MODELLING TRANSIENT POPULATION DYNAMICS AND THEIR ROLE IN ECOLOGY AND EVOLUTION

Submitted by

IAIN MICHAEL STOTT

to

THE UNIVERSITY OF EXETER

as a thesis for the degree of
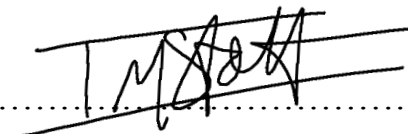
DOCTOR OF PHILOSOPHY IN BIOLOGICAL SCIENCES

in

JUNE 2012

I certify that all the material in this thesis which is not my own work has been identified and that no material has been previously been submitted and approved for the award of a degree by this or any other university.

Signature: ……………………………………..

ABSTRACT

_ _ _ _ _ _ _ _ _ _ _ _ _ _

Population projection matrix (PPM) models are a central tool in ecology and evolution. They are widely used for devising population management practises for conservation, pest control, and harvesting. They are frequently employed in comparative analyses that seek to explain demographic patterns in natural populations. They are also a key tool in calculating measures of fitness for evolutionary studies. Yet, demographic analyses using projection matrices have, in some ways, failed to keep up with prevailing ecological paradigms. A common focus on long-term and equilibrium dynamics when analysing projection matrix models fits better with the outmoded view of ecosystems as stable and immutable. The more current view of ecosystems as dynamic and subject to constant extrinsic disturbances has bred new theoretical advances in the study of short-term 'transient' dynamics. Transient dynamics can be very different to long-term trends, and given that ecological studies are often conducted over short timescales, they may be more relevant to research. This thesis focuses on the study of transient dynamics using population projection matrix models. The first section presents theoretical, methodological and computational advances in the study of transient dynamics. These are designed to enhance the predictive power of models, whilst keeping data requirements to a minimum, and borrow from the fields of engineering and systems control. Case studies in this section provide support for consideration of transient dynamics in population management. The second section applies some of these new methods to answer pertinent questions surrounding the ecology and evolution of transient dynamics in plants. Results show that transient dynamics exhibit patterns according to life form and phylogenetic history. Evidence suggests that this can be linked to the stage-structuring of life cycles, which opens up the possibility for new avenues of research considering the evolution of transient dynamics in nature.

ACKNOWLEDGMENTS

It goes without saying that there are a great many people without whom I would never have been able to achieve this. But, I'm going to say it anyway because I want to and because I've been looking forward to writing something that's not going to be peer-reviewed for once. So, it's the night before hand-in, I've come to Gylly beach and I'm sitting watching the sea with a glass of gin in one hand and a pen in the other.

First of all, there are the many people who have had a direct hand in this work. Dave and Stuart, you have both been genuinely great supervisors. I'm very fortunate to have had you two to guide me through my PhD, and there's no way I would have been able to achieve what I have were it not for your excellent supervision. You've had my back since I was an undergraduate, and I can't express how grateful I am for the opportunities you have afforded me. So thank you, for being supportive, and critical, and understanding, and enthusiastic, and hard-working, and grounded in just the right measures. I really hope that I can continue to work with you guys in the future.

There are a few co-authors to this work, who have provided a helping hand in areas where it was greatly needed. Miguel Franco had a great input in building plant phylogenies and giving advice on plant biology and demography. Thank you Miguel for being so thorough, and for turning work around so quickly! David Carslake helped establish the database of matrix models and hence the foundation of a lot of this work, so thank you David for all your hard work. Thanks also to Vicky Warwick-Evans and Jonathan Ramalheira-Tsu for their inputs to the matrix database.

Several others have provided a critical eye and/or a helping hand where required. Thanks to Jonathan Ramalheira-Tsu, Chris Coles, Mel Smee, Kim Stokes, Chris Beirne and Jenni Graham for your help with testing and presenting the R package. Thanks also to Xav Harrison, Fiona Ingleby, Lucy Wright and Yvonne Buckley for your help with MCMCglmm analyses… it truly is a tricky beast.

Thanks too to the Hodgson group: Mel, Cheryl, Erika, Jenni, Chris, Nicole, your input in group meetings has been much appreciated.

Now I come to the countless others who have helped indirectly with this work, by being such an important and invaluable part of my life over the last few years. You are, of course, my wonderful friends and family. I don't say it often enough, but I love you all.

I wouldn't have stayed sane if it wasn't for my friends. The all-too-infrequent times I get to see you all are invariably the highlights of my weeks, months and years. It doesn't matter whether it's a night out in Falmouth, Newton Abbot, Glasgow, Sheffield or Swansea, playing mini-golf in the rain when it was definitely supposed to be sunny, sitting under duvets whilst watching House and eating crisps, going to London for a concert, rockpooling on the beach, a trip to the zoo or aquarium, learning salsa on a hot and sweaty night in beautiful Kuzey Kıbrıs, cooking a giant roast dinner at Christmastime, going birdwatching (with the omnipresent birdwatching bag!), drinking gin and watching Studio Ghibli films, playing on the swan pedalos, drinking Malibu and hot chocolate in front of the fire, a midnight sea swim, sitting hung-over on the sofa and watching all the episodes of Miranda (Garryyyyyyy!), staying in all weekend and watching Grey's anatomy in bed, sitting on the rocks by the sea and watching the world go by, a gay old time of it at pride… I want to go on forever, and I could. These are the moments that have kept me going when work got too much. Beth, Sarah, Jonathan, Helen, Hattie, Rachel, Zoe, Anna, Steve, Anderson, Andrea, Sarah, Dan, Krish, Laura, and everyone else, you are all bloody wonderful. You are the people that make me E, and for that I am eternally grateful.

I must give particular thanks to two very special people. Beth and Sarah, you have been my rocks over the past few years. I'm struggling to vocalise just how important you have been in helping me through everything. Beth, I'm so grateful that you go out of your way to come and see me so often still, you breathe life into Falmouth. Sarah, I don't get to see you nearly often enough, but I just couldn't do without our once-, twice-, or three- or four-times weekly phone conversations. You guys have kept my life sunny even when the outlook was gloomy.

I also need to thank Jonathan. You have been such a special part of my life. Admittedly, the source of pleasure and pain in varying measures, but I could never imagine what everything would have been like without you. You changed my life, you have taught me so much, you have grounded me, and you made the first couple of years of this experience the best fun ever.

From friends brings me to family. It's not been the easiest few years. So much has changed, and yet I am grateful every day that we've all managed to surface from the turmoil, still intact. You've all helped mould me into the person I am today. Mum, Dad, I owe you so much. Thank you for being so unwaveringly supportive of me. There's a damn good chance I wouldn't even have ended up doing this if it wasn't for you, and an even bigger chance that I wouldn't have gotten where I am with it without you there behind me. Thank you for always being so proud of me. I find it hard to be proud of myself, and I think you more than make up for that.

Alec and Rory, thank you for being so bloody brilliant. When I started this PhD, you were both just teenagers. Now I arrive at the end, and you're both twenty-something (twenty-something!), intelligent, mature and accomplished young men. I am immensely proud of you both.

Nanny, thank you for always being there. I've always known, throughout everything, that I can come to you for help and support. Thank you too for being so proud of me. I haven't forgotten the promise I made to you on your eightieth birthday (despite how drunk I was): I look forward to sitting with you on your ninetieth birthday and I hope you will still be as proud of me then.

Thanks to everyone for providing fun times the past few years. Whenever we get together we have a blast (especially when the red wine is flowing, Auntie Fran), but I don't get to see enough of you all.

This PhD has been one hell of an experience. There have been countless others that have had such important contributions to make. There just isn't enough space. Thanks to all the housemates over the years for making my home life so fun and interesting. Thanks to all the people at work over the years for making Tremough such a wonderful place to be. Thanks to Falmouth for being Falmouth, with all the ups and all the downs. It's time for me to sign off now and get home, because Gylly is getting cold, I finished my drink a long time ago, and that's enough sentimentality poured onto paper for one evening.

Everybody, this thesis is because of you.

CONTENTS
- - - - - - - - - - - - - -

PART 2: THE ROLE OF TRANSIENT POPULATION DYNAMICS

IN ECOLOGY AND EVOLUTION

"STAGE-STRUCTURED LIFE CYCLES FAVOUR SHORT-TERM DEMOGRAPHIC RESILIENCE IN PLANT POPULATIONS"

_____

INTRODUCTION

– – – – – – – – – – – – – – – – – – – –

A fundamental aim in ecology and evolution is to create mathematical models that are predictive of future system dynamics. Ecological and evolutionary models may span scales of biological organisation from genes (Galindo, Olson & Palumbi 2006) to ecosystems (McGinnis *et al.* 1969), scales of time from days (Carslake, Townley & Hodgson 2009a) to millennia (Ezard *et al.* 2012), and scales of space from a single field (Valverde *et al.* 2004) to entire continents (Thomas *et al.* 2004). Such systems inevitably have one thing in common: their dynamics are noisy, subject to both exogenous and endogenous sources of variation that complicate our understanding of how they work and hinder our ability to accurately model them. Of course, different sources of variation are important at different scales: levels of gene expression will have a great deal of effect on an individual's phenotype (Smith *et al.* 2009), but probably very little impact on ecosystem dynamics. Individual weather patterns spanning a several months may seriously impact population growth (Smee *et al.* 2011), but are less likely to be highly influential on evolutionary scales. Certain aspects of microclimate may be highly important to individual insect populations (Lawson *et al.* 2012), but may be inconsequential to global insect diversity. In any case, variation presents a significant obstacle in developing models of natural systems: it is no coincidence that development of the fields of ecology, evolution, mathematics and statistics are often tightly linked.

Remarkably however, the foundations of mathematical models are often very similar. Individual classes of model can be applicable to a great variety of systems. Network models can describe disease dynamics (Lion & Boots 2010) or food webs (Ings *et al.* 2008); differential equations can describe chemical networks (Mincheva & Roussel 2007) or spatial population dynamics (Holmes *et al.* 1994); matrix models can describe metabolic networks (Förster *et al.* 2003) or macroevolutionary processes (Ezard *et al.* 2012). Moreover, modelling frameworks often transcend traditional disciplinary boundaries: ecological models have often proven relevant when applied to economic problems (Haldane & May 2011). Given the generality of modelling techniques, it may pay sub-disciplines within ecology and evolution to borrow methods from one another, or to look to other subject fields for solutions to modelling problems.

One ecological discipline that has seen a particular wealth of modelling literature is that of population ecology. The earliest prospective models of population dynamics were developed in the 19th Century, with the inception of the logistic equation (Verhulst 1838), although studies of population dynamics did not become popular until the 20th Century, when these equations were rediscovered and developed (Reed & Pearl 1927). Early models of population dynamics were

simple. Every individual was considered equal in its contribution to the population. Dynamics were considered to be constant over time. Density dependence was included in its most basic form. Development of more complex methods was slow, impeded by the fact that calculation was necessarily done by hand. Nevertheless, over time population models became steadily more complex, with the incorporation of new methods such as differential equation models (Lotka 1932). A particular breakthrough was the introduction of population projection matrix (PPM) models; Leslie 1945; Lefkovitch 1965). These introduced stage-structuring into population models, recognising that not all individuals in the population contribute equally to population dynamics. Matrix models of population dynamics grew to be perhaps the most widely-used models in population ecology, remaining highly popular today.

The popularity of matrix models may lie in their tractability. First of all, it is relatively easy to understand how a life cycle graph is coerced into matrix form: matrix columns describe the current life cycle stage of an individual, and matrix rows describe the stage an individual may move into within the next timestep. Entries in the matrix describe how probable movement between different life stages is. The demographic structure of the population is described by a column vector of numbers or densities of individuals, and multiplying the matrix by this vector yields the demographic structure of the population in the next timestep. Repeating this process gives a population projection; a time series of population size or density. Hence, the projection equation is simple: $\mathbf{n}_t = \mathbf{A}^t\mathbf{n}_0$, where $\mathbf{A}$ is the PPM and $\mathbf{n}_t$ and $\mathbf{n}_0$ are the demographic vectors at time t and time 0 respectively. Most importantly, there are a number of emergent properties of this model that describe long-term population dynamics, foregoing the requirement for model projection (see Caswell 2001). In the long term the population is predicted to settle to a stable state with stable growth or decline and a stable demographic structure. The dominant eigenvalue of the matrix λ_{max} is the value of stable geometric long-term growth. The dominant right eigenvector $\mathbf{w}$ of the matrix describes the proportions of life stage densities in the stable demographic structure. The dominant left eigenvector $\mathbf{v}$ of the matrix describes the long-term reproductive value of each stage. It is also possible to compute how changes in the life cycle might influence these dynamics, using simple sensitivity and elasticity analyses. As PPM models were conceived in a time when the presiding paradigm of ecology was one of stability in natural systems (Cuddington 2001), these properties made PPM models a highly attractive prospect.

However, over time ecological paradigms changed and stability theory largely fell out of favour. Technological developments revolutionised science as a whole, as computational power grew exponentially. For population ecology, this meant that greater sources of natural variation could (and should) be incorporated into matrix models. Ecologists fell into two broad camps: those that believed density-dependent processes contribute more significantly to noisy population dynamics (Dennis *et al.* 1997), and those that believed environmental stochasticity is the driver

of variation in population density and growth (Fieberg & Ellner 2001). This argument is not trivial: by this time PPM models were a key tool in numerous areas of ecological and evolutionary research. An accurate understanding of population dynamics was important when using PPM models to inform population management and policy for conservation (Price & Kelly 1994), pest control (Smith & Trout 1994), invasive species (Shea & Kelly 1998), fisheries (Sable & Rose 2011), and harvesting (Pinard 1993). In many such cases, studies will have influenced the dissemination of significant economical investment. Simultaneously, PPM models were widely used in comparative ecological and evolutionary studies (Silvertown *et al.* 1996; Crone 2001), with demographic measures such as long-term growth or reproductive value used as measures of fitness (Hunt & Hodgson 2010). Hence PPM models were not only instrumental in an applied sense, but also important to our understanding of how ecological and evolutionary processes work.

Density-dependent and stochastic models have both seen success in explaining complex time series of population dynamics. Two classic systems provide the most rigorous evidence for density dependent regulation of populations: in the laboratory, overcompensating density dependence has been shown to drive both limit cycles and chaos in populations of flour beetle of the genus *Tribolium* (Dennis *et al.* 1997; Costantino, Desharnais & Cushing 1997; Dennis *et al.* 2001). In the field, there is ample evidence to suggest that density-dependent processes drive the cyclic population dynamics of many species of rodent, particularly voles (Hanski *et al.* 1993; Turchin 1993). However, the importance of such nonlinear dynamics in most natural systems has been hotly debated (Turchin & Taylor 1992), whilst stochastic effects are arguably more ubiquitous. Countless studies of stochastic demography have demonstrated that vital rates vary over both time and space under differing environmental conditions. Such studies span a wealth of taxa in both plants (Nantel, Gagnon & Nault 1996; Morris & Doak 2005) and animals (Nakaoka 1997; Hunter *et al.* 2010). More recently, it has been accepted that both density-dependent and stochastic mechanisms are likely to be important, with the description of models that include both types of process (Bjørnstad & Grenfell 2001).

All of these analyses have retained one thing in common with analyses of earlier, basic PPM models: they continue to focus on the long-term properties of the model. Density dependent analyses consider attractors: stable equilibria such as the carrying capacity of the population and nonstable equilibria including limit cycles and chaos (Dennis *et al.* 2001). Stochastic models concern themselves with mean and variance of long-term stochastic growth rate (Fieberg & Ellner 2001), with stochastic sensitivity and elasticity analyses describing how stochastic growth is affected by changes in vital rates of the population (Tuljapurkar, Horvitz & Pascarella 2003).

