

## REVIEW AND SYNTHESIS

# A framework for studying transient dynamics of population projection matrix models

Iain Stott,<sup>1</sup> Stuart Townley<sup>2</sup> and  
David James Hodgson<sup>1\*</sup>

<sup>1</sup>Centre for Ecology and  
Conservation, Biosciences, College  
of Life and Environmental Sciences,  
University of Exeter Cornwall  
Campus, Tremough, Treliever Road,  
Penryn, Cornwall, TR10 9EZ, UK

<sup>2</sup>College of Engineering,  
Mathematics and Physical Sciences,  
University of Exeter, Harrison  
Building, Streatham Campus, Exeter,  
Devon, EX4 4QF, UK

\*Correspondence: E-mail:  
d.j.hodgson@exeter.ac.uk

## Abstract

Empirical models are central to effective conservation and population management, and should be predictive of real-world dynamics. Available modelling methods are diverse, but analysis usually focuses on long-term dynamics that are unable to describe the complicated short-term time series that can arise even from simple models following ecological disturbances or perturbations. Recent interest in such transient dynamics has led to diverse methodologies for their quantification in density-independent, time-invariant population projection matrix (PPM) models, but the fragmented nature of this literature has stifled the widespread analysis of transients. We review the literature on transient analyses of linear PPM models and synthesise a coherent framework. We promote the use of standardised indices, and categorise indices according to their focus on either convergence times or transient population density, and on either transient bounds or case-specific transient dynamics. We use a large database of empirical PPM models to explore relationships between indices of transient dynamics. This analysis promotes the use of population inertia as a simple, versatile and informative predictor of transient population density, but criticises the utility of established indices of convergence times. Our findings should guide further development of analyses of transient population dynamics using PPMs or other empirical modelling techniques.

## Keywords

Amplification, attenuation, damping ratio, demography, distance measures, population inertia, population projection matrix, reactivity, short-term dynamics, transient dynamics.

Ecology Letters (2011) 14: 959–970

## INTRODUCTION

Our aim is to promote a framework for the analysis of transients emerging from empirical models of population dynamics. Models of prospective population dynamics are integral to conservation and management (Menges 1990; Fujiwara & Caswell 2001; Wilson 2003; Baxter *et al.* 2006) and should ideally be predictive of real-world population dynamics. Numerous population modelling methods now exist, including simple linear or logistic equations (e.g. Verhulst 1838; Volterra 1926; Lotka 1932), difference equations (e.g. May 1975), matrix models (e.g. Leslie 1945; Lefkovich 1965), integral projection models (e.g. Childs *et al.* 2004; Ellner & Rees 2006, 2007) and individual-based models (e.g. van Winkle *et al.* 1993). Most models have simple density-independent, time-invariant forms, but many models may include drivers of more complicated population dynamics: nonlinear density-dependent forms incorporate intrinsic drivers, such as density dependence in vital rates or Allee effects (e.g. Costantino *et al.* 1997; Dennis *et al.* 2001; Fowler & Ruxton 2002), whereas time-varying stochastic forms incorporate extrinsic drivers, such as variation in climate or resource abundance (e.g. Fieberg & Ellner 2001; Tuljapurkar *et al.* 2002). Nonlinear, time-varying forms combine both these density dependent and stochastic approaches (e.g. Bjørnstad & Grenfell 2001; Costantino *et al.* 2005).

One particular class of model, the population projection matrix (PPM), has held enduring popularity in population modelling. PPM models benefit from being intuitive and tractable, and from the availability of a mature literature on their parameterisation, analysis

and interpretation. Although density-dependent and stochastic forms exist (Costantino *et al.* 1997; Fieberg & Ellner 2001), many research projects are unable to collect the data required to parameterise such models, especially for populations of conservation concern. Thus, it is linear, time-invariant PPM models that dominate the applied demographic literature (e.g. Pavlik & Barbour 1988; Crooks *et al.* 1998; Grenier *et al.* 2007), despite criticisms that they have limitations with respect to describing observed dynamics of natural populations (Bierzychudek 1999; Stephens *et al.* 2002). Historically, analysis of these models (and indeed of many other classes of population model) has focused on long-term population dynamics. Simple models tend to concentrate on analysing properties of stable asymptotic equilibria such as long-term growth rate and population structure (e.g. Pinard 1993; Shea & Kelly 1998; Otway *et al.* 2004). Density-dependent models largely focus on analysing attractors including stable equilibria such as carrying capacity or unstable equilibria such as limit cycles and chaotic dynamics (e.g. Turchin 1993; Dennis *et al.* 2001). Stochastic models aim to simulate or provide analytical solutions to expected values of and variation in long-term stochastic growth rate and population size (e.g. Tuljapurkar 1990; Morris & Doak 2005; Nantel *et al.* 1996). The tendency to focus on equilibria and long-term dynamics is perhaps a hangover from early theoretical paradigms that perceived ecological systems as 'balanced' (Cuddington 2001). In addition, because such long-term dynamics are largely independent of population attributes such as initial population size or structure, they lend themselves to relatively easy calculation.

However, there has been a recent surge of interest in short-term, TRANSIENT DYNAMICS of populations (see Glossary for definition of capitalised terms). Density-independent, time-invariant PPM models predict that if a population experiences a constant environment with unlimited resources, then it settles to a long-term stable rate of ASYMPTOTIC GROWTH (or decline) and a theoretical STABLE DEMOGRAPHIC DISTRIBUTION. However, in reality, populations experience a changeable and heterogeneous world, where extrinsic disruptions to population structure of biotic origin (e.g. disease, predation pressure or competition), abiotic origin (e.g. changing climate, extreme weather events or fire) and anthropogenic origin (e.g. harvesting or management intervention) lead to a realised INITIAL DEMOGRAPHIC DISTRIBUTION that is different from the population's stable demographic distribution. This can be a result of either DISTURBANCES to population structure that are asymmetric across the life cycle (changing the initial demographic distribution) and/or PERTURBATIONS to vital rates of the population (changing the stable demographic distribution). Discrepancies between initial and stable distributions will result in short-term increases in population density (population AMPLIFICATION), decreases in population density (population ATTENUATION), and/or fluctuations in density that are very different to those that might be expected in an immutable environment (Hastings 2004; Townley *et al.* 2007; Tenhumberg *et al.* 2009). In the absence of further disturbance or perturbation, transient dynamics would dampen and the population would settle back to stable state. The time taken for stable state to be reached following disturbance or perturbation is termed the TRANSIENT PERIOD (Fig. 1). The ability to understand and quantify such transient dynamics would enable managers to both ameliorate adverse transient response to natural disturbance and perturbation, and deliberately manipulate transient response through anthropogenic disturbance and perturbation. A thorough understanding of transients may improve the predictive power of the simple density-independent, time-invariant PPM models that dominate the literature and, combined with other approaches, may aid in our comprehension of how complicated population dynamics are shaped. The transient dynamics that we discuss here form a middle-ground of empirical modelling: they describe deterministic responses to (possibly stochastic) disturbances or perturbations, allowing a consideration of

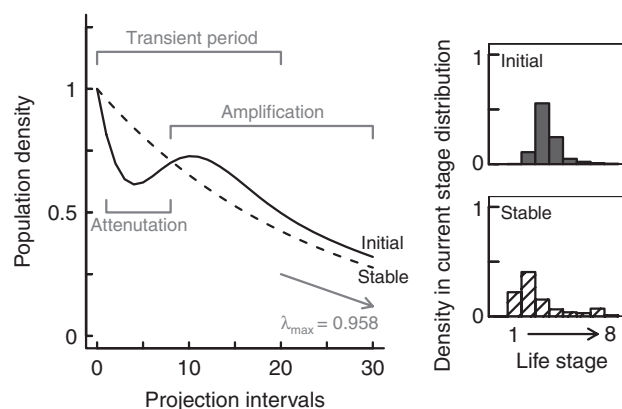
non-equilibrium dynamics without recourse to the computationally expensive study of fully stochastic systems. In a predictive sense, they are perhaps most useful for populations that usually experience relatively stable conditions, but which are occasionally subject to significant disturbance or perturbation.

Transient dynamics have already been shown to have important consequences for population management. Anthropogenic fires cause increased transient growth of the reproductive proportion of populations of endangered golden mountain heather (*Hudsonia Montana*) in North Carolina (Gross *et al.* 1998). Following hunting cessation, a managed population of red deer (*Cervus elaphus*) on the Isle of Rum showed prolonged transient fluctuations in size (Coulson *et al.* 2004). Analysis of transients also helps to improve our understanding of population invasion. In invasive plant populations, early life-stage vital rates strongly influence the transient dynamics that promote establishment and population growth (McMahon & Metcalf 2008; Ezard *et al.* 2010): this is intuitive considering seeds are the dispersive unit for plants. Conversely, in many animal populations, adults are more likely to disperse, and pea aphid (*Acyrtosiphon pisum*) populations may exhibit immediate population growth that is greater than predicted asymptotic growth, following experimentally induced adult invasion scenarios (Tenhumberg *et al.* 2009). Comparative studies of transient dynamics provide information that should help advise population management in the absence of sufficient data. Monocarpic herbs and trees have been shown to exhibit greater potential amplitudes of transient amplification and attenuation than perennial herbs and shrubs (Stott *et al.* 2010a). Long-lived animal species with slow reproduction have been shown to have greater variability in potential transient growth than short-lived species with fast reproduction (Koons *et al.* 2005). The importance of transients in shaping natural population dynamics is likely to become more apparent, as transient analyses become a more established part of the demographer's toolbox.

