analysis in conservation planning: an overview. *Ecological Bulletins* (eds P. Sjørgen-Gulve & T. Ebenhard), pp. 9–21. Munksgaard, Malden.

Anderson, C.N.K., Hsieh, C.H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M. & Sugihara, G. (2008) Why fishing magnifies fluctuations in fish abundance. *Nature*, **452**, 835–839.

Barbraud, C., Marteau, C., Ridoux, V., Delord, K. & Weimerskirch, H. (2008) Demographic response of a population of white-chinned petrels *Procerallia aequinoctialis* to climate and longline fisheries. *Journal of Applied Ecology*, **45**, 1460–1467.

Baxter, P.W.J., McCarthy, M.A., Possingham, H.P., Menkhorst, P.W. & McLean, N. (2006) Accounting for management costs in sensitivity analyses of matrix population models. *Conservation Biology*, **20**, 893–905.

Bierzychudek, P. (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications*, **9**, 1278–1287.

Bruna, E.M. & Oli, M.K. (2005) Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. *Ecology*, **86**, 1816–1824.

Bullock, J.M., Clear Hill, B. & Silvertown, J. (1994) Demography of *Cirsium vulgare* in a grazing experiment. *Journal of Ecology*, **82**, 101–111.

Bullock, J.M., Pywell, R.F. & Coulson-Phillips, S.J. (2008) Managing plant population spread: prediction and analysis using a simple model. *Ecological Applications*, **18**, 945–953.

Carslake, D., Townley, S. & Hodgson, D.J. (2009) Predicting the impact of stage-specific harvesting on population dynamics. *Journal of Animal Ecology*, **78**, 1076–1085.

Caswell, H. (2000) Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology*, **81**, 619–627.

Caswell, H. (2001) *Matrix Population Models: Construction, Analysis and Interpretation*, 2nd edn. Sinauer Associates Inc., Sunderland, MA.

Caswell, H. (2007) Sensitivity analysis of transient population dynamics. *Ecology Letters*, **10**, 1–15.

Caswell, H. & Neubert, M.G. (2005) Reactivity and transient dynamics of discrete-time ecological systems. *Journal of Difference Equations and Applications*, **11**, 295–310.

Caswell, H., Lensink, R. & Neubert, M.G. (2003) Demography and dispersal: life table response experiments for invasion speed. *Ecology*, **84**, 1968–1978.

Clutton-Brock, T. & Coulson, T. (2002) Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **357**, 1285–1298.

Clutton-Brock, T. & Pemberton, J. (2004) *Soay Sheep*. Cambridge University Press, Cambridge.

Cohen, J.C. (1979a) The cumulative distance from an observed to a stable age distribution. *Siam Journal of Applied Mathematics*, **36**, 169–175.

Cohen, J.C. (1979b) Ergodic theorems in demography. *Bulletin of the American Mathematical Society*, **1**, 275–295.

Cooch, E., Rockwell, R.F. & Brault, S. (2001) Retrospective analysis of demographic responses to climate change: a lesser snow goose example. *Ecological Monographs*, **71**, 377–400.

Coulson, T., Guinness, F., Pemberton, J. & Clutton-Brock, T. (2004) The demographic consequences of releasing a population of red deer from culling. *Ecology*, **85**, 411–422.

Crone, E.E., Marler, M. & Pearson, D.E. (2009) Non-target effects of broadleaf herbicide on a native perennial forb: a demographic framework for assessing and minimizing impacts. *Journal of Applied Ecology*, **46**, 673–682.

Ezard, T.H.G., Gaillard, J.-M., Crawley, M.J. & Coulson, T. (2008) Habitat dependence and correlations between elasticities of long-term growth rates. *American Naturalist*, **172**, 424–430.

Fox, G.A. & Gurevitch, J. (2000) Population Numbers Count: tools for Near-Term Demographic Analysis. *American Naturalist*, **156**, 242–256.