However, the past decade has seen the spotlight turned upon analyses of short-term, or 'transient', population dynamics (Neubert & Caswell 1997; Hastings 2001, 2004; Townley *et al.*

12

2007). The concepts underlying transient theory are relatively simple. Transient dynamics can be very different to long-term dynamics: for example, a population that declines in the long term may increase in the short term or *vice versa* (Hastings 2001, 2004; Townley *et al.* 2007). Long-term dynamics are independent of population structure, but transient dynamics depend heavily on population structure (Townley & Hodgson 2008). Therefore transients are likely to be a common feature of stochastic systems, where the environment induces frequent changes in population structure. As such, transient analyses may be important to population management if transients preside in the population, standing alongside asymptotic analyses as a means of evaluating population models. Additionally, transients may aid in our understanding of complex ecological time series, standing alongside density dependence and stochasticity as an important driver of variation in population dynamics.

However, transient analyses don't benefit from the simple analytical solutions and intuitive interpretations enjoyed by asymptotic analyses. Early development in the field saw a great diversity of methodologies for quantifying both transient dynamics *per se* (Neubert & Caswell 1997; Koons, Holmes & Grand 2007; Townley *et al.* 2007; Townley & Hodgson 2008) and their sensitivity to perturbation (Fox & Gurevitch 2000; Yearsley 2004; Caswell 2007). The emerging body of literature was fragmented: whilst there existed a diverse range of methodologies for analysing transients, these differed greatly in their approach and amongst them there was even little consensus on what constitutes 'transient dynamics'. Without a broad understanding of how best to analyse transients, let alone what transient dynamics are and what they mean, transient analyses remained elusive in studies of population management and comparative demography.

This thesis aims to build some coherence in the approach to studying transient population dynamics, and to explore some ecological and evolutionary patterns in transient dynamics. The thesis is comprised of a number of standalone papers written throughout the course of my PhD. Each chapter is a study in its own right, although hopefully they also come together as a logical whole.

The first part of the thesis, "Modelling Transient Population Dynamics" consists of four chapters that deal with methods behind the study of transients. The first chapter provides a literature review that aims to synthesise a framework within which to study transients. It is within this framework that the rest of the thesis is conducted. The second chapter presents novel methods for analysing transient dynamics that borrow from control systems engineering. These help to increase the accuracy of model prediction, but crucially demand no extra data for their implementation. The third chapter explores some of the core assumptions of PPM models, assessing how their violation affects predicted dynamics and how often they are adhered to. The fourth chapter presents a software package for transient analysis in the program R that includes all modelling methodology used in this thesis, and more. This software makes transient analyses

freely available to ecologists, conservationists and researchers the world over. Throughout this first section, I heavily utilise worked examples, using models for natural populations. These demonstrate, on a case-by-case basis, the importance of considering transient dynamics in population management.

The second section of the thesis, "The Role of Transient Population Dynamics in Ecology and Evolution", consists of two chapters that seek to explore patterns of transient dynamics in natural plant populations, and assess how important these patterns may be to ecological and evolutionary processes. Mainly, this concerns how transients vary according to both life history and phylogenetic relatedness. The fifth chapter explores how large transients can get, asking the questions, do plants exhibit boom-and-bust transient dynamics, do plants with similar life forms exhibit similar potential transient dynamics, and are these dynamics heritable? The sixth chapter explores the role transient dynamics play in the response of populations to disturbance, asking do populations tend to rebound quickly from disturbance events, do different life forms show different patterns of response to disturbance, and are such patterns of response heritable? This section draws upon a large database of PPM models for plant species. Results indicate that patterns of transient dynamics differ according to both life form and phylogenetic relatedness, unearthing the possibility that transients may be an important target of selection in natural populations.

Finally, the general discussion draws together information presented in the thesis, and debates the future of transient dynamics in ecology and evolution. This includes a discussion on how the results presented here contribute to our understanding of population dynamics, and a venturing of some important questions that need to be explored. It also includes a consideration of how transient dynamics fit into the general study of demography, and specifically how transient theory may contribute in density dependent and stochastic systems. Important methodological requirements are suggested, including the extension of transient dynamics to other modelling frameworks. Last, the discussion touches upon the possibility of using transient analyses to predict dynamics of other stage-structured biological systems spanning all levels of biological organisation across various scales of time and space.

CHAPTER 1

– – – – – – – – – – – – – –

Early experience of working with transient dynamics revealed the diversity of approaches to their study. Many indices of transient dynamics existed, but there was often confusion surrounding their exact meaning. Some studies would forego the use of specific indices altogether, analysing transient dynamics over arbitrary scales of time and/or density. Continued disparity in approach risked inability to compare results between studies, and would have increased difficulties for newcomers to the field. Chapter 1 reviews the literature on the study of transient dynamics in population projection matrix models, and synthesises a framework in which to work. Although the first chapter presented here, this was the third paper published as part of this thesis. With this paper, we aimed to promote methods that would be useful in many different contexts and identify important indices, with concrete mathematical and biological interpretations, which capture a large amount of the variability in transient dynamics of populations. At the very least, we hoped that synthesising the available literature into a coherent framework would help identify where different methods sit in the context of the overall study of transient dynamics.

Chapter 1:

A FRAMEWORK FOR STUDYING TRANSIENT DYNAMICS OF POPULATION PROJECTION MATRIX MODELS

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.

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; Lefkovitch 1965), integral projection models (e.g. Childs *et al.* 2004; Ellner & Rees 2006, 2007) and individual-based models (e.g. van Winkle, Rose & Chambers 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, Desharnais & Cushing 1997; Dennis *et al.* 2001; Fowler & Ruxton 2002), whereas time-varying stochastic forms incorporate extrinsic drivers, such as variation in climate

17

or resource abundance (e.g. Fieberg & Ellner 2001; Tuljapurkar, Horvitz & Pascarella 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, Desharnais & Cushing 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, Sanjayan & Doak 1998; Grenier, McDonald & Buskirk 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, Bradshaw & Harcourt 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, Gagnon & Nault 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, Tyre & Rebarber 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. 1.1). 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 (*Acyrthosiphon pisum*) populations may exhibit immediate population growth that is greater than predicted asymptotic growth, following experimentally induced adult invasion scenarios (Tenhumberg, Tyre & Rebarber 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 [Chapter 5]). 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 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 λ_{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 Appendix 1.1). 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 λ_{max} to become x times as great as λ_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 Δ* (Keyfitz 1968) measures the proportional difference between the initial and stable demographic distribution vectors (Appendix 1.1), 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 (Appendix 1.1), utilising the reproductive value vector **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 λ_{max}); however, this is a relatively computationally intensive solution to the problem.

POPULATION DENSITY AND 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, Rockwell & Grand 2007). 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 [Chapter 5]) 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, Horvitz & Williams 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. 1.2a). 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. 1.2b). 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 1.2a 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. 1.2b 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. 1.2b). Third, relative measures enable fair comparative study of transient dynamics among populations or species with widely varying asymptotic growth (Stott *et al.* 2010a [Chapter 5]). Therefore, relative measures 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, Holmes & Grand 2007; 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 λ_{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, Holmes & Grand 2007). 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 (Appendix 1.1) is to use the 'standardised' PPM **Â**, which is equal to the PPM **A** divided by λ_{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. 1.2b). 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 [Chapter 5]).

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. 1.2b). 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. 1.2), 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. 1.2, 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*,* Horvitz & Williams 2010; Koons *et al.* 2005; Townley *et al.* 2007; Townley & Hodgson 2008; Stott *et al.* 2010a [Chapter 5]) 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. 1.2b, for example, it is easy to see how different initial demographic distributions result in different transient responses when each starts with at an initial overall density of 1. Second, it enables fair comparative study of transient dynamics among models for different populations or species (Maron, Horvitz & Williams 2010; Stott *et al.* 2010a [Chapter 5]). 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. 1.2b, 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, Horvitz & Williams 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; Appendix 1.1). 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; Appendix 1.1). 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; Appendix 1.1), the latent increase in human population size following an immediate decrease in birth rates to the level of replacement. *Population inertia* (Koons, Holmes & Grand 2007; Appendix 1.1) 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. 1.2b). Therefore, population momentum is a special case of population inertia (Koons, Holmes & Grand 2007; Appendix 1.1). 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; Appendix 1.1) 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; Appendix 1.1) and the *lower Kreiss bound* is an upper bound on maximal possible attenuation (Townley & Hodgson 2008; Appendix 1.1). 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 [Chapter 5]). We exploit a database of 563 published, irreducible (Stott *et al.* 2010b [Chapter 3]) PPM models for 202 species of

animals and plants (Appendix 7) 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 (Appendix 1.1). However, where the maximum/minimum occurs at r→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 1.1). 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. 1.3. 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. 1.3. 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. 1.3. It appears that for both transient bounds and case-specific indices, amplified measures show very tight positive correlations with one another (upper-left quadrant of Fig. 1.3), whereas attenuated measures show tight positive correlations, but not to the same degree as among amplified measures (lower-right quadrant of Fig. 1.3). However, amplified measures are not good predictors of attenuated measures and *vice versa* (upper-right and lower-left quadrants of Fig. 1.3). 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 λ_{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 1.1 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 1.1). 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. 1.4). Figure 1.4a shows two projections for the subcanopy tree *Styrax obassia* in central Japan (Abe, Nakashizuka & Tanaka 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: λ_{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 λ_{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 1.4b 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. λ_{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 λ_{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 is 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.

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 λ_{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, Holmes & Grand 2007) 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 (Tuljapurkar 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, Holmes & Grand 2007). 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, Townley & Hodgson 2008, 2009a). 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 epidemical cycles becoming multiannual cycles following an increase in recovery rates (Rohani, Keeling & Grenfell 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.

TABLES

TABLE 1.1: 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. $\mathbf{\hat{A}}$ represents the standardised population projection matrix and is equal to $\mathbf{A}/\lambda_{max}$ (where $\mathbf{A}$ is the PPM and λ_{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); $\mathbf{\hat{n}}_0$ represents the initial demographic distribution, standardised to sum to 1. minCS denotes the minimum column sum of a matrix and $\|m\|_1$ is the one-norm of a vector $\mathbf{m}$ (equal to the sum of its entries). m_{min} and m_{max} are the smallest and largest entries of a vector $\mathbf{m}$ respectively. We have chosen to use the Greek ρ to represent transient bounds (in accordance with Townley & Hodgson 2008), whereas the Latin 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 ∞ for asymptotic indices.

INDEX	FORMULA		BIOLOGICAL MEANING
REACTIVITY	*TRANSIENT BOUND*	$\overline{\rho}_1 = \|\mathbf{\hat{A}}\|_1$	*TRANSIENT BOUND* – maximum population growth in a single timestep, relative to stable growth rate.
	CASE-SPECIFIC	$\overline{P}_1 = \|\mathbf{\hat{A}\hat{n}_0}\|_1$ when $\|\mathbf{\hat{A}\hat{n}_0}\|_1 > 1$	*CASE-SPECIFIC* – 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	*TRANSIENT BOUND*	$\underline{\rho}_1 = \min CS(\widehat{\mathbf{A}})$	*TRANSIENT BOUND* - minimum population growth in a single timestep, relative to stable growth rate.
	CASE-SPECIFIC	$\underline{P}_1 = \|\widehat{\mathbf{A}}\widehat{\mathbf{n}}_0\|_1$ when $\|\widehat{\mathbf{A}}\widehat{\mathbf{n}}_0\|_1 < 1$	*CASE-SPECIFIC* – population growth achieved by a given population in a single timestep, relative to stable growth rate. Assumes the population will attenuate immediately.
MAXIMUM AMPLIFICATON	*TRANSIENT BOUND*	$\overline{\rho}_{max} = \max_{t>0}\left(\|\widehat{\mathbf{A}}^t\|_1\right)$	*TRANSIENT BOUND* – the largest possible future population density achievable, relative to a population with stable growth rate and same initial density.
	CASE-SPECIFIC	$\overline{P}_{max} = \max_{t>0}\left(\|\widehat{\mathbf{A}}^t\widehat{\mathbf{n}}_0\|_1\right)$ when $\|\widehat{\mathbf{A}}^t\widehat{\mathbf{n}}_0\|_1 > 1$ for some t	*CASE-SPECIFIC* – 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	*TRANSIENT BOUND*	$\underline{\rho}_{min} = \min_{t>0}\left(\min CS(\widehat{\mathbf{A}}^t)\right)$	*TRANSIENT BOUND* – the smallest possible future population density achievable, relative to a population with stable growth rate and same initial density.

	CASE-SPECIFIC	$\underline{P}_{min} = \min_{t>0}\left(\left\|\widehat{A}^t\widehat{n}_0\right\|_1\right)$ when $\left\|\widehat{A}^t\widehat{n}_0\right\|_1 < 1$ for some t	*CASE-SPECIFIC* – 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	*TRANSIENT BOUND*	$\overline{\rho}_\infty = \dfrac{v_{max}\|w\|_1}{v^T w}$	*TRANSIENT BOUND* – the largest possible long-term population density, relative to a population with stable growth rate and same initial density.
	CASE-SPECIFIC	$\overline{P}_\infty = \dfrac{v^T\widehat{n}_0\|w\|_1}{v^T w}$ when $\dfrac{v^T\widehat{n}_0\|w\|_1}{v^T w} > 1$	*CASE-SPECIFIC* – 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	*TRANSIENT BOUND*	$\underline{\rho}_\infty = \dfrac{v_{min}\|w\|_1}{v^T w}$	*TRANSIENT BOUND* – the smallest possible long-term population density, relative to a population with stable growth rate and same initial density.
	CASE-SPECIFIC	$\underline{P}_\infty = \dfrac{v^T\widehat{n}_0\|w\|_1}{v^T w}$ when $\dfrac{v^T\widehat{n}_0\|w\|_1}{v^T w} < 1$	*CASE-SPECIFIC* – 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.