Unfortunately, the emerging literature on transient analysis is disparate and rather fragmented, lacking the coherence of approaches to the analysis of long-term dynamics in population models. A large number of methodologies have been developed in recent years for quantifying transient dynamics and their relationship to vital rates, and these have almost exclusively focused on density-independent, time-invariant PPM models: this class of model lends itself readily to development of transient analyses. A coherent approach to the analysis of transient dynamics in such models is warranted. In this article, we provide a critical review of existing methodologies that focuses on indices that have been developed, how they are calculated, their interpretation and potential applications. We highlight differences, similarities and even mathematical equivalences among such published indices. Our primary aim is to consolidate this information into a common framework for transient analysis and identify important indices that capture much of the variation in transient dynamics of a population. Although our focus is on linear, time-invariant models, we anticipate that this emerging framework will inform the development of transient analyses for density-dependent and stochastic PPM models and wider classes of population model. Throughout, we provide necessary mathematical methodology and clarify terminology surrounding the study of transient dynamics and wider population ecology.

## TRANSIENT DYNAMICS IN PPM MODELS

Transient dynamics in density-independent, time-invariant PPM models do not benefit from the simple analytical solutions available



**Figure 1** Illustration of transient population dynamics arising from a density-independent, time-invariant PPM model. A population with stable demographic distribution (dashed line; hatched bar plot) declines at a rate equal to  $\lambda_{\max}$  each time interval. However, real-world populations have initial demographic distributions that differ from the stable demographic distribution (solid line; grey bar plot) and exhibit transient dynamics.

for asymptotic dynamics. For the model  $\mathbf{n}_t = \mathbf{A}^t \mathbf{n}_0$  (where  $\mathbf{A}$  is the PPM,  $\mathbf{n}_t$  is the demographic distribution vector of the population at time  $t$  and  $\mathbf{n}_0$  is the initial demographic distribution vector of the population), the rate of asymptotic growth (or decline) is simply equal to  $\lambda_{\max}$  (the dominant eigenvalue of  $\mathbf{A}$ ). The dominant right eigenvector  $\mathbf{w}$  represents the relative proportions of life stages in the stable demographic distribution, and the dominant left eigenvector  $\mathbf{v}$  represents the relative reproductive value of each life stage (see Caswell 2001). Once the population settles to stable state, asymptotic properties have sole influence over population density, growth and structure. They are independent of the initial demographic distribution of the population, and they are insensitive to time. However, transient dynamics (and the indices used to describe them) vary in two dimensions: first, along the 'time' axis of the population projection (i.e. in rate of convergence to stable state) and second, along the 'population density' axis of the population projection (i.e. in whether they amplify, attenuate and/or oscillate and in the magnitude of these fluctuations). Variation along both axes depends strongly on the initial demographic distribution. However, variation along both axes is also limited: transient dynamics are bounded both in rate of convergence and in possible amplification and attenuation. Therefore, indices of transient dynamics focus either on convergence time or transient population density, and can differ in their measurement of either TRANSIENT BOUNDS or CASE-SPECIFIC indices of transient dynamics.

### Convergence rates

The earliest widely used transient index focuses on model convergence rate. The *damping ratio* (Caswell 2001 p. 95) of a PPM model is calculated as the ratio of the dominant eigenvalue to the magnitude of the first subdominant eigenvalue (see Table S1). It can be considered as a measure of the intrinsic resilience of the population, describing how quickly transient dynamics decay following disturbance or perturbation, regardless of population structure (the larger the damping ratio, the quicker the population converges). It is certainly a useful measure in comparing relative resilience across populations or species, and has been employed as such in many comparative analyses. For example, slower-growing corals may have a higher damping ratio than faster-growing corals (Hughes & Tanner 2000), indicating that slower-growing corals may be more susceptible to disturbance or perturbation. Similarly, late-successional plant species such as trees or shrubs tend to have a lower damping ratio than early-successional species such as perennial herbs (Franco & Silvertown 2004). Many other comparative analyses have also used the damping ratio to infer population resilience (e.g. O'Connor 1993; Mollet & Cailliet 2002; Salguero-Gómez & Casper 2010).

The damping ratio itself is a dimensionless measure and does not provide a direct quantification of the transient period. However, it can be implemented in equations that will provide this information. For example, the time for the influence of  $\lambda_{\max}$  to become  $x$  times as great as  $\lambda_2$  is equal to the logarithm of  $x$  divided by the logarithm of the damping ratio (Caswell 2001 p. 96). In a strict mathematical sense, the population never reaches stable state, but merely continues to approach it indefinitely. Therefore, considering quasi-convergence of the model in this way is perhaps the only way of prescribing a finite timeframe to the transient period. However, the length of the transient period depends not only on the inherent resilience of the population but also on its structure: the damping ratio ignores the

initial distribution of the population, and so cannot provide information on convergence and the transient period given a particular disturbance scenario. As such, it is likely to be of limited use for population managers and researchers interested in population response to specific natural or anthropogenic disturbance. Indeed, we use a large set of empirical PPM models to show below that the damping ratio correlates relatively weakly with convergence times of realistic population projections.

Another class of convergence measures makes it possible to incorporate specific disturbance scenarios. Distance measures calculate the 'distance' to stable state, incorporating explicitly the degree of difference between the initial and stable demographic distributions in their calculation. Each distance measure has a different interpretation and corresponding strengths and weaknesses. The simplest distance measures suffer from the opposite problem to the damping ratio in that they do not consider intrinsic resilience of the population to disturbance. For example, *Keyfitz's  $\Delta$*  (Keyfitz 1968) measures the proportional difference between the initial and stable demographic distribution vectors (Table S1), ignoring other PPM parameters in its calculation. Some distance measures incorporate further PPM parameters: for example, *projection distance* (Haridas & Tuljapurkar 2007) measures the difference in the reproductive value of the initial and the stable demographic distributions (Table S1), utilising the reproductive value vector  $\mathbf{v}$  in its calculation. Other distance measures are even more informative: *Cohen's cumulative distance metric* (Cohen 1979) incorporates the intrinsic resilience of the population to disturbance, with a formula that incorporates the 'path' taken by the initial demographic distribution, as it converges towards stable demographic distribution through time.

With each distance metric having a different interpretation, the utility of each will depend on the nature of the study under consideration. One drawback common to all distance measures is that they cannot give an objective estimate of convergence time given a particular disturbance scenario. As such, they are most useful in comparative analyses, comparing case-specific response to disturbance or perturbation. Despite this, distance measures have not seen the same popularity as the damping ratio in comparative analyses. There is a clear need for an index that can provide an estimate of time to convergence given a particular disturbance scenario. Quasi-convergence given a specific population structure can be simulated by projecting the model and calculating the time taken to achieve asymptotic growth to a specified accuracy (e.g. for the model to exhibit growth within 1% of  $\lambda_{\max}$ ); however, this is a relatively computationally intensive solution to the problem.

### Population density & growth

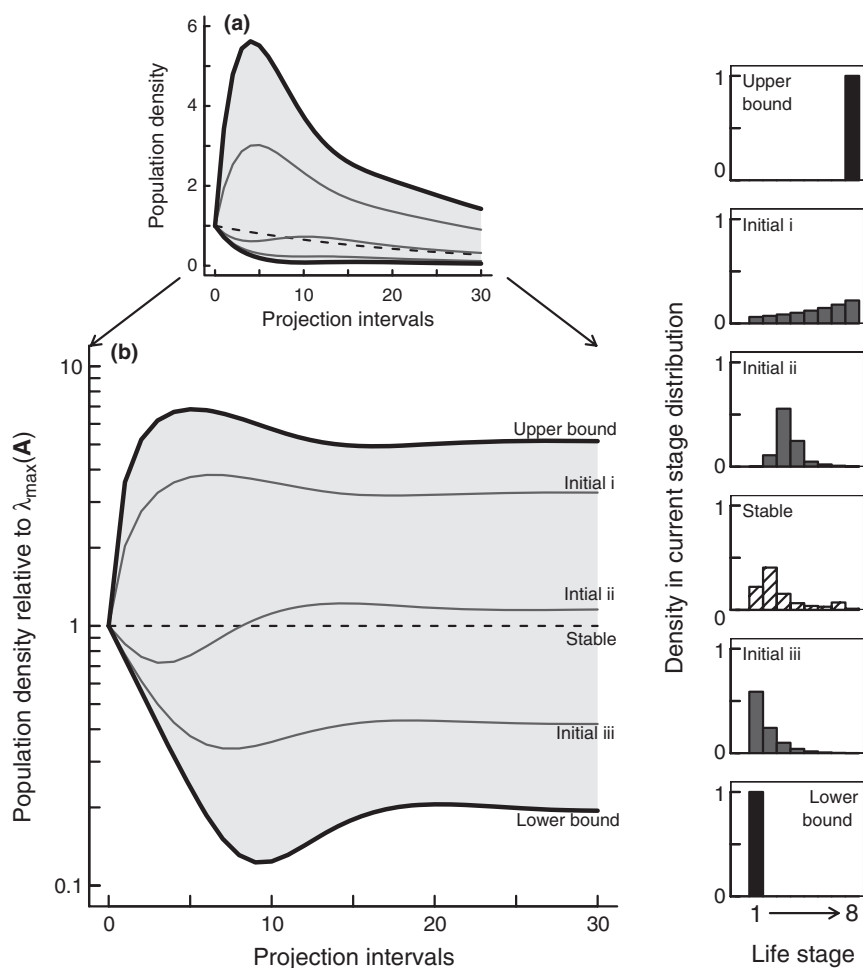
There are a number of benefits to studying transient population size, density and growth. Population managers will often aim either to boost the density and growth of populations (e.g. for conservation or harvesting) or to curb them (e.g. for control of pests and invasive species). Understanding transient response to natural or induced disturbance and perturbation can help to achieve these aims; indeed an ignorance of transient responses could hinder progress when employing management strategies developed using asymptotic analysis (Koons *et al.* 2007a). When studying resistance and resilience to disturbance and perturbation, measuring immediate changes in population density following disturbance or perturbation is an