Gaillard, J.-M., Boutin, J.-M., Delorme, D., Laere, G.V., Duncan, P. & Lebreton, J.-D. (1997) Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia*, **112**, 502–513.

Ghimire, S.K., Gimenez, O., Pradel, R., McKey, D. & Aumeeruddy-Thomas, Y. (2008) Demographic variation and population viability in a threatened Himalayan medicinal and aromatic herb *Nardostachys grandiflora*: matrix modelling of harvesting effects in two contrasting habitats. *Journal of Applied Ecology*, **45**, 41–51.

Hanski, I. & Gaggiotti, O.E. (2004) Metapopulation biology: past, present, and future. *Ecology, Genetics, and Evolution of Metapopulations* (eds L. Hansson & O.E. Gaggiotti), pp. 3–22. Elsevier, London.

Haridas, C.V. & Tuljapurkar, S. (2007) Time, transients and elasticity. *Ecology Letters*, **10**, 1143–1153.

Hastings, A. (2004) Transients: the key to long-term ecological understanding. *Trends in Ecology and Evolution*, **19**, 39–45.

Henden, J.-A., Bårdsen, B.-J., Yoccoz, N.G. & Ims, R.A. (2008) Impacts of differential prey dynamics on the potential recovery of endangered arctic fox populations. *Journal of Applied Ecology*, **45**, 1086–1093.

Hodgson, D.J. & Townley, S. (2004) Linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. *Journal of Applied Ecology*, **41**, 1155–1161.

Hunter, C.M. & Caswell, H. (2005) The use of the vec-permutation matrix in spatial matrix population models. *Ecological Modelling*, **188**, 15–21.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, **94**, 234–242.

Jongejans, E., Shea, K., Skarpaas, O., Kelly, D., Sheppard, A.W. & Woodburn, T.L. (2008) Dispersal and demography contributions to population spread of *Carduus nutans* in its native and invaded ranges. *Journal of Ecology*, **96**, 687–697.

Keyfitz, N. (1971) On the momentum of population growth. *Demography*, **8**, 71–80.

Koons, D.N., Grand, J.B., Zinner, B. & Rockwell, R.F. (2005) Transient population dynamics: relations to life history and initial population state. *Ecological Modelling*, **185**, 283–297.

Koons, D.N., Grand, J.B. & Arnold, J.M. (2006a) Population momentum across vertebrate life histories. *Ecological Modelling*, **197**, 418–430.