FIGURES
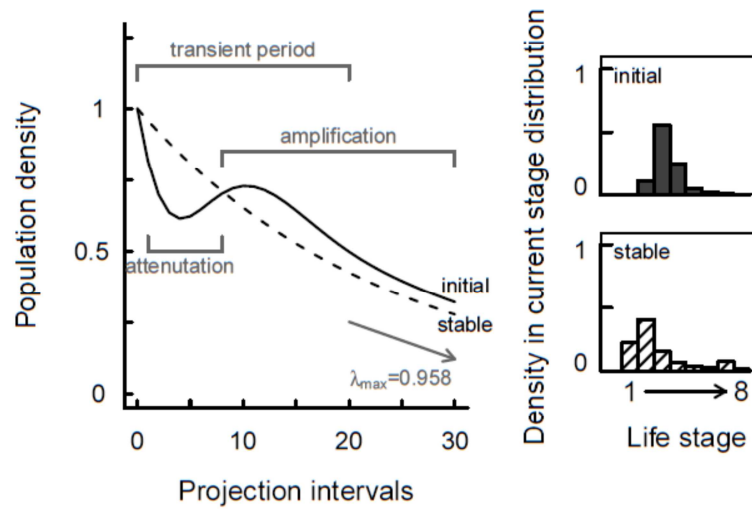
FIG. 1.1: Illustration of transient population dynamics arising from a density-independent, time-invariant PPM model. A population with stable demographic distribution (dashed line; hatched bar plot) declines at a rate equal to λ_{max} each time interval. However, real-world populations have initial demographic distributions that differ from the stable demographic distribution (solid line; grey bar plot) and exhibit transient dynamics.
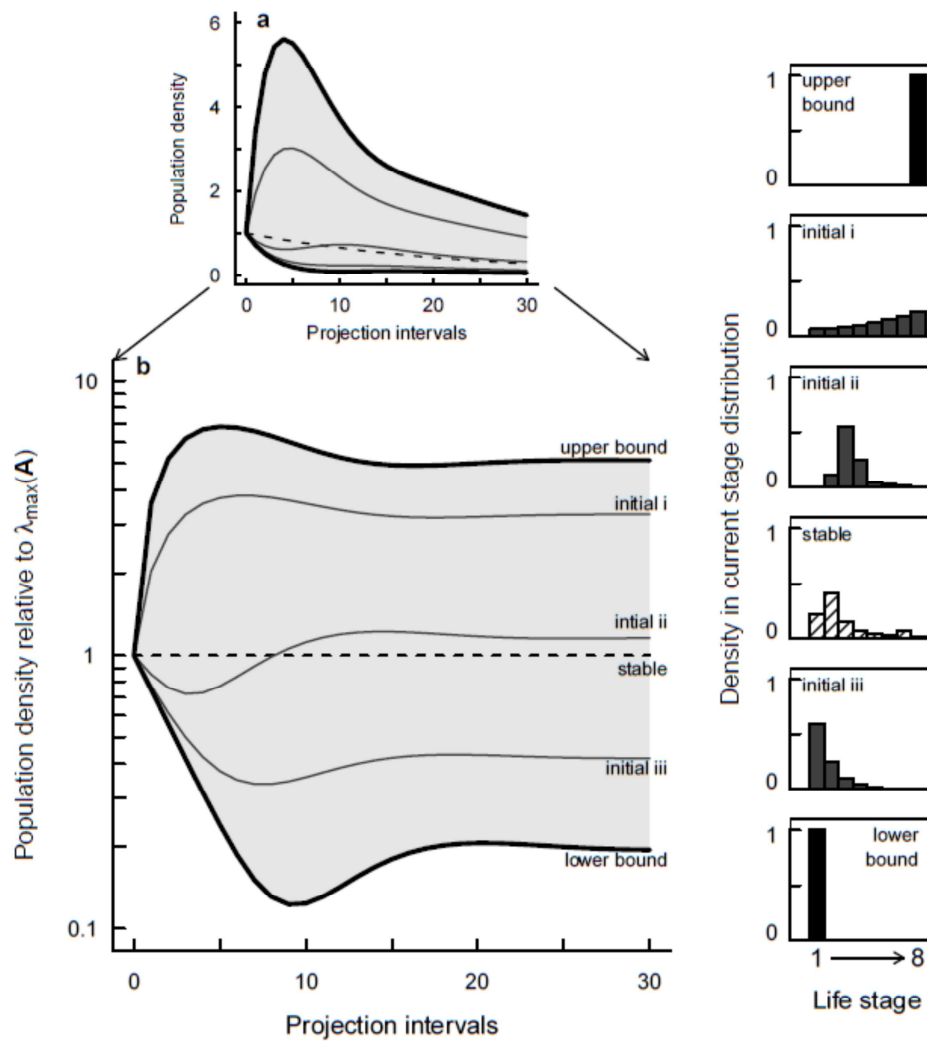
FIG. 1.2: Transient dynamics of the desert tortoise *Gopherus agassizii* with medium fecundity (Doak, Kareiva & Klepetka 1994). **(a)** Absolute population dynamics, including both transient and asymptotic influences; **(b)** standardised transient dynamics, excluding the influence of asymptotic growth. 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.
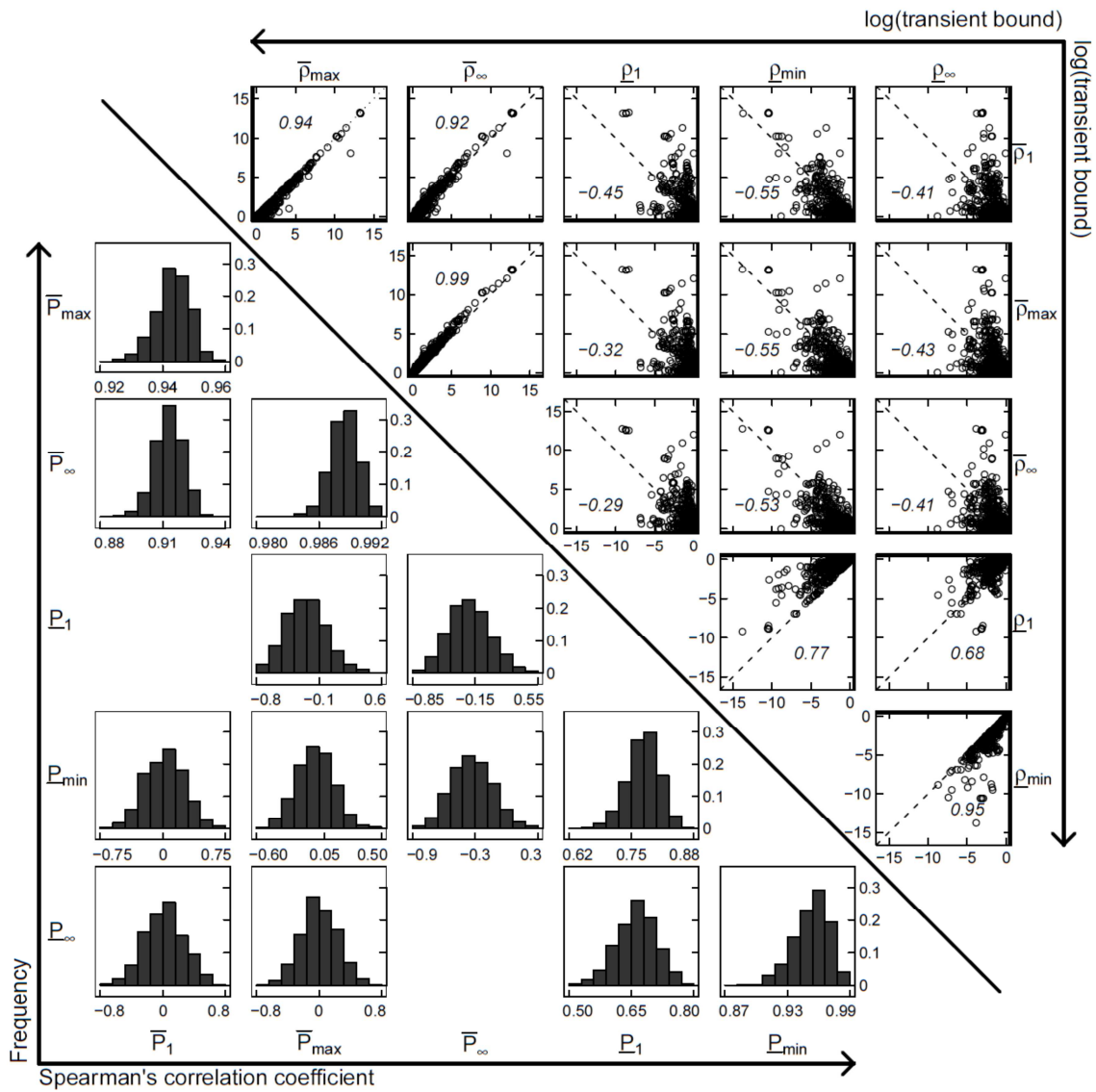
FIG. 1.3: Correlations between transient bounds and case-specific indices for 563 published population projection matrix models. The upper-right triangle shows pairwise correlations between six transient bounds and their associated Spearman's rho values; both axes are on a log scale. The lower-left triangle 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.
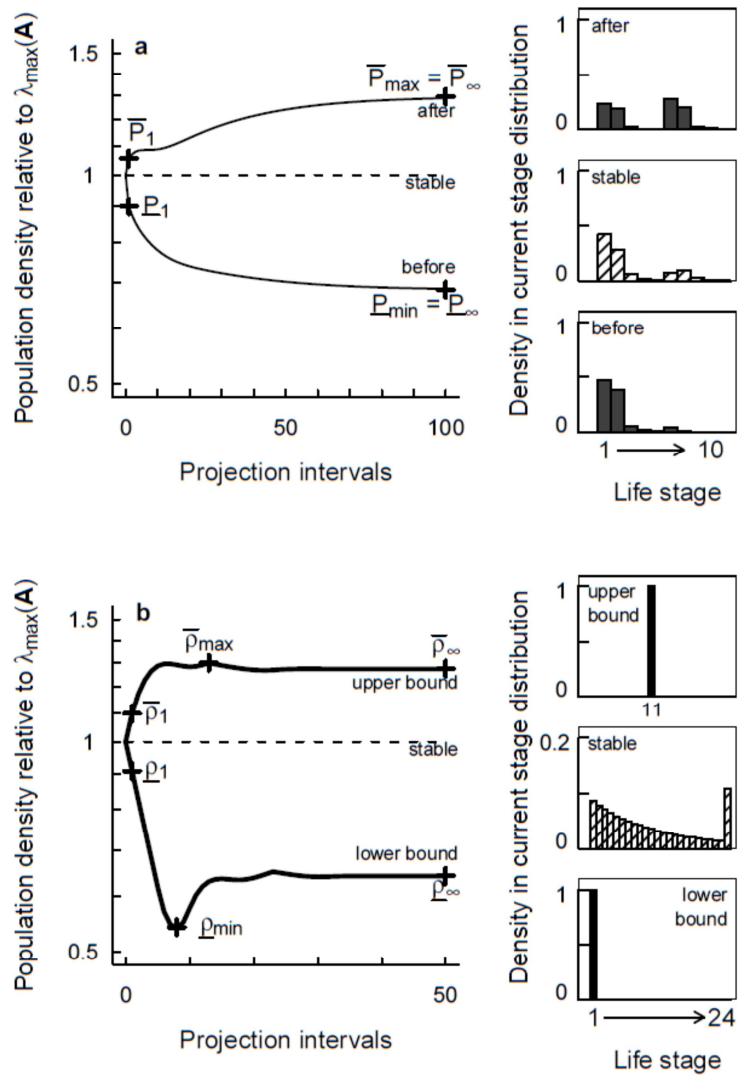
FIG 1.4: Case studies of transient dynamics in natural populations. **(a)** Case-specific dynamics of the subcanopy tree *Styrax obassia*; **(b)** transient bounds of the Amsterdam albatross *Diomedea amsterdamensis*. Bold lines and black barplots indicate transient bounds; thin lines and grey barplots indicate case-specific initial demographic distributions; dashed lines and hatched barplots indicate the stable demographic distribution.

CHAPTER 2

Understanding the dynamics of a model is important. However, management often also requires knowledge of the best way to change population dynamics to achieve management goals. Chapter 2, the fourth paper published as part of this thesis, confronts this issue for transient population dynamics. Having identified population inertia as a holistic and effective descriptor of transient density, this chapter describes methods to evaluate how changes to vital rates of the life cycle affect inertia. We borrow from engineering systems control theory to achieve this, employing use of transfer function analyses. Most crucially, this method accurately describes nonlinearity in the relationship between changes to vital rates and resulting changes in inertia. As we demonstrate, this is an important consideration when planning management regimes.

BEYOND SENSITIVITY: NONLINEAR PERTURBATION ANALYSIS OF TRANSIENT DYNAMICS

ABSTRACT

1. Perturbation analyses of population models are integral to population management: such analyses evaluate how changes in vital rates of members of the population translate to changes in population dynamics. Sensitivity and elasticity analyses of long-term (asymptotic) growth are popular, but limited: they ignore short-term (transient) dynamics and provide a linear approximation to nonlinear perturbation curves.

2. Population inertia measures how much larger or smaller a non-stable population becomes compared with an equivalent stable population, as a result of transient dynamics. We present formulae for the transfer function of population inertia, which describes nonlinear perturbation curves of transient population dynamics. The method comfortably fits into wider frameworks for analytical study of transient dynamics, and for perturbation analyses that use the transfer function approach.

3. We use case studies to illustrate how the transfer function of population inertia may be used in population management. These show that strategies based solely on asymptotic perturbation analyses can cause undesirable transient dynamics and/or fail to exploit desirable transient dynamics. This highlights the importance of considering both transient and asymptotic population dynamics in population management.

4. Our case studies also show a tendency towards marked nonlinearity in transient perturbation curves. We extend our method to measure sensitivity of population inertia and show that it often fails to capture dynamics resulting from perturbations typical of management scenarios.

INTRODUCTION

A thorough understanding of how external factors shape population density and growth is essential to population management. Management goals will often explicitly incorporate elements of density and growth, for example, to promote growth and persistence of populations of conservation concern (e.g. Esparza-Olguín, Valverde & Vilchis-Anaya 2002), reduce density and spread of pests and invasive species (e.g. De Walt 2006), or sustain optimal yields from exploited populations (e.g. Pinard 1993). Commonly, it is necessary to explore how potential management actions may impact population density and growth, to evaluate the most ecologically and economically effective means of achieving management goals (e.g. Baxter *et al.* 2006). Alternatively, an assessment of how potential environmental change may impact population density and growth may be required, to explore the possible detrimental impacts of

43

uncontrolled events that are antagonistic to management goals (e.g. Mumby, Vitolo & Stephenson 2011). It is important in either case to know which vital rates or stages of the life cycle should be targeted during management, to ensure optimum outcomes for minimum effort and cost.

In practise, these assessments are commonly carried out using perturbation analyses of empirical population models. Such analyses evaluate how changes in the vital rates of a population (survival, growth, regression, fecundity, or underlying parameters that influence these) affect measures of population density and growth. Frequently, analytical methods have focussed on linear approximations of the effect of small perturbations on long-term growth. Termed asymptotic sensitivity and elasticity analyses (Caswell 2001), these are typically mathematically and computationally simple and easily interpreted.

However, asymptotic sensitivity and elasticity analyses have two major drawbacks. First, long-term growth is often a very poor predictor of real population dynamics, as short-term 'transient' dynamics are often very different to long-term trends (Hastings 2001; Townley *et al.* 2007). There is an increasing awareness of the need to incorporate analyses of transient dynamics into ecological and evolutionary studies (Ezard *et al.* 2010; Stott *et al.* 2010a [Chapter 5]), and many methods have been developed in the last decade to quantify the sensitivity of transient dynamics to perturbation. Most of these have focussed on population projection matrix (PPM) models, which are arguably the most widely used empirical models in population ecology. Methods vary in their approach and may focus on time-invariant, density-independent models (Fox & Gurevitch 2000; Yearsley 2004), stochastic models (Tuljapurkar, Horvitz & Pascarella 2003), density-dependent models (Tavener *et al.* 2011) or combinations thereof (Caswell 2007). A second drawback of asymptotic sensitivity and elasticity analyses is that the linear approximations they offer may be very poor predictors of population dynamic response to large perturbations. The actual relationship between a perturbation to the life cycle and resultant population dynamics is often substantially nonlinear (Townley & Hodgson 2008), and there has been interest in modelling nonlinearity in perturbation analyses of long-term growth (Hodgson & Townley 2004; Hodgson, Townley & McCarthy 2006; Miller *et al.* 2011). These methods have been limited to non-stochastic, density-independent PPM models, which is more a by-product of the tractability of analytical nonlinear perturbation analysis than an ignorance of the need for such analyses in stochastic and density-dependent models. That said, given the relatively data-demanding nature of even basic PPM models, it is likely that non-stochastic, density-independent models dominate the literature, especially in conservation.

However, to date, there do not exist any analytical methods that can assess nonlinear perturbation of transient dynamics. In this paper, we address this issue to conceive a formula that calculates the transfer function of population inertia for linear, time-invariant PPM models. This builds on existing methods that use population inertia as an index of transient dynamics and that use transfer function methods for nonlinear perturbation analysis of population models.