alternative to evaluating convergence rate (Neubert & Caswell 1997). Populations may never reach stable state in the natural environment (Townley *et al.* 2007; Buckley *et al.* 2010; Stott *et al.* 2010a) and in any case, most ecological studies are conducted on timescales that are shorter than the time it would take to do so (Hastings 2004). Hence, there is a conceptual flaw in analysing asymptotic population density and growth whilst ignoring transients, and studying convergence rate alone will be of limited use. Consequently, recent literature has been concerned with quantifying transient population size, structure, density and growth.

However, the quantification of transient population density and growth requires a number of decisions to be made. The first decision is simply how to define 'transient'. It is difficult to objectively delimit the transient period (Maron *et al.* 2010), and the length of the transient period is highly variable among different models. Defining 'transient' in terms of population density and structure is equally difficult: asymptotic model properties always exert some influence over the population projection, albeit a decreasing influence, the nearer-term the analysis. Furthermore, by their very nature, transient dynamics are highly sensitive to the demographic population structure used in the model. Considering these issues, we have identified three main problems to overcome in quantifying transients: (1) disentangling transient and asymptotic effects, (2) choosing an initial demographic distribution and (3) choosing the timeframe for analysis. We discuss existing methodologies with respect to how they deal with these three problems.

#### Disentangling transient and asymptotic effects

There are two approaches to the study of transient amplification or attenuation in population density. First, absolute measures of transient population density describe how big or small a population can become in the short term: such measures describe the combined influence of transient growth rates and asymptotic dynamics (Fig. 2a). Second, relative measures of transient population density describe how big or small a population can become in the short term, relative to asymptotic dynamics (Fig. 2b). Relative measures of transient dynamics hold several advantages over absolute measures of transient population density. First, they clarify the concept of attenuation in asymptotically declining populations (attenuation is short-term decline in density at a faster rate than asymptotic decline) and amplification in asymptotically increasing populations (amplification is short-term increase in density at a faster rate than asymptotic increase). Figure 2a illustrates how, for an asymptotically declining population of the desert tortoise *Gopherus agassizii*, it is difficult to capture attenuation as the population approaches extinction. Conversely, Fig. 2b demonstrates that attenuation of the population is much easier to understand when the influence of asymptotic growth is discounted. Second, relative measures enable the fair comparison of both amplified and attenuated dynamics of a single population, through projection of different initial demographic distributions through the same PPM (Fig. 2b). Third, relative measures enable fair comparative study of transient dynamics among populations or species with widely varying asymptotic growth (Stott *et al.* 2010a). Therefore, relative measures



**Figure 2** Transient dynamics of the desert tortoise *Gopherus agassizii* with medium fecundity (Doak *et al.* 1994). (a) Absolute population dynamics, including both transient and asymptotic influences; (b) standardised transient dynamics, excluding the influence of asymptotic growth. All demographic distributions are scaled, so that overall initial population density equals 1. Bold lines and black barplots indicate transient bounds (note that sometimes, unlike in this case, different stage-biased projections define the amplification envelope at different times in the projection); thin lines and grey barplots indicate case-specific initial demographic distributions; dashed lines and hatched barplots indicate the stable demographic distribution. Areas shaded in light grey indicate the transient envelope, which is the range of values in which all case-specific projections will lie.



add to the list of standardised, emergent properties of a PPM model that are both qualitatively and quantitatively comparable within and across studies and models. Relative measures do not lack an intuitive biological interpretation: discounting asymptotic growth yields values for population density, relative to those of a population with the same initial density that grows at its predicted asymptotic rate (Koons *et al.* 2007b; Townley *et al.* 2007). In addition, relative measures of density can easily be converted back to absolute measures of density if required, simply by multiplying relative density by  $\lambda_{\max}^t$ .

The process of removing the influence of asymptotic dynamics can be done very easily in practice. An intuitive solution may be to project two models, one with the initial and one with the stable demographic distribution, and compare the two. However, this is unnecessarily computationally intensive. A second solution is to incorporate the correction into formulae for transient indices, for example, by scaling the eigenvectors of the matrix (e.g. Koons *et al.* 2007b). This solution, although adequate for individual indices, is lacking in generality: it does not allow for more detailed study, such as of other transient timeframes or of lifestage-specific dynamics. A third solution used by Townley & Hodgson (2008) in calculating their transient indices (Table S1) is to use the 'standardised' PPM  $\hat{\mathbf{A}}$ , which is equal to the PPM  $\mathbf{A}$  divided by  $\lambda_{\max}$ . This is a computationally simple solution, and enables complete projection of population dynamics in the absence of asymptotic dynamical effects. Hence, any analysis that can be applied to the PPM can also be applied to the standardised PPM, including analysis at any timeframe of the projection or analysis of lifestage-specific dynamics. We promote this as the simplest and most comprehensive solution to the problem of disentangling transient from asymptotic effects.

#### *Choosing an initial demographic distribution*

Transient dynamics are very sensitive to the initial demographic distribution used in the population projection (Koons *et al.* 2005; Caswell 2007; Townley & Hodgson 2008), and there are two established approaches available when it comes to choosing an initial demographic distribution to work with. First, case-specific measures of transient density describe the predicted dynamics of the population, given a known initial demographic distribution. Second, bounds on transient population density represent the most extreme possible values of amplification and attenuation, and require no prior knowledge of the population's demographic distribution. For effective population management, it will most often be better to study case-specific transient dynamics where possible (e.g. Zúñiga-Vega *et al.* 2007). However, estimating the demographic distribution of a population can prove to be costly and labour-intensive and so is often infeasible. Transient bounds provide an alternative approach to population management when the demographic distribution of the population is unknown, and provide best- and worst-case scenarios of transient change in population density (Townley & Hodgson 2008). The realised dynamics of the population will lie anywhere between the transient bounds on population density, and we call this range of possible values the TRANSIENT ENVELOPE (Fig. 2b). Transient bounds can also prove useful for comparative studies, both because they require no knowledge of population structure and because they invoke like responses among models (Stott *et al.* 2010a).

Calculation of case-specific transient dynamics merely requires projection of the known initial demographic distribution. Transient bounds on population density result from projection of STAGE-

BIASED VECTORS of demographic distribution (Townley & Hodgson 2008), where all individuals in the population are grouped in a single stage. In the *G. agassizii* model, maximal possible amplification is achieved from a population of just adults, whereas maximal possible attenuation is achieved from a population of just yearlings (Fig. 2b). Although there do exist situations where all individuals in a population might be in the same life stage (for example, in a biological invasion or reintroduction programme), it is unlikely that the dynamics of real populations will follow such extreme trajectories. The transient envelope is therefore useful in describing the range of possible transient densities, but fails to inform on the probability of certain population sizes being achieved. For example, a model might show an increased propensity for amplification over attenuation (indeed this is the case for the *G. agassizii* model in Fig. 2), but the transient envelope does not provide this vital information. Simulation of population dynamics over the entire range of possible demographic distributions (e.g. Koons *et al.* 2005) can provide this detailed information. Imagine the shaded areas in Fig. 2, but shaded darker for more likely transient population densities and lighter for less likely transient densities. This may be useful for population management, but is computationally demanding and an unwieldy output to use in comparative research.

Case-specific indices of transient dynamics and transient bounds are both valuable measures of transient dynamics, but it is important that both are comparable across models. Standardising the initial stage distribution so that overall population density is equal to 1 (e.g. Maron *et al.* 2010; Koons *et al.* 2005; Townley *et al.* 2007; Townley & Hodgson 2008; Stott *et al.* 2010a) achieves this. Initialising a population projection with an overall density of 1 holds several major advantages: first, it enables fair comparison of transient dynamics of different initial stage distributions projected through the same model. In Fig. 2b, for example, it is easy to see how different initial demographic distributions result in different transient responses when each starts with an initial overall density of 1. Second, it enables fair comparative study of transient dynamics among models for different populations or species (Maron *et al.* 2010; Stott *et al.* 2010a). Third, coupling this approach with the study of relative measures of transient dynamics yields values for projected population density that are not only relative to asymptotic dynamics but also relative to initial density. For example, in Fig. 2b, a projected density of 2 means that the population doubles in size relative to asymptotic growth, whereas a projected density of 0.5 means that the population halves in size relative to asymptotic growth.