- Koons, D.N., Rockwell, R.F. & Grand, J.B. (2006b) Population momentum: Implications for wildlife management. *Journal of Wildlife Management*, **70**, 19–26.
- Koons, D.N., Holmes, R.R. & Grand, J.B. (2007) Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology*, **88**, 2857–2867.
- Lande, R. (1982) A quantitative genetic history of life history evolution. *Ecology*, **63**, 607–615.
- Lande, R., Engen, S. & Sæther, B.-E. (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Levins, R. (1966) The strategy of model building in population biology. *American Scientist*, **54**, 421–431.
- Linares, C., Coma, R. & Zabala, M. (2008) Restoration of threatened red gorgonian populations: an experimental and modelling approach. *Biological Conservation*, **141**, 427–437.
- Lindström, J. & Kokko, H. (2002) Cohort effects and population dynamics. *Ecology Letters*, **5**, 338–344.
- Lopez, J.E. & Pfister, C.A. (2001) Local population dynamics in metapopulation models: implications for conservation. *Conservation Biology*, **15**, 1700–1709.
- McMahon, S.M. & Metcalf, C.J.E. (2008) Transient sensitivities of non-indigenous shrub species indicate complicated invasion dynamics. *Biological Invasions*, **10**, 833–846.
- Mertens, S.K., Yearsley, J.M., van den Bosch, F. & Gilligan, C.A. (2006) Transient population dynamics in periodic matrix models: methodology and effects of cyclic permutations. *Ecology*, **87**, 2238–2348.
- Milner-Gulland, E.J. & Rowcliffe, J.M. (2007) *Conservation and Sustainable Use*. Oxford University Press, Oxford.
- Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology: Theory and Practice of Population Viability Analysis*. Sinauer, Sunderland, MA.
- Neubert, M.G. & Caswell, H. (1997) Alternatives to resilience for measuring the response of ecological systems to perturbation. *Ecology*, **78**, 653–665.
- Neubert, M.G. & Caswell, H. (2000) Demography and dispersal: Calculation and sensitivity analysis of invasion speed for structured populations. *Ecology*, **81**, 1613–1628.
- Nicole, F., Brzosko, E. & Till-Bottraud, I. (2005) Population viability analysis of *Cypripedium calceolus* in a protected area: longevity, stability and persistence. *Journal of Ecology*, **93**, 716–726.
- Norris, K. & McCulloch, N. (2003) Demographic models and the management of endangered species: a case study of the critically endangered Seychelles magpie robin. *Journal of Applied Ecology*, **40**, 890–899.
- Ozgul, A., Oli, M.K., Armitage, K.B., Blumstein, D.T. & van Vuren, D.H. (2009) Influence of local demography on asymptotic and transient dynamics of a yellow-bellied marmot metapopulation. *American Naturalist*, **173**, 517–530.
- Pascarella, J.B. & Horvitz, C.C. (1998) Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. *Ecology*, **79**, 547–563.
- R Foundation for Statistical Computing. (2009). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Rogers-Bennett, L. & Leaf, R.T. (2006) Elasticity analyses of size-based red and white abalone matrix models: management and conservation. *Ecological Applications*, **16**, 213–224.
- Shea, K. & Kelly, D. (1988) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, **8**, 824–832.
- Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, Oxford.
- Silvertown, J., Franco, M. & Menges, E. (1996) Interpretation of elasticity metrics as an aid to the management of plant populations for conservation. *Conservation Biology*, **10**, 519–597.
- Sinclair, A.R.E., Mduma, S.A.R., Grant, J., Hopcraft, C., Fryxell, J.M., Hilborn, R. & Thirgood, S. (2007) Long-term ecosystem dynamics in the Serengeti: lessons for conservation. *Conservation Biology*, **21**, 580–590.
- Solberg, E.J., Sæther, B.-E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Stephens, P.A., Frey-Roos, F., Arnold, W. & Sutherland, W.J. (2002) Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology*, **71**, 343–361.
- Tenhumberg, B., Tyre, A.J. & Rebarber, R. (2009) Model complexity affects transient population dynamics following a dispersal event: a case study with pea aphids. *Ecology*, **90**, 1878–1890.
- van Tienderen, P.H. (1995) Life cycle trade-offs in matrix population models. *Ecology*, **76**, 2482–2489.
- van Tienderen, P.H. (2000) Elasticities and the link between demographic and evolutionary dynamics. *Ecology*, **81**, 666–679.
- Townley, S. & Hodgson, D.J. (2008) *Erratum et addendum*: transient amplification and attenuation in stage-structured population dynamics. *Journal of Applied Ecology*, **45**, 1836–1839.
- Townley, S., Carslake, D., Kellie-Smith, O., McCarthy, D. & Hodgson, D.J. (2007) Predicting transient amplification in perturbed ecological systems. *Journal of Applied Ecology*, **44**, 1243–1251.
- Tuljapurkar, S. (1990) *Population Dynamics in Variable Environments*. Springer, New York.
- Yearsley, J.M. (2004) Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling*, **177**, 245–258.

Received 23 November 2009; accepted 3 March 2010

Handling Editor: Andre Punt

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Population transition matrix and demographic rates for the *Carduus nutans* case study.

Appendix S2. MATLAB code to perform transient and asymptotic analysis.

Appendix S3. R code to perform transient and asymptotic analysis.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.