Transient dynamics of 'non-stable' populations (with non-stable demographic distributions) result in a phenomenon termed population inertia. A 'stable' population (with stable demographic distribution) is predicted to grow or decline at a fixed geometric rate. Population inertia occurs because non-stable populations exhibit very different patterns of transient growth and/or decline before eventually settling to this stable geometric rate. These transient dynamics mean that a non-stable population achieves long-term population densities at a fixed ratio either above or below that of an equivalent stable population. Population inertia (Koons, Holmes & Grand 2007) is the value of this ratio. Therefore, a population with inertia greater than 1 becomes and remains larger than had it started out with a stable demographic distribution, whilst a population with inertia smaller than 1 becomes and remains smaller. The magnitude of inertia indicates how much larger or smaller, relatively, the population becomes. Somewhat paradoxically, inertia is a measure of the asymptotic effects of transient dynamics that cause departures from asymptotic growth in the short term. Hence, it measures the persistency of transients, yet it has been shown to correlate very strongly with near-term transient indices such as reactivity and transient amplification (Stott, Townley & Hodgson 2011 [Chapter 1]). As an index of transient dynamics, population inertia has a number of strengths: it is standardised measure and thus can be easily compared among different models, and as we show here, it is amenable to analytical perturbation analysis.

Transfer function analyses help to elucidate relationships between system inputs, outputs and feedback mechanisms. Their application to PPM models in population ecology began with the modelling of nonlinear perturbations of asymptotic growth (Hodgson & Townley 2004; Hodgson, Townley & McCarthy 2006). A particular strength of transfer function methods is that they are able to model complex perturbation structures involving multiple simultaneous perturbations (for example, multiple management strategies or life cycle trade-offs). However, they require no extra data to calculate than traditional sensitivity and elasticity analyses.

Combining population inertia and the transfer function approach yields a method for nonlinear perturbation analysis of transient dynamics, which we show to be flexible in its ability to model realistic management regimes, and comparable both within and among models. We illustrate these methods using worked examples that demonstrate the importance of considering transient perturbation analysis alongside asymptotic perturbation analyses for population management. We derive measures of the linear sensitivity of population inertia, to compare these with their corresponding transfer functions. Examples show that transient dynamic response to perturbation is often extremely nonlinear, rendering sensitivity a poor approximation to nonlinear perturbation analysis of transient dynamics.

MATERIALS AND METHODS

TRANSFER FUNCTION FRAMEWORK

The transfer function analysis (TFA) framework is a powerful method for analysing linear, time-invariant mathematical systems (Ogata 2010). TFA describes relationships between system inputs, system outputs and the feedback mechanisms within the system. In the case of a PPM model, the 'system' is the PPM model itself, and a 'linear, time-invariant' model is one that is non-stochastic and density independent. An 'input' is the current demographic structure, the 'outputs' of interest are measures of population density or growth, and the 'feedbacks' being studied are the vital rates of the life cycle, that is, the elements of the PPM or underlying parameters that influence them. Thus, transfer functions may be used to determine the precise nonlinear relationship between a perturbation to vital rates of the life cycle and resulting population dynamics, which can then be used to inform management regimes or anticipate population response to environmental change.

When presenting transfer function formulae, we use a common notation throughout where matrices are presented upper-case bold (e.g. $\mathbf{A}$), vectors are presented lower-case bold (e.g. $\mathbf{a}$), numbers and scalars are presented in normal font (e.g. a) and functions are rendered in italics (e.g. $a(\lambda)$). The transfer function of long-term, or 'asymptotic', population growth has already been described (Hodgson & Townley 2004). For the purposes of population management, it may be desirable to know what the long-term growth of a perturbed PPM $\mathbf{A}_\delta$ is, where:

$$\mathbf{A}_\delta = \mathbf{A} + \delta \mathbf{d} \mathbf{e}^{\mathrm{T}}. \tag{1}$$

In this equation, the original PPM $\mathbf{A}$ is perturbed by magnitude δ using a 'perturbation structure' determined by column vectors $\mathbf{d}$ and $\mathbf{e}$, which when multiplied together as in equation 1 (with $\mathbf{e}^{\mathrm{T}}$ representing the transpose of $\mathbf{e}$ from a column to a row vector) form a matrix that determines which vital rates are perturbed. (It is noted that $\mathbf{d}$ and $\mathbf{e}$ are analogous to $\mathbf{b}$ and $\mathbf{c}$, respectively, of Hodgson & Townley 2004, although we have decided to change notation here to remain in line with the accepted norms of the control systems literature). $\mathbf{A}$ has some emergent properties relating to asymptotic population dynamics: the dominant eigenvalue λ_{max} represents the long-term (asymptotic) growth of the population, the dominant right eigenvector $\mathbf{w}$ represents the ratio of stages in the stable demographic distribution and the dominant left eigenvector $\mathbf{v}$ represents the reproductive value of each stage. $\mathbf{A}_\delta$ in turn has its own, different, asymptotic growth rate, stable stage structure and reproductive value that are determined by the structure and magnitude of perturbation.

If δ is used to represent a continuous set of perturbation values, then there is a corresponding set of numbers λ that represents all of the associated $\lambda_{max}(\mathbf{A}_\delta)$. The exact relationship between δ and λ can be described using:

$$\delta^{-1} = \mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d},\qquad(2)$$

where $\mathbf{I}$ is the identity matrix of same dimension as $\mathbf{A}$ (Hodgson & Townley 2004; please see Appendix 2.1 for all proofs). This equation is the transfer function for asymptotic growth. It is possible therefore to specify a range of perturbation magnitudes (δ_{min} to δ_{max}), calculate $\lambda_{max}(\mathbf{A}+\delta_{min}\mathbf{de}^{\mathrm{T}})$ and $\lambda_{max}(\mathbf{A}+\delta_{max}\mathbf{de}^{\mathrm{T}})$ to find the maximum and minimum of the associated range of λ, and use equation 2 to easily evaluate the precise relationship between λ and δ. As $\mathbf{d}$, $\mathbf{e}$ and the range of δ are user-specified, the only required known parameter is the PPM. Hence, transfer function analysis of asymptotic growth may be executed with the same basic information as sensitivity and elasticity analysis. Another strength of TFA is that it may be used to perturb more than one vital rate at a time, as illustrated later (and whilst we concentrate here on single-parameter, rank-one perturbations, TFA may also be extended to model multiple perturbations simultaneously: we refer to Hodgson & Townley 2004 and Hodgson, Townley & McCarthy 2006 for more information on specifying these complex perturbation structures).

THE TRANSFER FUNCTION OF POPULATION INERTIA

An extension to equation 2 allows evaluation of the transfer function of population inertia. Population inertia (P_∞) is calculated using:

$$P_\infty = \frac{\mathbf{v}^{\mathrm{T}}\hat{\mathbf{n}}_0\|\mathbf{w}\|_1}{\mathbf{v}^{\mathrm{T}}\mathbf{w}}.\qquad(3)$$

Here, $\mathbf{v}$ is the dominant left eigenvector of $\mathbf{A}$ and $\mathbf{w}$ is the dominant right eigenvector of $\mathbf{A}$ (as described earlier), $\hat{\mathbf{n}}_0$ is the vector representing the demographic distribution of the population (scaled to sum to 1) and $\|\mathbf{w}\|_1$ denotes the one-norm, or column sum, of $\mathbf{w}$ (Koons, Holmes & Grand 2007; Stott, Townley & Hodgson 2011 [Chapter 1]). Replacing $\hat{\mathbf{n}}_0$ with $\mathbf{v}_{max}$ or $\mathbf{v}_{min}$, the standard basis vectors that maximise and minimise population inertia, will give the upper bound ($\overline{\rho}_\infty$) or lower bound ($\underline{\rho}_\infty$) on population inertia, respectively (Stott, Townley & Hodgson 2011 [Chapter 1]), and this is true for all subsequent formulae. Working with this basic equation, it can be shown that population inertia of the perturbed matrix $\mathbf{A}_\delta$ is equivalent to:

$$P_\infty = \frac{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\hat{\mathbf{n}}_0\mathbf{c}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}}{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-2}\mathbf{d}},\qquad(4)$$

where **I** is the identity matrix of same dimension as **A** and **c** is a column vector of ones of equal dimension to **A** (see Appendix 2.1 for proofs). Hence, given the same parameters as before (**d**, **e** and a range of δ), plus one extra parameter ($\hat{\mathbf{n}}_0$, $\mathbf{v}_{\max}$ or $\mathbf{v}_{\min}$), it is possible to first use equation 2 to evaluate the relationship between λ and δ as described earlier and then use equation 4 to evaluate the relationship between population inertia and λ. The result is three sets of numbers: a set of δ values (the perturbation magnitude), a set of λ values (the corresponding asymptotic growth) and a set of population inertia values (the corresponding transient population density). It is then possible to plot the precise relationships between population inertia and δ, between population inertia and λ, and between λ and δ.

SENSITIVITY OF POPULATION INERTIA

Transfer functions are extremely useful for informing population management, but sensitivity measurements may remain useful for comparative statistical analyses among models, populations or species (e.g. Franco & Silvertown 2004; McMahon & Metcalf 2008). In such analyses, the scalar value of sensitivity is more amenable than a complex, nonlinear transfer function. Using the transfer function method, it is fairly simple to obtain an estimate for the sensitivity of population inertia through differentiation of the transfer functions themselves. Equation 4 may be represented as:

$$P_\infty = \frac{f_1(\lambda)f_2(\lambda)}{f_3(\lambda)} \, , \tag{5}$$

Where

$$f_1(\lambda) = \mathbf{e}^T(\lambda \mathbf{I} - \mathbf{A})^{-1}\hat{\mathbf{n}}_0 \quad , \quad f_2(\lambda) = \mathbf{c}^T(\lambda \mathbf{I} - \mathbf{A})^{-1}\mathbf{d}$$
$$\text{and} \quad f_3(\lambda) = \mathbf{e}^T(\lambda \mathbf{I} - \mathbf{A})^{-2}\mathbf{d} \, . \tag{6}$$

The derivatives of the functions $f_1(\lambda)$, $f_2(\lambda)$ and $f_3(\lambda)$ separately are:

$$f_1'(\lambda) = -\mathbf{e}^T(\lambda \mathbf{I} - \mathbf{A})^{-2}\hat{\mathbf{n}}_0 \quad , \quad f_2'(\lambda) = -\mathbf{c}^T(\lambda \mathbf{I} - \mathbf{A})^{-2}\mathbf{d}$$
$$\text{and} \quad f_3'(\lambda) = -2\mathbf{e}^T(\lambda \mathbf{I} - \mathbf{A})^{-3}\mathbf{d} \, . \tag{7}$$

Then, the product rule and the quotient rule are used to differentiate equation 5 with respect to λ:

$$\frac{\partial P_\infty}{\partial \lambda} = \lim_{\lambda \to \lambda_{\max}} \left\{ \frac{f_1'(\lambda)f_2(\lambda)f_3(\lambda) + f_1(\lambda)f_2'(\lambda)f_3(\lambda) - f_1(\lambda)f_2(\lambda)f_3'(\lambda)}{f_3(\lambda)^2} \right\} . \tag{8}$$

Here, using the limit as λ approaches λ_{max} is a necessary step, as matrices used in the equation become singular (i.e. their inverse cannot be computed), when $\lambda = \lambda_{max}$.

Equation 2 can be directly differentiated with respect to δ to give the sensitivity of λ to δ:

$$\frac{\partial \lambda}{\partial \delta} = \lim_{\lambda \to \lambda_{max}} \left\{ \frac{\left(\mathbf{e}^{\mathrm{T}} (\lambda \mathbf{I} - \mathbf{A})^{-1} \mathbf{d} \right)^2}{\mathbf{e}^{\mathrm{T}} (\lambda \mathbf{I} - \mathbf{A})^{-2} \mathbf{d}} \right\}. \tag{9}$$

Again, the limit as λ approaches λ_{max} must be used to avoid singularities. Third, the chain rule is used to find the sensitivity of population inertia to δ:

$$\frac{\partial P_{\infty}}{\partial \delta} = \frac{\partial P_{\infty}}{\partial \lambda} \frac{\partial \lambda}{\partial \delta} \tag{10}$$

(see Appendix 2.1 for proofs). All code used in analyses is freely available as part of the R package `popdemo` (R Development Core Team 2011; Stott, Hodgson & Townley 2012a [Chapter 4]).

RESULTS

In this section, we provide two worked examples using the analyses outlined earlier. Both are empirical PPM models parameterised from field data, and previous studies of both populations have led to very clear management recommendations based on asymptotic perturbation analyses. We explore the transfer function for population inertia of each, using parameter inputs based on their recommended management strategies, and discuss how the results from these analyses might affect the outcome of proposed management. We highlight how the nonlinear predictions of transfer functions compare with the linear predictions of sensitivity analysis. For each model, we evaluate the effect of management on the predicted inertia of the current population structure, which provides the most accurate prediction of perturbed dynamics. We also explore the effect of management on the upper and lower bounds on inertia. Management is often unlikely to operate near the inertia boundaries, although there are some notable scenarios when this may be the case: for example, in population invasions and reintroductions, individuals are likely to be concentrated in a single stage class. For the case studies presented here, the bounds on inertia provide a good indication of the effect of perturbation on the range of transient dynamics, which is useful knowledge if there is uncertainty in the estimation of current population structure or if there is the potential for disturbance to cause that structure to change.

CACTUS (*NEOBUXBAUMIA MACROCEPHALA*)

Neobuxbaumia macrocephala is a rare species of columnar cactus, endemic to the Tehuacan valley, central Mexico. Esparza- Olguín, Valverde & Vilchis-Anaya (2002) parameterised two size-based PPM models for the species using data collected in the field from 1997 to 1999. Based on elasticity analysis and simulated perturbation analysis of long-term growth, they recommended prolonging survival of the largest individuals as the best management strategy to increase population growth of the species.

Here, we work with the 1997-1998 matrix (the same matrix used in simulation analyses in Esparza-Olguín, Valverde & Vilchis-Anaya 2002), which we call $\mathbf{A}_{cactus}$ (Table 2.1). We perturb stasis of the largest size class (element [10,10]), in accordance with the recommended management regime: therefore, the perturbation structure is determined by the vectors $\mathbf{d}_{cactus}$ and $\mathbf{e}_{cactus}$ (Table 2.1). The population structure $\hat{\mathbf{n}}_{cactus}$ is known (Table 2.1; Fig. 2.1a), and we use this to calculate the transfer function of case-specific population inertia. However, there is uncertainty in the number of seedlings in the population: none were detected, but this is likely a result of the fact that they are small and hard to find. Therefore, evaluation of the transfer functions of the outer bounds on inertia provides an indication of the range of values of transient dynamics that may result from any population structure. Given that stasis of the largest individuals is 0.869, we perturb over a realistic range of $-0.1 \leq \delta \leq 0.1$, to give a maximum perturbed stasis value of 0.969.

The population currently has a relatively large inertia and is expected to increase to a density around 400% of that predicted by λ_{max} (Fig. 2.1b). Given that the goal is to increase population density and growth, this is good news: although the population is predicted to decline in the long term, current population structure dictates that it will in fact increase rapidly in the short term and should not dip below current density within the next 70 years (Fig. 2.1b). The recommended management regime is beneficial in the long term; however, it has a negative impact on population inertia: any increase in stasis of the largest stage class will cause a drop in the value of population inertia (Fig. 2.1d). The magnitude of this decline is not captured by sensitivity, which predicts a far less pronounced decline in inertia. Thus, a significant benefit of management is not seen for several decades, because of the dampening of transient dynamics. Evaluation of the outer bounds on population inertia indicates further detriment of managing for adult survival. Fluctuations in the upper bound on inertia (Fig. 2.1c) and a decrease in the lower bound (Fig. 2.1e) cause an increase in the range of potential transient density. Sensitivity analyses do not accurately describe these changes over large perturbation range – in particular, the upper bound shows highly nonlinear dynamics that are far from those predicted by sensitivity.