#### *Choosing the timeframe for analysis*

Transient dynamics can be measured at any point along the population projection. The first, and perhaps most intuitive, approach is to measure near-term, time-dependent transient dynamics: in this case, the timeframe chosen is very important. Very near-term measurements risk overlooking the full extent of transient dynamics if the population continues to amplify or attenuate beyond the timeframe studied. Conversely, measurements taken further along the projection will risk increased dilution by asymptotic dynamics as the population converges to stable state. Choosing arbitrary time points along the projection at which to analyse transient dynamics has been the solution of many comparative studies (e.g. Koons *et al.* 2005; McMahon & Metcalf 2008; Maron *et al.* 2010), but often such measurements are not comparable as they are not necessarily

indicative of preceding or subsequent dynamics. A second approach is to measure the asymptotic effects of transient dynamics: although this may seem paradoxical, this method provides easily calculable and amenable indices that can supply very useful information. A third approach is to do away with time altogether in calculations, with time-independent measures of transient dynamics. The benefits and drawbacks of each method depend on the context in which they are used.

For near-term transient analysis, an intuitive solution is to study immediate transient response, i.e. population density and growth in the first time interval. *Reactivity* and *first-timestep attenuation* are the maximal possible amplification and attenuation in the first timestep (Neubert & Caswell 1997; Townley *et al.* 2007; Townley & Hodgson 2008; Table S1). This instantaneous transient response will always be in the transient period, but limiting evaluation to the first time interval risks missing the full extent of transient dynamics. A complementary solution to this problem is to measure maximal transient response alongside first-timestep response. *Maximal amplification* and *maximal attenuation* are the largest possible amplification and attenuation that may be achieved at any time point of population projection (Neubert & Caswell 1997; Townley *et al.* 2007; Townley & Hodgson 2008; Table S1). Measuring this 'biggest' transient response is effective for capturing the full extent of transient dynamics: population density should always be smaller than maximal amplification and larger than maximal attenuation. These four near-term indices were all originally defined as transient bounds, but they also exist for case-specific projections and collectively capture the majority of variation in near-term transient response, as we show below. However, they are not particularly amenable: maximal amplification and attenuation must be calculated numerically, and are therefore not readily disposed to PERTURBATION ANALYSIS. Analytical perturbation analyses of reactivity and first-timestep attenuation are more feasible, but will do little to inform on transient response beyond the first timestep.

Alternatively, studying the asymptotic effects of transient dynamics can prove to be very informative. Early demographic studies of human populations considered *population momentum* (Keyfitz 1971; Table S1), the latent increase in human population size following an immediate decrease in birth rates to the level of replacement. *Population inertia* (Koons *et al.* 2007b; Table S1) is a logical extension of this: a population with any given demographic distribution, following any disturbance or perturbation, will settle asymptotically to a fixed ratio above or below what is expected from a similar population growing at asymptotic rate (Fig. 2b). Therefore, population momentum is a special case of population inertia (Koons *et al.* 2007b; Table S1). Population inertia was originally defined for case-specific projections, but bounds on population inertia also exist. *Amplified asymptotic multiplication* and *attenuated asymptotic multiplication* (Townley & Hodgson 2008; Table S1) are bounds on population inertia, despite being calculated differently. Although more a consequence of transient dynamics than a measure of transient dynamics *per se*, population inertia can be thought of as a holistic measure that results from the combined effect of dynamics over the whole transient period and we show below that population inertia correlates tightly with the other indices of transient dynamics. A final strength of inertia is that it is very amenable to perturbation analysis, as it is a simple function of the initial stage distribution and the dominant eigenvectors of the PPM.

A final method for overcoming the problem of time is to do away with it in calculations altogether. The *upper Kreiss bound* is a lower bound on maximal possible amplification (Townley *et al.* 2007;

Townley & Hodgson 2008; Table S1) and the *lower Kreiss bound* is an upper bound on maximal possible attenuation (Townley & Hodgson 2008; Table S1). These measures are time-independent and, thanks to the existence of analytical formulae for their calculation, provide a gateway to perturbation analysis for transient bounds on maximal amplification and attenuation. However, the Kreiss bounds also suffer from drawbacks: first, they have no precise biological interpretation. Second, they are currently defined only as transient bounds and not for case-specific dynamics (although the necessary algebraic adjustment is not complicated). Last, they are somewhat redundant when considering their relationship to other indices, as we show below.

## A FRAMEWORK FOR TRANSIENT ANALYSIS

The transient analysis of density-independent, time-invariant PPM models would benefit from a coherent framework within which to work. When measuring transient population density and growth, the discounting of asymptotic model properties has a number of benefits, and this is most easily done by using the standardised PPM  $\hat{\mathbf{A}}$ , where  $\hat{\mathbf{A}} = \mathbf{A}/\lambda_{\max}$ . In addition, standardising the initial demographic distribution  $\mathbf{n}_0$  to give  $\hat{\mathbf{n}}_0$ , where  $\|\hat{\mathbf{n}}_0\|_1 = 1$  means that transient dynamics can be studied relative to both initial density as well as to asymptotic growth. In combination, these standardisations make transient indices more meaningful both for population management and comparative analysis, and allow fair comparison of results both within and among models.

Deciding the timeframe for analysis of transient density and growth is a harder problem to solve: different transient indices have different interpretations, but often show highly correlated relationships with one another (Stott *et al.* 2010a). We exploit a database of 563 published, irreducible (Stott *et al.* 2010b) PPM models for 202 species of animals and plants (Appendix S1) to further explore the relationships between transient indices measured using different timeframes. All mathematical and statistical modelling was conducted using R version 2.12.1 (R Development Core Team 2011). First of all, we note a special relationship between the Kreiss bound and transient bounds on population inertia. The derivation of the Kreiss bounds involves maximising or minimising over a scaling factor  $r$  for  $r > 1$  (Table S1). However, where the maximum/minimum occurs at  $r \rightarrow 1$ , the upper and lower Kreiss bounds are identical to the upper and lower bounds on population inertia respectively. We calculated these measurements for each PPM in our database and found that in 76.1% of cases, the upper Kreiss bound was identical to the upper bound on population inertia, whereas in 99.8% of cases, the lower Kreiss bound was identical to the lower bound on population inertia. In both cases, Spearman's rank correlations between the Kreiss bounds and their respective bound on inertia yielded coefficients of greater than 0.99. So, the Kreiss bounds are somewhat redundant in comparison to population inertia, which is easier to interpret, simpler to calculate and more flexible.

Given this information, we would consider first-timestep (*reactivity*, *first-timestep attenuation*), maximal (*maximal amplification*, *maximal attenuation*) and asymptotic (*amplified inertia*, *attenuated inertia*) indices of transient dynamics to be the most useful measurements of transient population density and growth (Table 1). These indices and their bounds together describe the majority of variation in transient population density, are comparable within and across models and all have a definite biological interpretation. Relationships between these measurements are presented in Fig. 3. To study relationships between

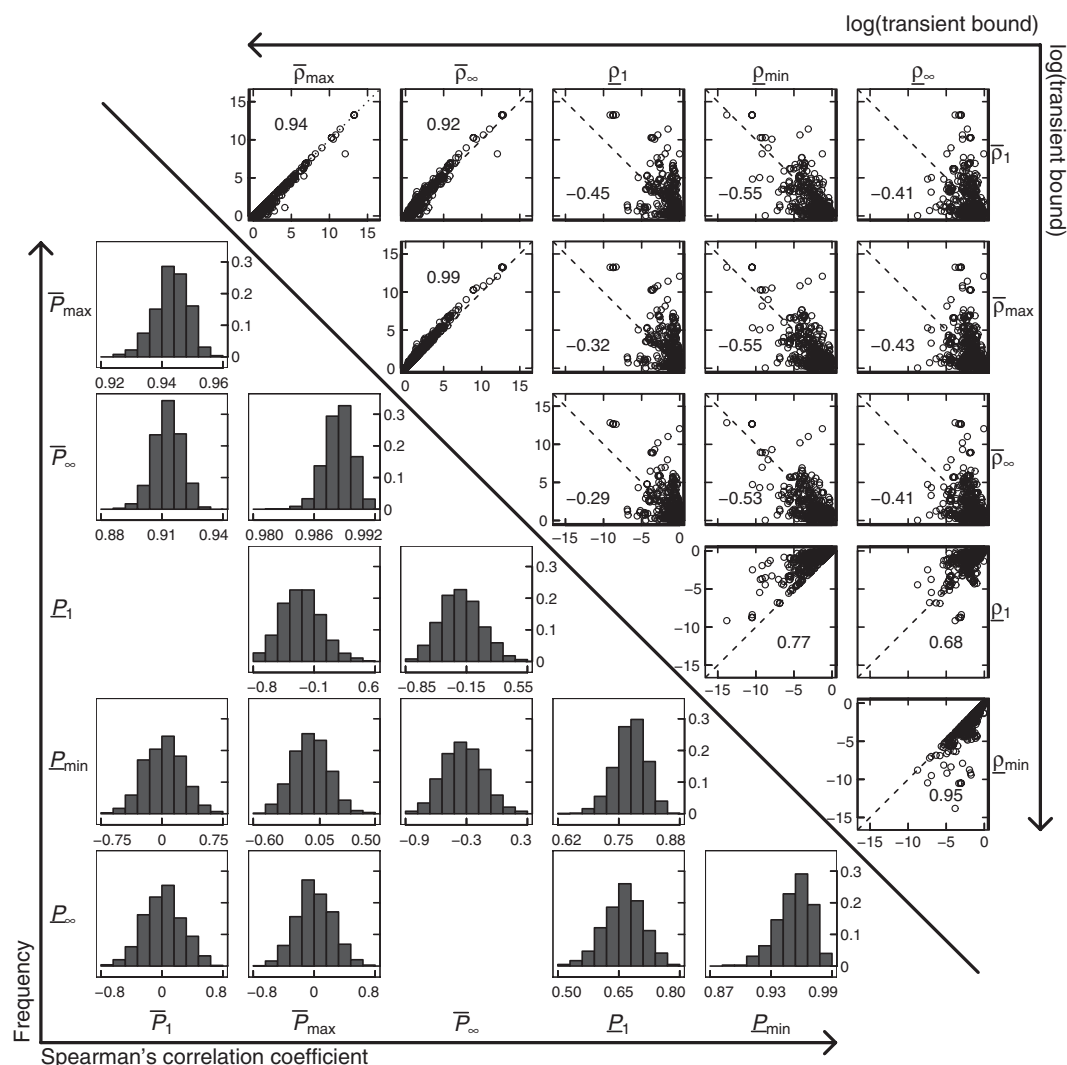
bounds on transient dynamics, we calculated the six bounds for each PPM and correlated them against one another, the results of which are presented in the upper-right triangle of Fig. 3. To study relationships between case-specific indices, we generated random demographic distribution vectors for each PPM by drawing numbers from uniform distributions, standardised these vectors to sum to 1, calculated the six case-specific transient indices for each model and performed Spearman's rank correlations on each pairwise combination of indices.

We repeated this process 1000 times to obtain distributions of correlation coefficients for the pairwise comparisons. Although the use of a uniform distribution is somewhat artificial given that relative densities of life stages are likely to co-vary in natural populations, it allowed exploration of a wide range of potential stage structures. The results are presented in the lower-left triangle of Fig. 3. It appears that for both transient bounds and case-specific indices, amplified measures show very tight positive correlations with one another

**Table 1** Important indices of transient population dynamics. Matrices are presented as capitalised, and in bold. Vectors are in small type and in bold. Numbers and scalars are in normal font

INDEX	FORMULA	BIOLOGICAL MEANING
REACTIVITY	<i>TRANSIENT BOUND</i> $\bar{\rho}_1 = \ \hat{\mathbf{A}}\ _1$	<i>TRANSIENT BOUND</i> – maximum population growth in a single timestep, relative to stable growth rate.
	<i>CASE-SPECIFIC</i> $\bar{\mathbf{P}}_1 = \ \hat{\mathbf{A}}\hat{\mathbf{n}}_0\ _1$ when $\ \hat{\mathbf{A}}\hat{\mathbf{n}}_0\ _1 > 1$	<i>CASE-SPECIFIC</i> – population growth achieved by a given population structure in a single timestep, relative to stable growth rate. Assumes the population will amplify immediately.
FIRST-TIMESTEP ATTENUATION	<i>TRANSIENT BOUND</i> $\underline{\rho}_1 = \min \text{CS}(\hat{\mathbf{A}})$	<i>TRANSIENT BOUND</i> – minimum population growth in a single timestep, relative to stable growth rate.
	<i>CASE-SPECIFIC</i> $\underline{\mathbf{P}}_1 = \ \hat{\mathbf{A}}\hat{\mathbf{n}}_0\ _1$ when $\ \hat{\mathbf{A}}\hat{\mathbf{n}}_0\ _1 < 1$	<i>CASE-SPECIFIC</i> – population growth achieved by a given population in a single timestep, relative to stable growth rate. Assumes the population will attenuate immediately.
MAXIMUM AMPLIFICATION	<i>TRANSIENT BOUND</i> $\bar{\rho}_{\max} = \max_{t>0} (\ \hat{\mathbf{A}}^t\ _1)$	<i>TRANSIENT BOUND</i> – the largest possible future population density achievable, relative to a population with stable growth rate and same initial density.
	<i>CASE-SPECIFIC</i> $\bar{\mathbf{P}}_{\max} = \max_{t>0} (\ \hat{\mathbf{A}}^t\hat{\mathbf{n}}_0\ _1)$ when $\ \hat{\mathbf{A}}^t\hat{\mathbf{n}}_0\ _1 > 1$ for some $t$	<i>CASE-SPECIFIC</i> – the largest possible future density of a given population structure, relative to a population with stable growth rate and same initial density. Assumes the population amplifies at some point in the future.
MAXIMUM ATTENUATION	<i>TRANSIENT BOUND</i> $\underline{\rho}_{\min} = \min_{t>0} (\min \text{CS}(\hat{\mathbf{A}}^t))$	<i>TRANSIENT BOUND</i> – the smallest possible future population density achievable, relative to a population with stable growth rate and same initial density.
	<i>CASE-SPECIFIC</i> $\underline{\mathbf{P}}_{\min} = \min_{t>0} \ \hat{\mathbf{A}}^t\hat{\mathbf{n}}_0\ _1$ when $\ \hat{\mathbf{A}}^t\hat{\mathbf{n}}_0\ _1 < 1$ for some $t$	<i>CASE-SPECIFIC</i> – the smallest possible future density of a given population structure, relative to a population with stable growth rate and same initial density. Assumes the population attenuates at some point in the future.
AMPLIFIED INERTIA	<i>TRANSIENT BOUND</i> $\bar{\rho}_{\infty} = \frac{\mathbf{v}_{\max}^T \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}}$	<i>TRANSIENT BOUND</i> – the largest possible long-term population density, relative to a population with stable growth rate and same initial density.
	<i>CASE-SPECIFIC</i> $\bar{\mathbf{P}}_{\infty} = \frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}}$ when $\frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}} > 1$	<i>CASE-SPECIFIC</i> – the long-term population density of a given population structure, relative to a population with stable growth and same initial density. Assumes the population amplifies in the long term.
ATTENUATED INERTIA	<i>TRANSIENT BOUND</i> $\underline{\rho}_{\infty} = \frac{\mathbf{v}_{\min}^T \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}}$	<i>TRANSIENT BOUND</i> – the smallest possible long-term population density, relative to a population with stable growth rate and same initial density.
	<i>CASE-SPECIFIC</i> $\underline{\mathbf{P}}_{\infty} = \frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}}$ when $\frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \ \mathbf{w}\ _1}{\mathbf{v}^T \mathbf{w}} < 1$	<i>CASE-SPECIFIC</i> – the long-term population density of a given population structure, relative to a population with stable growth and same initial density. Assumes the population attenuates in the long term.

$\hat{\mathbf{A}}$  represents the standardised population projection matrix and is equal to  $\mathbf{A}/\lambda_{\max}$  (where  $\mathbf{A}$  is the PPM and  $\lambda_{\max}$  is the dominant eigenvalue of  $\mathbf{A}$ );  $\mathbf{w}$  represents the dominant right eigenvector of  $\mathbf{A}$  (the stable demographic distribution vector);  $\mathbf{v}$  represents the dominant left eigenvector of  $\mathbf{A}$  (the reproductive value vector);  $\hat{\mathbf{n}}_0$  represents the initial demographic distribution, standardised to sum to 1.  $\min \text{CS}$  denotes the minimum column sum of a matrix and  $\|\mathbf{m}\|_1$  is the one-norm of a vector  $\mathbf{m}$  (equal to the sum of its entries).  $\mathbf{m}_{\min}$  and  $\mathbf{m}_{\max}$  are the smallest and largest entries of a vector  $\mathbf{m}$  respectively. We have chosen to use the Greek  $\rho$  to represent transient bounds (in accordance with Townley & Hodgson 2008), whereas the Latin  $\mathbf{P}$  represents case-specific indices of transient dynamics. An overbar indicates a bound or index of amplification, whereas an underbar represents a bound or index of attenuation (Townley & Hodgson 2008). A subscript provides information on the timeframe of study: 1 for first-timestep indices; max or min for maximal amplification or attenuation, respectively, and  $\infty$  for asymptotic indices.



**Figure 3** Correlations between transient bounds and case-specific indices for 563 published population projection matrix models. The upper-right triangle shows pairwise correlations between six transient bounds and their associated Spearman's rho values; both axes are on a log scale. The lower-left triangle consists of histograms that show distributions of Spearman's rho values for 1000 pairwise correlations of case-specific indices for randomly generated case-specific demographic distributions.

(upper-left quadrant of Fig. 3), whereas attenuated measures show tight positive correlations, but not to the same degree as among amplified measures (lower-right quadrant of Fig. 3). However, amplified measures are not good predictors of attenuated measures and *vice versa* (upper-right and lower-left quadrants of Fig. 3). The correlation coefficients of transient bounds lie comfortably within the modal range for those of case-specific transient indices, which indicates that in relation to one another, bounds on transient dynamics behave similar to case-specific indices of transient dynamics. Of the three pairs of indices, population inertia correlates best with its amplified or attenuated partner indices.