Managing for transient dynamics can yield a better result. Transfer functions of inertia across the life cycle (Appendix 2.2) indicate that fecundity has the most positive impact on transient dynamics. Using a perturbation structure that acts on fecundity across all reproductive

life stages (Table 2.1) increases population inertia (Fig. 2.2d). A doubling of fecundity significantly increases short-term population size (Fig. 2.2b), giving much more rapid results than managing for increased adult survival, despite the fact that this management scheme has a negligible effect on long-term growth. Additionally, this management practise increases both upper (Fig. 2.2c) and lower (Fig. 2.2e) bounds on inertia: given uncertainty in the population structure, this is favourable as it shifts the potential range of transient dynamics upwards on the scale of transient density. Therefore, it may be favourable in this case to manage for increased fecundity rather than increased adult survival, as the immediate returns are better. Alternatively, it may be desirable to implement two different management strategies: first, to manage for transient dynamics to boost population density and then to manage for asymptotic dynamics to maintain population persistence. However, this will of course inevitably depend on the relative costs of each management strategy.

KOALA (*PHASCOLARCTOS CINEREUS*)

The Koala, *Phascolarctos cinereus*, is an arboreal marsupial native to Australia. It is widespread within the country, although the status of populations varies from region to region: in some areas, it is overabundant, whilst in others, populations are in persistent decline. Baxter *et al.* (2006) explore potential management strategies for an overabundant population on Snake Island, with a goal of reducing population density. They parameterise a stage-based PPM with stages defined by the tooth wear of koalas, which is an indication of age. The study uses asymptotic elasticity analysis that explicitly incorporates costs of management, therefore identifying those strategies that are both ecologically and economically viable. Based on these analyses, they recommend investing in reduction of both fecundity and survival, in an approximate 0.3:1 ratio. Subdermal contraceptives are considered as a mechanism to decrease fecundity, whilst translocation of adults to more sparsely populated areas is recommended to decrease survival by proxy, without the need for culls.

It is possible to evaluate the precise impact of this management strategy on the transient dynamics of the population using transfer function analysis. We perturb the koala PPM $\mathbf{A}_{koala}$ using a structure determined by vectors $\mathbf{d}_{koala}$ and $\mathbf{e}_{koala}$ (Table 2.2). Recommended management targets all adult life stages, but modelling this would require a multi-parameter, multi-rank perturbation structure. As an analytical compromise, we have chosen to focus on the vital rates of stage 2 individuals, as they have both largest fecundity and highest survival. The perturbation structure acts on several vital rates simultaneously: fecundity of stage 2 individuals (element [1,2]) is perturbed by factor 0.3, whilst stasis and growth of stage 2 individuals (elements [2,2] and [3,2], the life cycle transitions that incorporate survival) are both perturbed by factor 0.5 each. This gives the 0.3:1 investment ratio recommended by the study. We evaluate transfer functions based on the known structure of the population $\hat{\mathbf{n}}_{koala}$ (McLean 2003; Table 2.2), although again we evaluate the transfer functions of bounds on inertia to get an idea of the range

of uncertainty surrounding this estimate. We perturb over the range $-0.3 \leq \delta \leq 1$, to evaluate the short-term impact of management over a wide range of investment, whilst keeping vital rates of the perturbed matrix within realistic limits.

Population structure is very close to the stable structure predicted by the model (Fig. 2.3a), and as such population dynamics closely follow long-term growth from the outset (Fig. 2.3b). Hence, population inertia is small, with the population becoming at most up to 3% larger than predicted by λ_{max}. A reduction in survival and fecundity using the recommended management regime increases population inertia (Fig. 2.3d), which is directly antagonistic to management goals. The absolute increase in inertia is small, but it is important to note that recommended management does not result in an immediate halt to growth: the population will continue to grow for 2-3 years before stabilizing (Fig. 2.3b). Nonlinearity of the transfer function means that the larger the magnitude of perturbation, the less accurate sensitivity analysis is at describing the magnitude of change in inertia. The potential range of transient dynamics is decreased overall, with management decreasing the upper bound on inertia (Fig. 2.3c) and increasing the lower bound on inertia (Fig. 2.3e). This indicates that management can decrease the uncertainty surrounding short-term population density, although again these changes are small in their magnitude. Sensitivity analysis would have overestimated this effect: both transfer functions show diminishing returns, which is not captured by sensitivity approximations.

Managing for transient dynamics would suggest that focusing on survival alone is a better option: decreasing fecundity tends to increase inertia, whereas decreasing survival tends to decrease inertia. It appears that targeting stage 3 individuals would have the largest impact (Appendix 2.2). Decreasing survival of stage 3 individuals does reduce population inertia (Fig. 2.4d), and it is possible to manipulate this to stop population growth, despite long-term growth being above unity (Fig. 2.4b). This management option also results in a significantly decreased upper bound on inertia (Fig. 2.4c) and a barely altered lower bound on inertia (Fig. 2.4e). However, the effort and cost required to implement this management scheme would be far greater than that recommended by Baxter *et al.* (2006), and within a few years, the population resumes growth. As a long-term management scheme, this proves therefore to be inadequate. However, it may be desirable to first, manage for transient dynamics through translocation of adults, and then phase in contraceptive measures to manage for asymptotic dynamics. This exploits the population reductions that can be achieved through transient dynamics and then maintains those reductions in the long term.

DISCUSSION

The transfer function for population inertia provides a means of nonlinear perturbation analysis of transient population dynamics. We have illustrated the importance of considering this

alongside asymptotic perturbation analyses in population management, which adds to other studies that have demonstrated that an ignorance of transient dynamics can work against management goals (Koons, Rockwell & Grand 2007).

A notable outcome of our analyses is the extreme nonlinearity that can be exhibited in perturbation curves of population inertia. Many of the transfer functions generated in the case studies showed a marked nonlinearity that may render the linear approximations of sensitivity analysis ineffective except for very small perturbation magnitude. Figure 2.5 illustrates some more examples of extreme nonlinearity exhibited in transfer functions of the cactus and koala models, and Appendix 2.2 explores these further. Our evaluation of many other PPM models not presented here suggests that such nonlinearity is perhaps the rule rather than the exception. It has been argued that sensitivity analyses of asymptotic growth may be fairly robust to model assumptions, including linearity of perturbation response (Caswell 2001 p.613-615), and this warrants further study. Our preliminary evidence suggests that this may not be the case for transient dynamics. Targets of conservation and management often require large magnitude of perturbation, and so sensitivity may prove too poor an approximation for predicting their impact on transient dynamics.

In the light of this, nonlinear perturbation of transient dynamics could prove to be very important, and working with population inertia and the transfer function framework has a number of benefits. In a previous paper (Stott, Townley & Hodgson 2011 [Chapter 1]), we identified an emerging framework for analysis of transient dynamics with choices to make regarding: (i) standardising dynamics to remove asymptotic effects, (ii) choosing an initial demographic distribution to use in the model and (iii) choosing a timeframe to evaluate. Population inertia (Koons, Holmes & Grand 2007) is an index of transient dynamics that is robust to all of these choices: as it is possible to evaluate upper and lower bounds on inertia (Stott, Townley & Hodgson 2011 [Chapter 1]), there is no need to know the population's demographic distribution, although it is possible to evaluate sensitivity of case-specific dynamics using a given demographic distribution if desired. Population inertia correlates very well with other measures of transient dynamics (Stott, Townley & Hodgson 2011 [Chapter 1]), indicating that it should be a good proxy index to use in perturbation analyses, especially when it is unclear what timeframe of the projection to analyse. Lastly, in the equation for population inertia, the influence of asymptotic dynamics is removed, so that perturbation analysis of inertia is a standardised approach that may be compared across models, regardless of differences in their asymptotic dynamics. The transfer function framework works well with population inertia: matrix eigendata are easy to express in terms of transfer functions and population inertia is expressed in terms of matrix eigendata. As illustrated, the methods we present are flexible, compared with classic approaches, in their ability to model complex management regimes involving simultaneous perturbation to many matrix elements.We have focussed here on single-parameter, rank-one perturbations, whilst multiparameter, multi-rank perturbations may offer

the option to study yet more complicated perturbation structures (Hodgson, Townley & McCarthy 2006). We are working on the more complicated algebraic expansion for this method.

An alternative approach of nonlinear perturbation analysis is to use matrix determinants to represent the transfer function (and derivatives thereof) in terms of characteristic polynomials (Lubben *et al.* 2009; Miller *et al.* 2011). This affords a more flexible specification of perturbation structure without the need for complex algebraic expansion and offers another benefit in its ability to evaluate polynomials at $\lambda = \lambda_{max}$. However, when using this approach to attempt analysis of population inertia, we discovered numerical calculation and evaluation of polynomials to be inherently unstable, in both R (R Development Core Team 2011) and MATLAB (Mathworks 2011), using the polynom package in R and the ss2tf function in MATLAB. It is possible that the use of symbolic algebra (as advocated in Miller *et al.* 2011) will lessen this instability.

The methods discussed here would benefit from application to other population models. It would certainly be useful to have analytical transient indices and nonlinear perturbation methods for stochastic and density-dependent models. Another important challenge is to migrate transient analyses and nonlinear perturbation analyses to integral projection models (Easterling, Ellner & Dixon 2000). It is argued that these models require less data than PPMs so are better for data-deficient systems (Ramula, Rees & Buckley 2009), and as they do not rely on an arbitrary discretisation of the life cycle, they may be robust to many of the analytical problems associated with matrix dimension (see Easterling, Ellner & Dixon 2000; Salguero-Gómez & Plotkin 2010; Stott *et al.* 2010a [Chapter 5]), and matrix reducibility (Stott *et al.* 2010b [Chapter 3]). Stochastic and density-dependent applications exist (Ellner & Rees 2006, 2007), but the study of transient dynamics and use of nonlinear perturbation analysis requires development.

Meanwhile, it is becoming increasingly easy to incorporate complex analyses into studies that use linear, time-invariant PPM models. Many studies rely on such basic models, as parameterisation of stochastic or density-dependent models often requires more data than it is feasible to provide, especially under constraints on time and finance. But, perhaps analytical approaches need to move beyond sensitivity when it comes to informing population management: methods for nonlinear perturbation analysis of both asymptotic and transient dynamics are now freely available. These vastly increase the information that can be provided by simple models, without any demand for further data. Most importantly, as many studies are starting to show, an ignorance of these dynamics may even be detrimental to management goals.

TABLES

	Stage→ ↓	1	2	3	4	5	6	7	8	9	10
A$_{cactus}$	1	0	0	0	0	0	0	4.130	11.456	10.238	31.370
	2	0.013	0.435	0	0	0	0	0	0	0	0
	3	0	0.217	0.677	0	0	0	0	0	0	0
	4	0	0	0.097	0.865	0	0	0	0	0	0
	5	0	0	0	0.108	0.875	0	0	0	0	0
	6	0	0	0	0	0.025	0.900	0	0	0	0
	7	0	0	0	0	0	0.050	0.850	0.077	0	0
	8	0	0	0	0	0	0	0.150	0.615	0	0
	9	0	0	0	0	0	0	0	0.308	0.700	0.091
	10	0	0	0	0	0	0	0	0	0.300	0.869
n̂$_{cactus}$		0	0.1116	0.1505	0.1797	0.1942	0.0971	0.0971	0.0631	0.0485	0.0582
d$_{cactus}$	Long term	0	0	0	0	0	0	0	0	0	1
	Transient	1	0	0	0	0	0	0	0	0	0
e$_{cactus}$	Long term	0	0	0	0	0	0	0	0	0	1
	Transient	0	0	0	0	0	0	0.13	0.36	0.32	1

TABLE 2.1: Parameters used in the *Neobuxbaumia macrocephala* (cactus) case study. **A**$_{cactus}$ is the population projection matrix, **n̂**$_{cactus}$ is the population vector standardised to sum to 1, and the vectors **d**$_{cactus}$ and **e**$_{cactus}$ determine the perturbation structure for recommended management based on either perturbation analyses of asymptotic dynamics (labelled 'long-term') or the transfer function of inertia (labelled 'transient').

	Stage→ ↓	1	2	3	4	5	6	7	8	9
	1	0	0.3026	0.1663	0.1244	0.0891	0.0556	0.0394	0.0226	0.0118
	2	0.9908	0.5359	0	0	0	0	0	0	0
	3	0	0.4580	0.4550	0	0	0	0	0	0
	4	0	0	0.5000	0.0655	0	0	0	0	0
$\mathbf{A}_{koala}$	5	0	0	0	0.7272	0.2216	0	0	0	0
	6	0	0	0	0	0.4617	0.2265	0	0	0
	7	0	0	0	0	0	0.3538	0.1267	0	0
	8	0	0	0	0	0	0	0.4693	0.4247	0
	9	0	0	0	0	0	0	0	0.1762	0.6090
$\hat{\mathbf{n}}_{koala}$		0.135	0.330	0.225	0.120	0.080	0.065	0.035	0.010	0
$\mathbf{d}_{koala}$	Long term	0.3	0.5	0.5	0	0	0	0	0	0
	Transient	0	0	0.5	0.5	0	0	0	0	0
$\mathbf{e}_{koala}$	Long term	0	1	0	0	0	0	0	0	0
	Transient	0	0	1	0	0	0	0	0	0

TABLE 2.2: Parameters used in the *Phascolarctos cinereus* (koala) case study. $\mathbf{A}_{koala}$ is the population projection matrix, $\hat{\mathbf{n}}_{koala}$ is the population vector standardised to sum to 1, and the vectors $\mathbf{d}_{koala}$ and $\mathbf{e}_{koala}$ determine the perturbation structure for recommended management based on either perturbation analyses of asymptotic dynamics ('long-term') or the transfer function of inertia ('transient').

FIGURES

FIG. 2.1: Analyses of the transfer function of inertia for the cactus population projection matrix based on management recommendations for long-term dynamics. Parameters for models are presented in Table 2.1. **(a)** Estimated current population structure and predicted stable population structure; **(b)** population projection showing dynamics of the stable stage structure (dashed), the current population structure (solid black) and perturbation of d = +0.358 acting on the current population structure to give $\lambda = 1$ (red); **(c)** transfer function of the upper bound on inertia; **(d)** transfer function of inertia of the current population structure; **(e)** transfer function of the lower bound on inertia. In panels c-e, sensitivity at $\delta = 0$ is indicated with dotted lines. In panel c, the change in the function at $\delta = 0.037$ is caused by the maximum entry of $\mathbf{v}$ changing from element 7 to element 10, thus altering $\mathbf{v}_{max}$ and changing the transfer function of the bound.