We also explored the relationships between the six indices and measures of convergence. For each randomly generated initial demographic distribution, we simulated the time taken for population growth to settle within 1% of  $\lambda_{\max}$ . We correlated transient bounds with the median simulated convergence time of the 1000 iterations for each PPM. For case-specific indices, we correlated the six transient indices with time to convergence at each iteration of the model, and 1000 iterations of this model provided distributions of Spearman's rho

values. Most correlations between bounds and median convergence time were significant, but all were relatively weak with absolute values of Spearman's rho ranging between 0.21 and 0.7. Distributions of correlation coefficients between case-specific transient dynamics and time to convergence were similarly weak and widely varying (see Appendix S2 for more detailed methodology and results from these analyses). This indicates that larger transient departures from asymptotic growth are not necessarily linked to a longer time to convergence, either for transient bounds or for case-specific transient indices. Studying the relationship between the damping ratio and the median simulated time to convergence also indicated that the damping ratio is a relatively poor predictor of convergence, with a Spearman's correlation coefficient of  $-0.66$  and high variability in the distribution of points (Appendix S2). The relationship between approximate time to convergence calculated using the damping ratio and simulated median time to convergence is similarly weak, although with median time to convergence rarely exceeding approximated time to convergence, there is a potential utility of the damping ratio in providing a weak bound on convergence rate. Nonetheless, there is a clear need



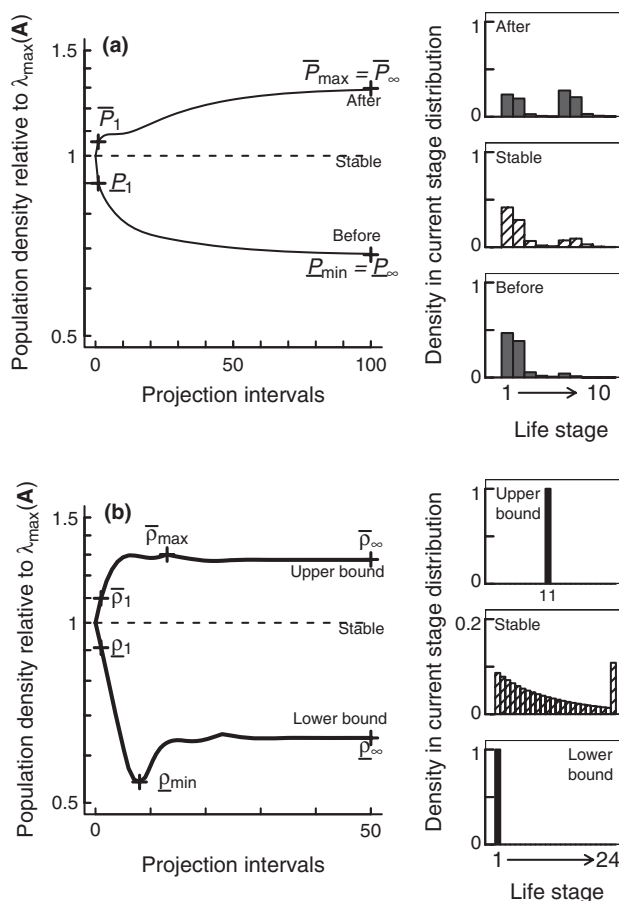
for an index that measures finite convergence time, which would fit into the framework for analysis we describe here. Such a measure would be qualitatively and quantitatively informative for population management, be calculable as both a bound and case-specific index and be a standardised index that is comparable among PPM models. Simulating quasi-convergence of the model goes some way to achieving these goals, but is computationally intensive and rather ill-defined.

## CASE STUDIES

The transient indices and bounds identified here provide standardised, comparable, qualitative and quantitative measures that can be used in conjunction with other model parameters to inform on population state and potential management (Fig. 4). Figure 4a shows two projections for the subcanopy tree *Syrax obassia* in central Japan (Abe *et al.* 1998). The PPM distinguishes between those individuals found in the shade and individuals found in canopy gaps: vital rates of individuals in each environment differ considerably. The 'before' projection uses the recorded demographic distribution, with only 6.2% of the canopy open. This population attenuates increasingly over time: the value for first-timestep attenuation indicates that the

population is expected to decrease by 10% compared with asymptotic growth in one year, whereas the value for attenuated inertia indicates that given environmental stability the population is expected to become up to 70% smaller than asymptotic growth predicts. This is important to consider:  $\lambda_{\max}$  for the population is 1.02, indicating that it will grow over time, when in fact the transient dynamics of the population may cause it to decline. Eventually (assuming no change in vital rates or canopy cover), population growth will settle to  $\lambda_{\max} = 1.02$ , but at much reduced density. The 'after' projection simulates disturbance caused by a hurricane opening up 50% of the existing canopy. Far from being damaging to the population, this would cause amplification, even with no change in the vital rates of the population. It would grow at a rate faster than  $\lambda_{\max}$  in the short term: reactivity indicates that within just 1 year, it is predicted to become 5% larger than asymptotic growth predicts, whereas amplified inertia predicts the density will eventually settle to be up to 30% larger than expected of a population initiated at stable stage structure (again, assuming environmental stability following the disturbance event).

Figure 4b illustrates transient bounds for the Amsterdam albatross *Diomedea amsterdamensis* on Amsterdam Island in the South-Eastern Indian Ocean (Inchausti & Weimerskirch 2001). This is one of the world's rarest species of bird, with the Amsterdam Island colony being the known population. Although the demographic structure of the species has previously been recorded in 1997, the exact demographic structure of the current population is unknown. In this case, transient bounds can provide vital information.  $\lambda_{\max}$  for the population is equal to 1.06, which is encouraging, and the values of bounds on reactivity and first-timestep attenuation indicate that in 1 year, the population should not decrease or increase within anything more than 10% of its size as predicted by asymptotic growth. However, despite having a positive  $\lambda_{\max}$ , the worst-case scenario is that the population almost halves relative to asymptotic growth within the next 10 years as indicated by the lower bound on maximal attenuation. So, despite having a positive predicted asymptotic growth, there is a real danger that the population may in fact decline in size. This worst-case scenario is unlikely as it results from a population composed entirely of chicks, but sets the goalposts for population management. Were a reintroduction programme to take place, the transient bounds indicate that age 11 individuals would be the best to translocate, as it is this age class that provides the largest overall population amplification both immediately and asymptotically.



**Figure 4** Case studies of transient dynamics in natural populations. (a) Case-specific dynamics of the subcanopy tree *Syrax obassia*; (b) transient bounds of the Amsterdam albatross *Diomedea amsterdamensis*. Bold lines and black barplots indicate transient bounds; thin lines and grey barplots indicate case-specific initial demographic distributions; dashed lines and hatched barplots indicate the stable demographic distribution.

## DISCUSSION

Transient population dynamics are important to consider in any management scenario: short-term fluctuations in population density and growth can swamp predicted asymptotic trends. Recent interest in transients has given rise to diverse methodologies for calculating transients for density-independent, time-invariant PPM models. However, the fragmented nature of this literature has left the field of transient analysis relatively inaccessible to non-specialists. We have identified an emerging framework, with a number of decisions to make when evaluating transient population density, growth and structure. We strongly recommend that transient dynamics be studied relative to both asymptotic growth and initial population density. The easiest ways to achieve this are to standardise the PPM by dividing it by  $\lambda_{\max}$  and standardise the initial demographic distribution by scaling it, so that overall population density is equal to 1. Analysing transient dynamics at arbitrary points along the population projection is

unsatisfactory, and so the three pairs of indices identified here can be used as comparable measures to capture the majority of variation in transient dynamics of a population. Our analysis of correlations between these indices reveals population inertia (Koons *et al.* 2007b) to be a simple yet versatile index that correlates strongly with other indices, both when measured for case-specific transient dynamics and bounds on transient dynamics. There are many available methods for analysing convergence of models, but the biological interpretation of most of these indices is questionable and we have identified a need for a more robust index of convergence in density-independent, time-invariant PPM models.

Although the study of transient dynamics is relatively well developed for density-independent, time-invariant PPM models, transients have received relatively little attention in density-dependent and stochastic models. We anticipate that the framework we identify here (i.e. study of relative transient dynamics, standardised initial conditions and first-timestep, maximal and asymptotic response) may be useful in informing development of transient indices in these areas. However, the nonlinear and/or time-varying nature of such models presents further obstacles to analytical solutions for transient dynamics. Nonlinear projection matrix models vary greatly in the form and influence of their attractors, therefore there is unlikely to be a single predictor of transient density or convergence rate that suits all situations. Nonlinear models demonstrating stable equilibrium density will prevent the phenomenon of asymptotic inertia in future population size as defined here for linear models, but timestep-specific amplification and attenuation (and bounds on these) will remain interesting and measurable. Stochastic models incorporate disturbance and perturbation as a result of small-scale fluctuations in the environment, but near-term dynamics following larger, more infrequent disturbances or perturbations may differ from long-term dynamic trends. It may be useful to have analytical formulae to approximate such dynamics, similar to those that exist for long-term stochastic dynamics (Tuljapourkar 1982), thereby reducing the need for full numerical simulation. The extension of transient analysis to classes of population model other than PPMs is another logical next step. In particular, integral projection models (Ellner & Rees 2006, 2007) would benefit from development of methods for transient analysis.

One of the most useful extensions to understanding population dynamics *per se* is to understand the interplay between the vital rates of the population and its dynamics. Perturbation analyses such as SENSITIVITY (Caswell 2001 p. 210), ELASTICITY (Caswell 2001 p. 227) and TRANSFER-FUNCTION (Hodgson & Townley 2004) analyses provide this important information for asymptotic population dynamics. A number of methods for transient perturbation analysis exist, particularly methods for analysing sensitivity of transient population density to changes in vital rates of the population. These methods must make the same decisions regarding standardisation of dynamics, choice of initial population structure and time point along the projection at which to analyse. However, they have an added decision to make in what form of projection equation to differentiate: methods have chosen to use matrix calculus to evaluate state-space form equations (Caswell 2007), to differentiate the solution to the projection equation as expressed using model eigenvalues and eigenvectors (Fox & Gurevitch 2000; Yearsley 2004) and to evaluate sensitivity of transient indices that are functions of the PPM (Townley *et al.* 2007; Koons *et al.* 2007b). A review and synthesis of these approaches is certainly needed. However, there is still a need for new approaches to transient perturbation analysis. Relationships between

asymptotic growth and changes in vital rates of populations are often markedly nonlinear (Hodgson & Townley 2004) and there is evidence to show that this may also be the case for transient dynamics (Townley *et al.* 2007). Sensitivity analysis, as a linear approximation, is not sufficient to describe population dynamic responses to non-negligible perturbations (Carslake *et al.* 2008, 2009). Therefore, there is a need for a transfer-function style approach to transient perturbation analysis that can model the nonlinear response of transient density to perturbation.

The majority of interest in transient dynamics has so far centred on their use in population management: far fewer studies have considered their potential impact in other areas of ecology and evolution. A better understanding of transients could provide opportunities to understand life-history evolution from a new perspective. A population that experiences unpredictable disturbance may need to evolve to be resistant to disturbance through having smaller transients, as an insurance against population decline. Conversely, a population that experiences regular disturbance of a particular type may evolve to have a larger transient dynamical response to that disturbance, maximising amplification to exploit opportunity to outcompete other genotypes. It is likely that the simultaneous optimisation of asymptotic and transient growth rates will combine to maximise long-term stochastic growth rate, but the mechanisms mapping life-history variation onto transient dynamics and potential trade-offs between selection on short- and long-term growth have not yet been explored. Transient dynamics also have relevance in ecological systems other than populations: indeed the application of transient theory could extend to any stage-structured biological system. Transients could help to better understand the dynamics of communities, for example in modelling tropic cascades in food webs. They may help to better understand the spread of infectious diseases in epidemiological models. They may help explain the rapid spread of novel genotypes through populations. They could be useful in modelling the responses of ecosystems to climate change, tracking the movement of energy or matter through different ecosystem compartments. There are some examples of transient dynamics in other ecological systems – the flow of matter through a rainforest ecosystem has been shown to exhibit transient dynamics (Neubert & Caswell 1997; Townley & Hodgson 2008) and models of whooping cough epidemiology in humans have shown significant transient response to perturbation, with annual epidemics becoming multiannual cycles following an increase in recovery rates (Rohani *et al.* 2002).

Transient analysis of population dynamics is still a young and emerging field of population ecology, likely to see many advances in coming years. Indeed, transient analysis should prove an essential part of any study of demography. However, relatively inaccessible literature and a lack of coherency could present a barrier to widespread use of some methodologies. With a common framework within which to develop methods, and the formulation of extra tools, transient analysis has the potential to provide great insight to the fields of conservation, population management and evolutionary ecology.

## ACKNOWLEDGEMENTS

We are grateful to David Carslake, Miguel Franco and Vicky Warwick-Evans for the provision of PPMs to the database, and for intellectual contributions. IS was supported by the European Social Fund.

## AUTHOR CONTRIBUTIONS

IS wrote the first draft of the manuscript, performed modelling work and statistical analyses and created figures, tables and supporting documents. IS, ST and DJH all provided intellectual contributions, and were together responsible for editing final versions of the manuscript, figures, tables and supporting documents.

## REFERENCES

- Abe, S., Nakashizuka, T. & Tanaka, H. (1998). Effects of canopy gaps on the demography of the subcanopy tree *Styrax obassia*. *J. Veg. Sci.*, 9, 787–796.
- Baxter, P.W.J., McCarthy, M.A., Possingham, H.P., Menkhurst, P.W. & McLean, N. (2006). Accounting for management costs and sensitivity analyses of matrix population models. *Conserv. Biol.*, 20, 893–905.
- Bierzychudek, P. (1999). Looking backwards: assessing the projections of a transition matrix model. *Ecol. Appl.*, 9, 1278–1287.
- Bjørnstad, O.N. & Grenfell, B.T. (2001). Noisy clockwork: time series analysis of population fluctuation in animals. *Science*, 293, 638–643.
- Buckley, Y.M., Ramula, S., Blomberg, S.P., Burns, J.H., Crone, E.E., Ehrlén, J. *et al.* (2010). Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. *Ecol. Lett.*, 13, 1182–1197.
- Carslake, D., Townley, S. & Hodgson, D.J. (2008). Nonlinearity in eigenvalue-perturbation curves of simulated population projection matrices. *Theor. Popul. Biol.*, 73, 498–505.
- Carslake, D., Townley, S. & Hodgson, D.J. (2009). Predicting the impact of stage-specific harvesting on population dynamics. *J. Anim. Ecol.*, 78, 1076–1085.
- Caswell, H. (2001). *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer, Sunderland, MA.
- Caswell, H. (2007). Sensitivity analysis of transient population dynamics. *Ecol. Lett.*, 10, 1–15.
- Childs, D.Z., Rees, M., Rose, K.E., Grubb, P.J. & Ellner, S.P. (2004). Evolution of size-dependent flowering in a variable environment: construction and analysis of a stochastic integral projection model. *Proc. R. Soc. Lond. B*, 271, 425–434.
- Cohen, J.E. (1979). The cumulative distance from an observed to a stable age structure. *SIAM J. Appl. Math.*, 36, 169–175.
- Costantino, R.F., Desharnais, R.A. & Cushing, J.M. (1997). Chaotic dynamics in an insect population. *Science*, 275, 389–391.
- Costantino, R.F., Desharnais, R.A., Cushing, J.M., Dennis, B., Henson, S.M. & King, A.A. (2005). Nonlinear stochastic population dynamics: the flour beetle *Tribolium* as an effective tool of discovery. *Adv. Ecol. Res.*, 37, 10–141.
- 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.
- Crooks, K.R., Sanjayan, M.A. & Doak, D.F. (1998). New insights on cheetah conservation through demographic modelling. *Conserv. Biol.*, 12, 889–895.
- Cuddington, K. (2001). The 'balance of nature' metaphor and equilibrium in population ecology. *Biol. Philos.*, 16, 463–479.
- Dennis, B., Desharnais, R.A., Cushing, J.M., Henson, S.M. & Costantino, R.F. (2001). Estimating chaos and complex dynamics in an insect population. *Ecol. Monogr.*, 71, 277–303.
- Doak, D., Kareiva, P. & Klept, B. (1994). Modeling population viability for the desert tortoise in the western Mojave desert. *Ecol. Appl.*, 4, 446–460.
- Ellner, S.P. & Rees, M. (2006). Integral projection models for species with complex demography. *Am. Nat.*, 167, 410–428.
- Ellner, S.P. & Rees, M. (2007). Stochastic stable population growth in integral projection models: theory and application. *J. Math. Biol.*, 54, 227–256.
- Ezard, H.G., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A. *et al.* (2010). Matrix models for a changeable world: the importance of transient dynamics in population management. *J. Appl. Ecol.*, 47, 515–523.
- Fieberg, J. & Ellner, S.P. (2001). Stochastic matrix models for conservation and management: a comparative review of methods. *Ecol. Lett.*, 4, 244–266.
- Fowler, M.S. & Ruxton, G.D. (2002). Population dynamic consequences of Allee effects. *J. Theor. Biol.*, 215, 39–46.
- Fox, G.A. & Gurevitch, J. (2000). Population numbers count: tools for near-term demographic analysis. *Am. Nat.*, 156, 242–256.
- Franco, M. & Silvertown, J. (2004). A comparative demography of plants based upon elasticities of vital rates. *Ecology*, 85, 531–538.
- Fujiwara, M. & Caswell, H. (2001). Demography of the endangered North Atlantic right whale. *Nature*, 414, 537–541.
- Grenier, M.B., McDonald, D.B. & Buskirk, S.W. (2007). Rapid population growth of a critically endangered carnivore. *Science*, 317, 779.
- Gross, K., Lockwood, J.R. III, Frost, C.C. & Morris, W.F. (1998). Modelling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conserv. Biol.*, 12, 1291–1301.
- Haridas, C.V. & Tuljapurkar, S. (2007). Time, transients and elasticity. *Ecol. Lett.*, 10, 1143–1153.
- Hastings, A. (2004). Transients: the key to long-term ecological understanding? *Trends Ecol. Evol.*, 19, 39–45.
- Hodgson, D.J. & Townley, S. (2004). Linking management changes to population dynamic responses: the transfer function of a projection matrix perturbation. *J. Appl. Ecol.*, 41, 1155–1161.
- Hughes, T.P. & Tanner, J.E. (2000). Recruitment failure, life histories and long-term decline of Caribbean corals. *Ecology*, 81, 2250–2263.
- Inchausti, P. & Weimerskirch, H. (2001). Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. *Biol. Conserv.*, 100, 337–386.
- Keyfitz, N. (1968). *Introduction to the Mathematics of Populations*. Addison-Wesley, Reading, MA.
- 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. *Ecol. Model.*, 185, 283–297.
- Koons, D.N., Rockwell, R.F. & Grand, J.B. (2007a). Population momentum: implications for wildlife management. *J. Wildlife Manage.*, 70, 19–26.
- Koons, D.N., Holmes, R.R. & Grand, J.B. (2007b). Population inertia and its sensitivity to changes in vital rates and population structure. *Ecology*, 88, 2857–2867.
- Lefkovich, L.P. (1965). The study of population growth in organisms grouped by stages. *Biometrics*, 21, 1–18.
- Leslie, P.H. (1945). On the use of matrices in certain population mathematics. *Biometrika*, 33, 183–212.
- Lotka, A.J. (1932). The growth of mixed populations: two species competing for a common food supply. *J. Wash. Acad. Sci.*, 22, 461–469.
- Maron, J.L., Horvitz, C.C. & Williams, J.L. (2010). Using experiments, demography and population models to estimate interaction strength based on transient and asymptotic dynamics. *J. Ecol.*, 98, 290–301.
- May, R.M. (1975). Biological populations obeying difference equations: stable points, stable cycles and chaos. *J. Theor. Biol.*, 51, 511–524.
- McMahon, S.M. & Metcalf, C.J.E. (2008). Transient sensitivities of non-indigenous shrub species indicated complicated invasion dynamics. *Biol. Invasions*, 10, 833–846.
- Menges, E.S. (1990). Population viability for an endangered plant. *Conserv. Biol.*, 4, 52–62.
- Mollet, H.F. & Cailliet, G.M. (2002). Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Mar. Freshwater Res.*, 53, 503–516.
- Morris, W.F. & Doak, D.F. (2005). How general are the determinants of the stochastic population growth rate across nearby sites? *Ecol. Monogr.*, 75, 119–137.
- Nantel, P., Gagnon, D. & Nault, A. (1996). Population viability analysis of American ginseng and wild leek harvested in stochastic environments. *Conserv. Biol.*, 10, 608–621.
- Neubert, M.G. & Caswell, H. (1997). Alternatives to resilience for measuring the responses of ecological systems to perturbations. *Ecology*, 78, 653–665.
- O'Connor, T.G. (1993). The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. *J. Appl. Ecol.*, 30, 119–132.
- Otway, N.M., Bradshaw, J.A. & Harcourt, R.G. (2004). Estimating the rate of quasi-extinction of the Australian grey nurse shark (*Carcharias taurus*) population using deterministic age- and stage-classified models. *Biol. Conserv.*, 119, 341–350.
- Pavlik, B.M. & Barbour, M.G. (1988). Demographic monitoring of endemic sand dune plants, Eureka valley, California. *Biol. Conserv.*, 46, 217–242.
- Pinard, M. (1993). Impacts of stem harvesting on populations of *Iriartea deltoidea* in an extractive reserve in Acre, Brazil. *Biotropica*, 25, 2–14.