FIG.2.2: Analyses of the transfer function of inertia for the cactus population projection matrix based on management recommendations for transient dynamics. Parameters for models are presented in Table 2.1. **(a)** Estimated current population structure and predicted stable population structure; **(b)** population projection showing dynamics of the stable stage structure (dashed), the current population structure (solid black) and a managed population with a perturbation of $\delta = +31$ acting on the current population structure (red); **(c)** transfer function of the upper bound on inertia; **(d)** transfer function of inertia of the current population structure; **(e)** transfer function of the lower bound on inertia. In panels c-e, sensitivity at $\delta = 0$ is indicated with dotted lines.
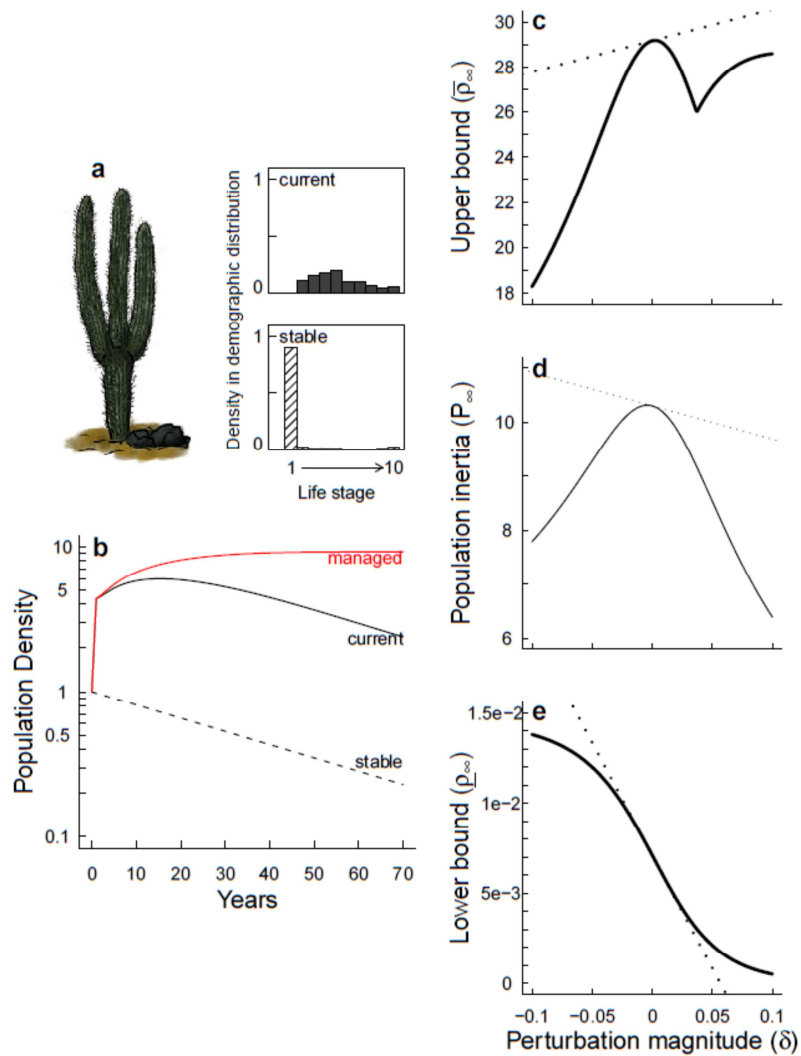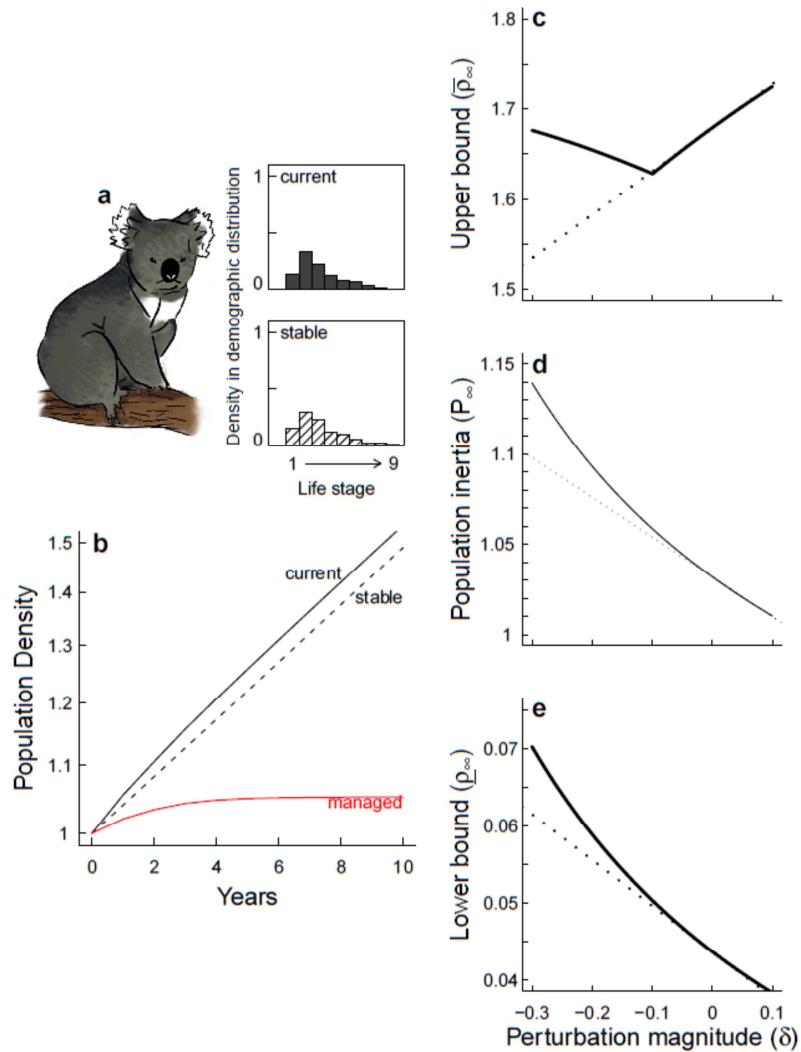
FIG.2.3: Analyses of the transfer function of inertia for the koala population projection matrix based on management recommendations for long-term dynamics. Parameters for models are presented in Table 2.2. **(a)** Estimated current population structure and predicted stable population structure; **(b)** population projection showing dynamics of the stable stage structure (dashed), the current population structure (solid black) and perturbation of $\delta = -0.081$ acting on the current population structure to give $\lambda = 1$ (red); **(c)** transfer function of the upper bound on inertia; **(d)** transfer function of inertia of the current population structure; **(e)** transfer function of the lower bound on inertia. In panels c-e, sensitivity at $\delta = 0$ is indicated with dotted lines. In panel c, the change in the function at $\delta = -0.1$ is caused by the maximum entry of v changing from element 2 to element 1, thus altering $\mathbf{v}_{max}$ and changing the transfer function of the bound.
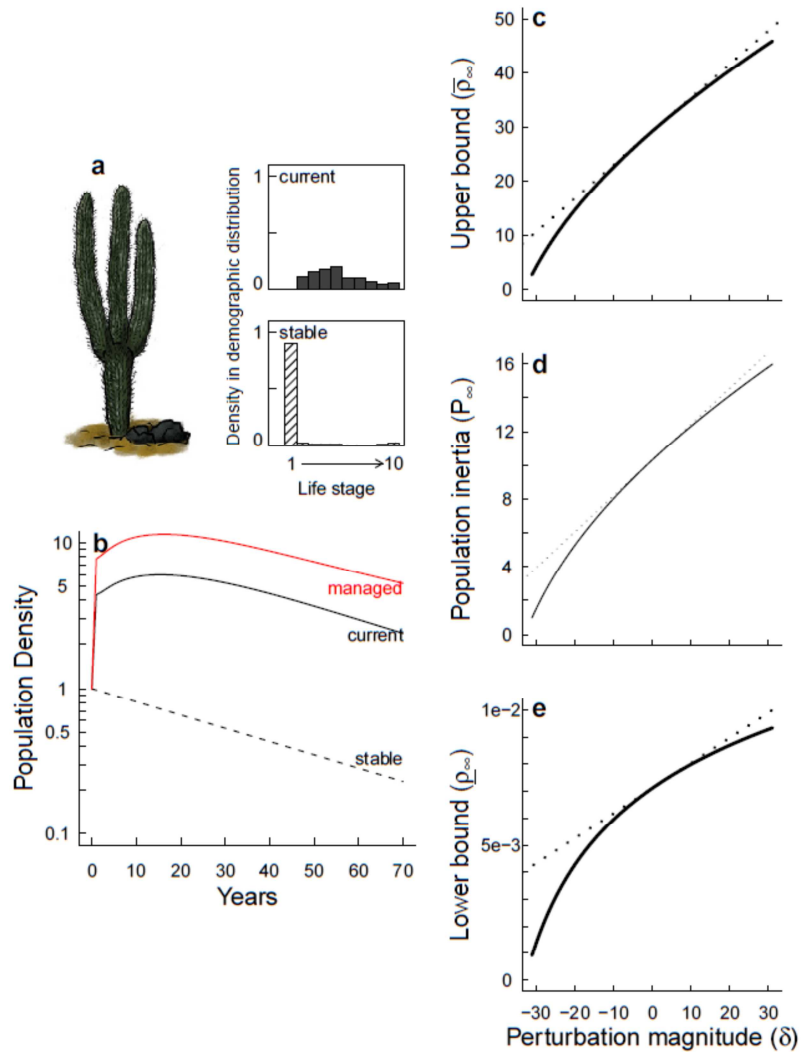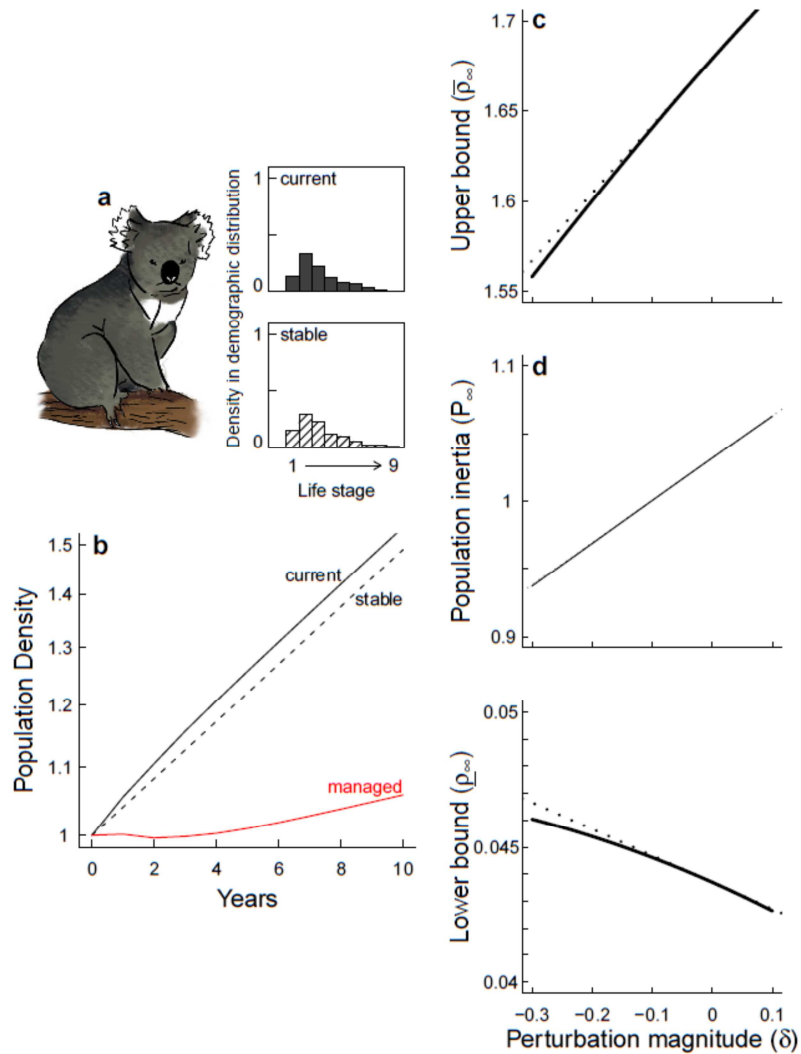
FIG. 2.4: Analyses of the transfer function of inertia for the koala population projection matrix based on management recommendations for transient dynamics. Parameters for models are presented in Table 2.2. **(a)** Estimated current population structure and predicted stable population structure; **(b)** population projection showing dynamics of the stable stage structure (dashed), the current population structure (solid black) and perturbation of $\delta = -0.24$ acting on the current population structure (red); **(c)** transfer function of the upper bound on inertia; **(d)** transfer function of inertia of the current population structure; **(e)** transfer function of the lower bound on inertia. In panels c-e, sensitivity at $\delta = 0$ is indicated with dotted lines.
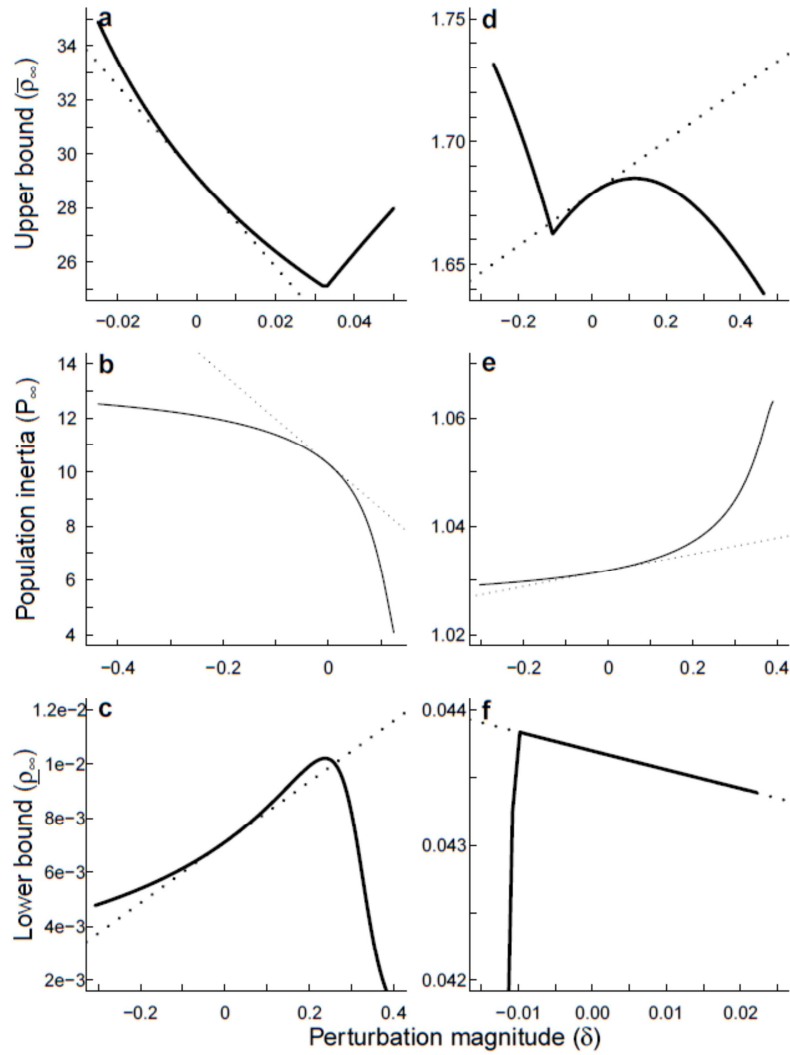
FIG. 2.5: Further examples of nonlinearity in the cactus and koala models. Transfer functions of inertia are represented by solid lines, and sensitivity values by dotted lines. Panels a-c represent transfer functions of the cactus model: **(a)** upper bound on inertia, perturbing element [7,6]; **(b)** case-specific inertia (using the current demographic structure in Figs 2.1a and 2.2a), perturbing element [5,5]; **(c)** lower bound on inertia, perturbing element [8,8]. Panels d-f represent transfer functions of the koala model: **(d)** upper bound on inertia, perturbing element [2,2]; **(e)** case-specific inertia (using the current demographic structure in Figs 2.3a and 2.4a), perturbing element [9,9]; **(f)** lower bound on inertia, perturbing element [1,8]. In all cases, perturbation achieves a minimum of half the element being perturbed and a maximum of twice the element being perturbed, but is bounded between 0 and 1.

CHAPTER 3

– – – – – – – – – – – – – – –

Advances in computation have opened up the opportunity for complex ecological models and analytical techniques, such as those presented in chapters 1 and 2. However, most models and analyses necessarily make certain basic assumptions, which if violated undermine their results. Various anomalies encountered when working with PPMs raised questions about reducibility and ergodicity of models. Core assumptions of most analyses are that the matrix is irreducible and ergodic. However, we discovered that up to a quarter of published PPM models violate these assumptions. Chapter 3 is the second paper published as part of this PhD. The chapter introduces the joint concepts of reducibility and ergodicity and what they mean in the context of PPM models. We explore the consequences of violating these assumptions for various types of model and various types of analysis, and use case studies to demonstrate how reducibility and non-ergodicity can affect model dynamics and analytical outcomes.

Chapter 3:

ON REDUCIBILITY AND ERGODICITY OF POPULATION PROJETION MATRIX MODELS

ABSTRACT

1. Population projection matrices (PPMs) are probably the most commonly used empirical population models. To be useful for predictive or prospective analyses, PPM models should generally be *irreducible* (the associated life cycle graph contains the necessary transition rates to facilitate pathways from all stages to all other stages) and therefore *ergodic* (whatever initial stage structure is used in the population projection, it will always exhibit the same stable asymptotic growth rate).

2. Evaluation of 652 PPM models for 171 species from the literature suggests that 24.7% of PPM models are *reducible* (parameterized transition rates do not facilitate pathways from all stages to all other stages). Reducible models are sometimes ergodic but may be *non-ergodic* (the model exhibits two or more stable asymptotic states with different asymptotic stable growth rates, which depend on the initial stage structure used in the population projection). In our sample of published PPMs, 15.6% are non-ergodic.

3. This presents a problem: reducible–ergodic models often defy biological rationale in their description of the life cycle but may or may not prove problematic for analysis as they often behave similarly to irreducible models. Reducible–non-ergodic models will usually defy biological rationale in their description of the both the life cycle and population dynamics, hence contravening most analytical methods.

4. We provide simple methods to evaluate reducibility and ergodicity of PPM models, present illustrative examples to elucidate the relationship between reducibility and ergodicity and provide empirical examples to evaluate the implications of these properties in PPM models.

5. As a prevailing tool for population ecologists, PPM models need to be as predictive as possible. However, there is a large incidence of reducibility in published PPMs, with significant implications for the predictive power of such models in many cases. We suggest that as a general rule, reducibility of PPM models should be avoided. However, we provide a guide to the pertinent analysis of reducible matrix models, largely based upon whether they are ergodic or not.

INTRODUCTION

Ecological dynamics are inherently complex. However, it is desirable in applications of population ecology to be able to accurately predict future dynamics of populations (Caswell 2001, 2007; Townley *et al.* 2007; Townley & Hodgson 2008). Population projection matrices

(PPMs) are possibly the most often used empirical population models, and much research in population ecology focuses on the design of increasingly accurate matrix modelling techniques. Factors such as spatial heterogeneity (e.g. Day & Possingham 1995; Hunter & Caswell 2005), density dependence (e.g. Jensen 1993; Grant & Benton 2000; Armsworth 2002), exogenous stochastic influence (e.g. Nakaoka 1997; Fieberg & Ellner 2001; Tuljapurkar, Horvitz, & Pascarella 2003) and transient dynamics (e.g. Koons *et al.* 2005; Townley & Hodgson 2008; Tenhumberg, Tyre, & Rebarber 2009; Stott *et al.* 2010a [Chapter 5]) are now commonly incorporated into modelling and analytical methods. However, for a building to be robust it must also have secure foundations. Equally, matrix model complexities are building blocks upheld by the basic grounding of the model itself – the life cycle.

Almost all life cycle models can be described as *irreducible*, meaning that they contain direct or indirect pathways from every stage class to every other stage class (Fig. 3.1a). A PPM associated with an irreducible life cycle can itself be described as irreducible. According to the Perron–Frobenius theorem (Perron 1907a,b; Frobenius 1912; for overviews, see Caswell 2001; Li & Schneider 2002; Elhashash & Szyld 2008), an irreducible, primitive matrix **A** will have a single, positive eigenvalue that is a simple root of the characteristic polynomial of **A** and whose modulus is greater than all other eigenvalues of the matrix (Caswell 2001; Li & Schneider 2002) – this is commonly known as the dominant eigenvalue of the matrix. It is this value – also known as λ_{max}– that describes the long-term (asymptotic) growth rate of the population and which has to date been studied in the majority of published PPM analyses (see, e.g. Esparza-Olguín, Valverde, & Vilchis-Anaya 2002; Grenier, McDonald, & Buskirk 2007; Zúñiga-Vega *et al.* 2007). It is simple to calculate, and conceptually easy to understand. Long-established methods of evaluating the effects of changes to vital rates on the long-term population growth rate exist in the forms of sensitivity and elasticity analyses (Caswell 2001), and these are often used to inform on population management and conservation decisions (Crowder *et al.* 1994; Crooks, Sanjauan, & Doak 1998; Runge, Langtimm, & Kendall 2004). Population projections from irreducible matrices are always *ergodic*– that is, they will always eventually exhibit the same outcome (i.e. the same stable growth as described by the dominant eigenvalue), irrespective of the initial conditions of the model (i.e. the initial population structure used in the projection).

By contrast, a *reducible* life cycle model is essentially not complete – transitions do not facilitate pathways from every stage class to every other stage class (Caswell 2001). Consequently, one or more portions of the life cycle are isolated from the rest of the cycle (Fig. 3.1b,c). Except in a few cases – for example, when modelling a species with post-reproductive stage classes (Caswell 2001; Fig. 3.1b) – a reducible life cycle model defies biological rationale. A reducible PPM associated with such a life cycle may undergo simultaneous row and column permutations (i.e. have its rows and columns simultaneously rearranged) so that it takes the form:

$$
\begin{array}{ccccc}
A_1 & A_{1,2} & \ldots & A_{1,n-1} & A_{1,n} \\
0 & A_2 & \ldots & A_{2,n-1} & A_{2,n} \\
\vdots & \vdots & \ddots & \vdots & \vdots \\
0 & 0 & \ldots & A_{n-1} & A_{n-1,n} \\
0 & 0 & \ldots & 0 & A_n
\end{array}
$$

That is, it may be divided into a number of submatrices (blocks), with those on the diagonal being irreducible (Caswell 2001; Li & Schneider 2002), and where '0' denotes a block of zeroes. The presence or absence of data in blocks at the top-right corner determines the position of the diagonal blocks relative to one another. We refer to this as the block-permuted matrix. Each diagonal block has a dominant eigenvalue, each of which will be an eigenvalue of the overall matrix, and the largest of these will be equal to the dominant eigenvalue of the overall matrix, λ_{max}. However, for some reducible matrices, the long-term stable growth rate may be described by eigenvalues other than the dominant (Caswell 2001), dependent on the initial stage structure of the population used in the projection. A reducible model that may exhibit more than one final state, dependent on initial conditions, may be described as *non-ergodic*. When using dominant eigenvalues or vectors to inform on management and conservation decisions, a reducible, non-ergodic model can hence prove problematic, as the asymptotic growth rate experienced by the population may be radically different from that predicted by the model. The ergodic properties of reducible non-negative matrices depend on the specific structure of the reducible model and the relative sizes of the dominant eigenvalues of its constituent blocks. This has been explored in the mathematical literature (e.g. Dietzenbacher 1991; Bapat 1998; Kolotilina 2004); however, its application has not yet extended to population biology. Indeed, the issue of reducibility *per se* is rarely explicitly considered in the biological literature (however, notable exceptions include Bierzychudek 1982; Caswell 2001; Ehrlén & Lehtilä 2002; Bode, Bode, & Armsworth 2006; Maron, Horvitz, & Williams 2010; Stott *et al.* 2010a [Chapter 5]).

Here, we present methods to easily evaluate reducibility and ergodicity of matrices. Using these methods, we show that a considerable proportion (approximately one-quarter) of existing published PPMs are reducible, many of which are non-ergodic. We elucidate the relationship between reducibility and ergodicity using illustrative theoretical models of reducible PPMs. We explore the real-world implications of reducibility and non-ergodicity of PPMs using three empirical examples of reducible matrices employing different analytical techniques. Lastly, we encourage population demographers to carefully consider their life cycle model and advise that reducibility should be avoided where possible; however, we discuss analytical approaches to unavoidably reducible models, based upon their ergodic properties.

ILLUSTRATIVE MODELS

To show how reducible non-negative matrix structure relates to ergodicity of the model, we present simulations of illustrative PPM models. These demonstrate the conditions under which a reducible model will be differentially ergodic or nonergodic and, at a greater resolution, reveal how matrix structure relates to the number of different asymptotic states that the model may achieve. We use, e.g. $\lambda(A_1)$ to refer to the dominant eigenvalue of a constituent block of a reducible matrix, whereas λ_{max} or $\lambda(\mathbf{A})$ refers to the dominant eigenvalue of the overall matrix.

ILLUSTRATIVE MODELS: METHODS

A theoretical, irreducible, six-stage matrix model was constructed. This model was designed to be similar to one that may be parameterized for a tree species (Fig. 3.2a). Transition rates were 'knocked out' of this model and replaced with zero values to create reducible models. The first of these may be subdivided to form two irreducible blocks on the diagonal (the two-block reducible model; Fig. 3.2b). The second may be subdivided to form three irreducible blocks on the diagonal (the three-block reducible model; Fig. 3.2c).

Ergodic properties of reducible non-negative matrices are determined by the relative sizes of the dominant eigenvalues of the constituent blocks of the matrix – specifically, it is the relative sizes of the blocks on the diagonal that are important (Bapat 1998). We manipulated the relative sizes of the dominant eigenvalues of these diagonal blocks by varying transition rates on the diagonal of the block (i.e. varying survival with stasis, the transition rate that measures the rate of survival without growth or regression to a different stage class). As a result, sets of matrices were generated with eigenvalues that varied on a continuous scale. Each single matrix in these sets was projected using six stage-biased initial population vectors, with all individuals in a single stage and a density of one, in a manner similar to that employed by Townley & Hodgson (2008). In practice, these are vectors of zeroes except for a one in one row only. This enabled an assessment of growth rate according to life cycle stage: as reducibility is related to connectivity between stages, it was important that the 'fate' of each individual stage was assessed independently. The actual, realized asymptotic growth rate of each stage-biased projection was calculated by dividing population size at time t+1 $[N_{(t+1)}]$ by population size at time t $[N_{(t)}]$ after the population had reached a stable growth rate. An ergodic model will exhibit the same realized asymptotic growth rate for every stage-biased projection, whereas a non-ergodic model will exhibit two or more growth rates among its set of stage-biased projections.

For the two-block reducible matrix, the modelling process was simple. $\lambda(A_1)$ was fixed at its 'natural' value (0·738), whilst $\lambda(A_2)$ was varied over the range 0·66–0·81. For the three-block reducible matrix, each of the block-specific eigenvalues had to be varied in order to assess every permutation of relative eigenvalue size. As such, in part 1 of the process $\lambda(A_1)$ and $\lambda(A_2)$

were fixed at their 'natural' values (0·711 and 0·611 respectively), whilst $\lambda(A_3)$ varied over the range 0·53–0·78. In part 2 of the process, $\lambda(A_3)$ was fixed at its highest value from part 1 (0·78), $\lambda(A_1)$ remained fixed at its 'natural' value (0·611) and $\lambda(A_2)$ was varied over the range 0·61–0·86. In part 3, $\lambda(A_2)$ was fixed at its highest value from part 2 (0·86), $\lambda(A_3)$ remained fixed at its highest value from part 1 (0·78) and $\lambda(A_1)$ was varied over the range 0·70–0·95. These values may seem somewhat arbitrary but were chosen so that all transition rates remained within biologically realistic limits, whilst still allowing all permutations of relative eigenvalue size to be assessed.

All modelling was carried out using R version 2.9.2 (R Development Core Team 2009). Realised λ values were calculated using the `truelambda` function in the R package `popdemo`.

ILLUSTRATIVE MODELS: RESULTS

Models showed that for both the two- and three-block reducible matrices, the models only exhibited ergodicity where $\lambda(A_1)$ was the largest eigenvalue, with all other cases exhibiting non-ergodicity (Figs 3.3 and 3.4).

More specifically, the models showed that the number of different asymptotic growth rates that may be achieved by a reducible PPM model depends on the relative magnitudes of the dominant eigenvalues of its constituent blocks. The two-block reducible matrix can only exhibit a maximum of two different growth rates. This will occur when $\lambda(A_1) < \lambda(A_2)$ (Fig. 3.3). The three-block reducible matrix can be thought of as a two-block reducible matrix within another two-block reducible matrix. Therefore, $\lambda(A_3)$ must be greater than both $\lambda(A_2)$ and $\lambda(A_1)$ to exhibit asymptotic independence (i.e. to exist as a potential asymptotic growth rate of the model). However, $\lambda(A_2)$ must only be greater than $\lambda(A_1)$ to exhibit asymptotic independence. As such, it is only when $\lambda(A_1) < \lambda(A_2) < \lambda(A_3)$ that the model exhibits three different long-term growth rates (Fig. 3.4). However, the model may exhibit two different long-term growth rates where $\lambda(A_2) < \lambda(A_1) < \lambda(A_3)$, where $\lambda(A_1) < \lambda(A_3) < \lambda(A_2)$ or where $\lambda(A_3) < \lambda(A_1) < \lambda(A_2)$ (Fig. 3.4). The same logic would therefore apply to any reducible model – for example, in a four-block reducible model, $\lambda(A_4)$ would have to be greater than $\lambda(A_3)$, $\lambda(A_2)$ and $\lambda(A_1)$ to exhibit asymptotic independence, and so on.

The only exception to this rule will occur when two diagonal blocks are not fixed relative to one another. Take a reducible matrix with the structure:

$$
\begin{array}{c|cc}
A_1 & \multicolumn{2}{c}{A_{1,2}} \\
\hline
 & A_2 & 0 \\
0 & \cline{2-3} \\
 & 0 & A_3 \\
\end{array}
$$

The matrix can be re-permuted so that blocks A_2 and A_3 are swapped but without changing the overall structure of the matrix:

$$
\begin{array}{c|cc}
A_1 & \multicolumn{2}{c}{A_{1,2}} \\
\hline
 & A_3 & 0 \\
0 & \hline 0 & A_2 \\
\end{array}
$$

For $\lambda(A_2)$ to exhibit asymptotic independence as illustrated by our models, the condition $\lambda(A_1) < \lambda(A_2)$ must be true, as usual. However, as there is no discernable difference between these two placements of A_2 and A_3, then for $\lambda(A_3)$ to exhibit asymptotic independence, the condition $\lambda(A_1) < \lambda(A_3)$ is necessary, but $\lambda(A_2) < \lambda(A_3)$ is no longer necessary. Note that whilst this affects the number of possible asymptotic growth rates where $\lambda(A_1)$ is not the largest eigenvalue, it does not affect the condition that for the model to exhibit ergodicity, $\lambda(A_1)$ must be the largest eigenvalue. Hence, if A_1 is not fixed relative to the other diagonal blocks, the model will be non-ergodic. It is worth mentioning also that whilst we have only illustrated this case with matrices where $\lambda_{max} < 1$, the rules we have described above apply to any non-negative matrix with $\lambda_{max} > 0$.