- R Development Core Team (2011). *R: A Language and Environment for Statistical Computing*, reference index version 2.12.1. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://cran.r-project.org>. Last accessed 16 December 2010.
- Rohani, P., Keeling, M.T. & Grenfell, B.T. (2002). The interplay between determinism and stochasticity in childhood diseases. *Am. Nat.*, 159, 469–481.
- Salguero-Gómez, R. & Casper, B.B. (2010). Keeping plant shrinkage in the demographic loop. *J. Ecol.*, 98, 312–323.
- Shea, K. & Kelly, D. (1998). Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecol. Appl.*, 8, 824–832.
- Stephens, P.A., Frey-Roos, F., Arnold, W. & Sutherland, W.J. (2002). Model complexity and population predictions. The alpine marmot as a case study. *J. Anim. Ecol.*, 71, 343–361.
- Stott, I., Franco, M., Carslake, D., Townley, S. & Hodgson, D.J. (2010a). Boom or bust? A comparative analysis of transient population dynamics in plants. *J. Ecol.*, 98, 302–311.
- Stott, I., Townley, S., Carslake, D. & Hodgson, D.J. (2010b). On reducibility and ergodicity of population projection matrix models. *Methods Ecol. Evol.*, 1, 242–252.
- 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.
- Townley, S. & Hodgson, D. (2008). Erratum et addendum: transient amplification and attenuation in stage-structured population dynamics. *J. Appl. Ecol.*, 45, 1836–1839.
- Townley, S., Carslake, D., Kellie-Smith, O., McCarthy, D. & Hodgson, D. (2007). Predicting transient amplification in perturbed ecological systems. *J. Appl. Ecol.*, 44, 1243–1251.
- Tuljapourkar, S.D. (1982). Population dynamics in variable environments. III. Evolutionary dynamics of  $r$  selection. *Theor. Popul. Biol.*, 21, 141–165.
- Tuljapourkar, S.D. (1990). Population dynamics in variable environments. *Lect. notes Biomath.*, 85. Springer-Verlag, New York.
- Tuljapourkar, S., Horvitz, C.C. & Pascarella, J.B. (2002). The many growth rates and elasticities of populations in random environments. *Am. Nat.*, 162, 489–502.
- Turchin, P. (1993). Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. *Oikos*, 68, 167–172.
- Verhulst, P.F. (1838). Notice sur la loi que la population suit dans son accroissement. *Correspondes Mathematiques et Physiques*, 10, 113–121.
- Volterra, V. (1926). *Variations and Fluctuations of the Numbers of Individuals in Animal Species Living Together*. McGraw Hill, New York. (Reprinted in 1931: R.N. Chapman, Animal Ecology)
- Wilson, P.H. (2003). Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. *Conserv. Biol.*, 17, 782–794.
- van Winkle, W., Rose, K.A. & Chambers, R.C. (1993). Individual-based approach to fish population dynamics: an overview. *T. Am. Fish. Soc.*, 122, 397–403.
- Yearsley, J.M. (2004). Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecol. Model.*, 177, 245–258.
- Zúñiga-Vega, J.J., Valverde, T., Rojas-González, R.I. & Lemos-Espinal, J.A. (2007). Analysis of the population dynamics of an endangered lizard (*Xenosaurus grandis*) through the use of projection matrices. *Copeia*, 2007, 324–335.

## GLOSSARY

**Amplification:** Short-term increase in population density relative to asymptotic growth.

**Asymptotic growth:** The long-term, geometric rate of population increase or decline that the model exhibits when it reaches stable state; mathematically, equal to the dominant eigenvalue of the PPM,  $\lambda_{\max}$ .

**Attenuation:** Short-term decrease in population density relative to asymptotic growth.

**Case-specific transient dynamics:** The transient dynamics resulting from a specified initial demographic distribution.

**Initial demographic distribution:** The actual ratios of life stages in the population; mathematically, the vector used to project population dynamics. Represented here using  $\mathbf{n}_0$ , where  $\|\mathbf{n}_0\|_1$  (the one-norm or column sum of  $\mathbf{n}_0$ ) is equal to overall population size or density.

**Disturbance:** A change to the demographic structure of the population (usually as a result of exogenous forces); mathematically, a change in the ratio of life stages in the initial demographic distribution vector.

**Elasticity:** The change in population density or growth resulting from a perturbation of one or more vital rates of a population, relative to the magnitude of the vital rate(s) perturbed.

**Perturbation:** A change to the vital rates of the population (usually as a result of exogenous forces); mathematically, a change in one or more PPM elements.

**Perturbation analysis:** Any analysis that considers the change of a model output with respect to the change of a model input; usually considering the change in population density or growth resulting from perturbation of one or more vital rates of the population.

**Sensitivity:** The absolute rate of change in population density or growth resulting from infinitesimal perturbations of one or more vital rates of a population.

**Stable demographic distribution:** The ratios of life stages in the population when it reaches stable state; mathematically, equal to the dominant right eigenvector of the PPM,  $\mathbf{w}$ .

**Stage-biased vector:** An initial demographic distribution vector that has all individuals in a single stage and an overall density of 1; mathematically, a standard basis vector with zeroes in each entry, except for a single entry that is equal to one.

**Transfer function:** A means of perturbation analysis derived from systems and control theory. Describes the exact nonlinear relationship between a perturbation to a vital rate and resultant change in population density or growth.

**Transient bound:** The most extreme values of transient dynamics that may result from a PPM. Any case-specific transient dynamics must lie between the bounds on amplification and attenuation.

**Transient dynamics:** The short-term dynamics of the population, which are dependent on the initial conditions of the model.

**Transient envelope:** The area between the transient bounds, in which case-specific transient dynamics must lie.

**Transient period:** The period of time in which the model exhibits transient dynamics, before it settles to stable state.

## SUPPORTING INFORMATION

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

**Table S1** Table of published indices of transient dynamics.

**Appendix S1** Database of population projection matrix models and associated data used in correlation analyses.

**Appendix S2** Detailed information on methodology and results of correlation analyses.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials are peer-reviewed and 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.

Editor, Michael Bonsall

Manuscript received 29 April 2011

First decision made 2 June 2011

Manuscript accepted 15 June 2011