INCIDENCE OF REDUCIBILITY AND NON-ERGODICITY IN PUBLISHED PPMS

INCIDENCE OF REDUCIBILITY AND NON-ERGODICITY IN PUBLISHED PPMS: METHODS

Population projection matrices were collected from the literature, with the database at the time of analysis numbering 652 matrices (152 animals and 500 plants) for 171 species (57 animals and 114 plants) across a diverse range of taxa (see Appendix 7). In the first instance, we sought out large comparative analyses of PPM models of plants and animals and sourced many PPMs from the original articles cited by those analyses. Online searches of ecological literature provided additional PPMs, although these searches were not systematic. PPMs were not chosen with any bias regarding reducibility or ergodicity. We feel that the database of PPMs represents a fair sample of the entire population of published PPMs; hence, any result described here may be interpreted as applicable to the wider PPM literature. The database held by the authors is being continually added to, and contains extra information on the species and models present. It is producible at any time upon request.

Each matrix was tested for reducibility using the argument that a square matrix $\mathbf{A}$ is irreducible if, and only if, $(\mathbf{I} + \mathbf{A})^{s-1}$ is positive (i.e. every element of $(\mathbf{I} + \mathbf{A})^{s-1}$ is greater than 0), where $\mathbf{I}$ is the identity matrix and s represents the number of columns or rows in the matrix, equal to the number of stage classes in the life cycle model (Caswell 2001).

Each matrix was tested for ergodicity using the argument that a non-negative matrix $\mathbf{A}$ is, under certain natural conditions, ergodic if and only if the dominant left eigenvector $\mathbf{v}$ of $\mathbf{A}$ is positive (i.e. every element of $\mathbf{v}$ is greater than 0). Biologically, this vector

is known as the 'reproductive value' vector, and satisfies the equation $\mathbf{v}^T\mathbf{A} = \lambda_{max}\mathbf{v}^T$, where λ_{max} is the dominant eigenvalue of $\mathbf{A}$ and $\mathbf{v}^T$ denotes the transpose of $\mathbf{v}$ (i.e. from a column vector to a row vector). The specific conditions and mathematical proof for this can be found in Appendix 3.1, and the subject is discussed at a greater depth in Dietzenbacher (1991). As this is a new method in population biology for evaluating ergodicity, each result was double checked with simulation of population dynamics using stage-biased vectors in the same manner described here for the illustrative model (see Illustrative models: methods). In every case, results from simulation of the model agreed with results from evaluation of the dominant left eigenvector.

All tests were carried out using R version 2.9.2 (R Development Core Team 2009). The necessary code to test reducibility and ergodicity of matrices using the above arguments is available in the R package `popdemo`.

INCIDENCE OF REDUCIBILITY AND NON-ERGODICITY IN PUBLISHED PPMS: RESULTS

Analysis of the matrix database showed that the incidence of reducibility in published PPMs is high, at 24·7%. Of the reducible models, 63·2% are non-ergodic, which makes 15·6% of our sample of published PPMs non-ergodic.

Some reducible models have been modelled with post-reproductive stage classes or have similar plausibly reducible life cycles, and thus do not defy biological rationale (as illustrated in Fig. 3.1b). However, most reducible models are lacking vital transition rates to complete the life cycle and as such defy biological rationale (as illustrated in Fig. 3.1c). Some reducible models showed a complete absence of certain stages in the model, and hence incorporated no transition rates whatsoever for those stages (so that the PPM contained columns of zeroes). In addition, many models included 100% rates of survival with stasis in adult stage classes, which although are not an origin of reducibility *per se*, effectively model immortal individuals and so clearly defy biological rationale.

EMPIRICAL EXAMPLES

We chose three reducible matrices from the literature to illustrate how reducibility may (or may not) affect model outcomes and conclusions, depending on the ergodic properties of the model and the analyses performed. These matrices were block permuted (code to block permute a reducible matrix may be found in the R package `popdemo` and further information on block permuting a reducible matrix by hand may be found in Appendix 3.2), and the eigenvalues of their diagonal blocks were calculated. These were then compared with the realized asymptotic growth rates of their stage-biased projections.

EMPIRICAL EXAMPLES: *NUTTALLIA OBSCURATA*

Nuttallia obscurata (the varnish clam) is a marine invasive species in British Columbia, Canada. Dudas, Dower, & Anholt (2007) parameterize two matrices for the species, in order to evaluate the dynamics of invasive populations and identify which life-history stages are the best to target with control strategies. By performing asymptotic sensitivity and elasticity analyses, they concluded that reducing the survival of adult individuals would be the most beneficial strategy to curb population growth.

The PPM for the Robbers' passage population of *N. obscurata* is shown in Fig. 3.5a. There was no observed growth of stage 1 individuals into stage 2 individuals – these instead all bypassed stage 2, becoming stage 3 individuals in 1 year. The authors noted this irregularity and corrected the estimates of transition rates accordingly but failed to note that the resulting matrix is reducible: individuals in stage 2 may grow and reproduce, but no individual in stages 1, 3, 4 or 5 can contribute in any way to stage 2 (whether through growth or reproduction).

Although reducible, the matrix is ergodic (Fig. 3.6a). Therefore, in this particular case, the conclusions of the study would not be greatly affected by the reducible structure of the model. Every population projection will eventually settle to a rate of geometric growth described by the dominant eigenvalue of the matrix, and so the asymptotic growth rate of the population can be safely defined as such. Therefore, the sensitivity and elasticity analyses conducted by Dudas, Dower, & Anholt (2007) correctly evaluate the effects of perturbations to vital rates on asymptotic population growth. This is not necessarily always the case, as other examples will show.

Perhaps in this case, individuals grew faster than anticipated. A re-definition of size classes to a lesser resolution might have produced an irreducible matrix that described population dynamics more effectively. This should be easy to do if data on sizes of individuals are available. When parameterizing models, it is worth bearing in mind that the life cycle model may have to be redefined in order to fit with the data collected. Information on parameterizing models according to data availability is available (Vandermeer 1978; Moloney 1986). Alternatively, for species such as the varnish clam that exhibit continuous state variables (e.g. where organism size is a strong determinant of survival and/or growth and/or fecundity), integral projection models (IPMs) offer a means of population projection that utilizes smooth, continuous relationships between such state variables and an organism's vital rates, which may be more accurate than the discrete-class approximations to such relationships provided by a PPM (Easterling, Ellner, & Dixon 2000; Ellner & Rees 2006, 2007).

EMPIRICAL EXAMPLES: *ARDISIA ESCALLONIOIDES*

Ardisia escallonioides (Marlberry) is a perennial understorey shrub found in the subtropical forests of southern Florida, as well as on islands and in coastal regions of the Caribbean Sea and the Gulf of Mexico. Pascarella & Horvitz (1998) collected data from the Florida populations in

order to parameterize models that would allow the assessment of the role of environmental variation in shaping population dynamics of the species. The environmental variation in question was the degree of forest canopy 'openness' as a result of hurricane damage. Patches were identified with varying degrees of canopy openness, and an individual matrix was parameterized for each. The individual matrices were then combined with a patch-transition matrix into a megamatrix that described dynamics of the population as a whole. Asymptotic growth rates, stable stage structures and sensitivity and elasticity analyses were conducted for individual matrices and the megamatrix and the results were compared and contrasted with one another.

The matrix representing the 5% open patch is presented in Fig. 3.5b. There is no growth of stage 7 or stage 8 individuals, and 100% stasis of stage 8 individuals. The authors noted that their original matrix parameterization was not 'full rank' (*sensu* Caswell 1989), so would not exhibit asymptotic behaviour comparable with other patch-specific matrices, and corrected it as such (by estimating fecundity values and juvenile survival rates). However, they did not note that the resulting model was reducible, and so may still not exhibit comparable asymptotic behaviour (although it is noteworthy that they realized and corrected this in later analyses that used the data – see Appendix A of Tuljapurkar, Horvitz, & Pascarella 2003).

The reducible model exhibits two possible asymptotic growth rates (Fig. 3.6b). Any projection that excludes stage 8 individuals in the initial population structure will follow $\lambda = 0.984$, and any projection that includes stage 8 individuals in the initial population structure will follow $\lambda = 1$. In this case, the asymptotic growth rate of the population has no single numerical definition, although it is assumed to equal the dominant eigenvalue of the matrix. Hence, it is not comparable with the other matrix models. Sensitivity and elasticity analyses measured the effect of perturbations on the dominant eigenvalue, but this is not necessarily equivalent to the effect that such perturbations have on asymptotic growth rate, as asymptotic growth rate is not always equal to the dominant eigenvalue. These analyses are therefore fundamentally flawed for the 5% open canopy patch. Having said that, the errors in this model are diluted by data from other patches in the megamatrix such that the megamatrix is irreducible, so that the conclusions of analyses based on the megamatrix will be little affected by the single reducible model.

The authors recognize that transition rates absent in such a model must occur in populations and that 'a much larger sample size would be needed to detect them empirically' (Pascarella & Horvitz 1998, p. 551). With constraints on the amount of data that can be collected, perhaps in such situations it may be necessary to estimate these transition rates (such as from historical data, or based upon observed rates in other (sub)populations where available) to ensure a reliable model. Again, IPMs may offer an alternative approach in such a situation, as they usually require less data than traditional PPM models (Easterling, Ellner, & Dixon 2000; Ellner & Rees 2006, 2007).

EMPIRICAL EXAMPLES: *PINUS JEFFREYI*

Pinus jeffreyi (the Jeffrey Pine) is a coniferous tree found in the south-eastern USA. van Mantgem & Stephenson (2005) constructed PPM models for a population of the species (along with numerous other species of coniferous tree) in the Sierra Nevada in order to assess the reliability of PPM models as predictors of the dynamics of populations of such species. They compared matrix model projections with empirical data on population size, and concluded that PPM models were good predictors of population size, short-term growth, survival and recruitment.

The PPM model for *P. jeffreyi* is presented in Fig. 3.5c. No stage 4 individuals progressed to become stage 5 individuals within the time frame of the study. The authors noted this, and recognized that this missing transition would be a problem when projecting over long time periods. However, as the study only looked at short-term dynamics (with models projected over a maximum of two time intervals), they concluded that it should not have great adverse effects on their analyses. That said, reducibility *per se* was not explicitly discussed.

The reducible model exhibits three possible asymptotic growth rates (Fig. 3.6c). The matrix, in its block-permuted form, has five irreducible blocks on the diagonal. This is a good example of how a model missing just one transition rate then becomes highly mathematically constrained as a result: eigenvalues are constrained to be equal to the values of survival with stasis (on the diagonal of the matrix). Eigenvectors are equally constrained by these eigenvalues. Hence, an analysis that uses any eigenvalues of the matrix will be adversely affected. These include not only asymptotic analyses such as sensitivity and elasticity but also some measures of transient dynamics, such as the damping ratio of the population (Caswell 2001) and certain measures of transient sensitivity and elasticity (Fox & Gurevitch 2000; Yearsley 2004).

van Mantgem & Stephenson (2005) are correct in that the reducibility of the matrix has little impact on the conclusions of their analyses – they wished merely to compare empirical with predicted population dynamics, and the models they present are an accurate representation of the demographic rates of the species in the time period considered. This example illustrates a case in which a reducible matrix, despite being non-ergodic and having highly constrained eigenvalues, should not pose a problem for the specific analyses being conducted. That said, the supplementary material does provide dominant eigenvalues of the PPMs as values of asymptotic population growth, and elasticity values are used in the manuscript to support certain conclusions (although are not presented) – these analyses will be flawed as a result of the model structure.

DISCUSSION

We have demonstrated that reducibility, and hence non-ergodicity, in published PPM models is common. We have illustrated how the structure of reducible models affects their ergodic properties, and provided some empirical examples showing how these properties may or may not affect model outcomes and conclusions, depending on the analyses implemented.

But why are so many published PPMs reducible? Whilst some models may plausibly be based upon a reducible life cycle (e.g. Brault & Caswell 1993), most are missing vital transition rates necessary for a complete life cycle. This leads to the question as to why such transition rates are missing from those models. The most likely explanation for this, as noted earlier by Pascarella & Horvitz (1998) in the *Ardisia* example, is that the relevant data required to fully parameterize the model are lacking. There are two possible explanations for this – either the data collected overlooked life cycle transitions that did occur, or the missing transitions did not occur during the time of study. Certain methods of data collection may result in poor estimates of transition rates, and perhaps a failure to capture a full set of transition rates – Münzbergová & Ehrlén (2005) note that commonly used methods may result in 'poor representation of some stages', and advise to collect data for an equal number of individuals per stage. However, even if the data collected do accurately represent the life cycle of the population during the time of study (with certain transition rates missing), this time is often limited to two consecutive years (Fieberg & Ellner 2001), comprising two population censuses: just enough to parameterize a single projection matrix. Such matrices will only represent demographic rates under the environmental conditions specific to that year. Under undesirable environmental conditions, it takes little stretch of the imagination to envisage that some life cycle transitions may not occur in a single year. Even under desirable environmental conditions, low transition rates (especially of growth) may be seen under certain life cycle models, especially for long-lived species (Enright, Franco, & Silvertown 1995). While the data collected in such an instance may adequately represent the demographics of that species in that particular year, it is clearly insufficient to describe the dynamics of the population over many years – this much seems intuitive. Additionally, as we have shown here with our illustrative and empirical examples, complications arise as reducible matrix models based upon such data have certain mathematical properties – such as eigenvalues that are constrained to equal those of the sub-blocks in all cases, and non-ergodicity in some cases – that may pose problems for analysis.

For these reasons, as a general rule it is best to avoid using reducible models. Having said that, if a reducible model is unavoidable, such a model will not always prove problematic for analysis (as was seen earlier in the *Pinus* example). It is important that demographers know how to: (1) identify reducible matrices, (2) evaluate the ergodic properties of those matrices and (3) discern whether the models will prove problematic for the analyses that are to be conducted. We propose that matrices should be defined as irreducible, reducible–ergodic or reducible–non-ergodic and that this information be used to guide analysis. Reducibility and ergodicity of a

matrix can be easily evaluated using the methods we present (see the Incidence of reducibility and non-ergodicity in published PPMs: methods section; Appendix 3.1) and analyses appropriate to that model structure can then be chosen.

For deterministic asymptotic analyses, a reducible–ergodic matrix can be analysed in very much the same way as an irreducible matrix. Analyses such as evaluation of the dominant eigenvalue and/or eigenvector and calculations of asymptotic sensitivity or elasticity will be largely unaffected by the model. On the other hand, deterministic asymptotic analyses of reducible–non-ergodic matrices will often prove spurious: there is no single definition of asymptotic stable population growth and structure. For an unavoidably reducible model, an alternative is to analyse the portion of the life cycle that one is interested in – for example, when analysing population growth rates of species with post-reproductive stage classes, one might want to only analyse the block for the reproductive part of the population (Caswell 2001, p. 89).

Reducible models have implications for stochastic analyses also. In stochastic analyses, sets of transition matrices are generated, with each single matrix representing transition rates under a certain environmental condition. This is usually done either by using matrices parameterized over different time intervals or by drawing transition rates from probability distribution functions with covarying parameters (Fieberg & Ellner 2001). A different matrix (emulating a unique set of environmental conditions) is chosen for each projection interval. In this case, it is clearly difficult to evaluate ergodicity of the model – each simulation is unique, as a different sequence of parameters or matrices is selected each time the simulation is run. However, reducibility of the combined matrix set can be evaluated. For the matrix set $\mathbf{A}(1), \mathbf{A}(2),\ldots, \mathbf{A}(n)$, the arithmetic average matrix $\mathbf{M}=(1/n)(\mathbf{A}(1) + \mathbf{A}(2) +\ldots+ \mathbf{A}(n))$. As ergodicity cannot be evaluated, reducibility of $\mathbf{M}$ should be avoided in stochastic analyses. Individual reducible matrices, while undesirable, should not usually be a problem provided that the missing transitions are present elsewhere in the matrix set. However, the impacts of individual reducible matrices on stochastic analyses warrant further exploration and we note that this rule of thumb may not always apply. An alternative to simulating stochastic models is to calculate Tuljapurkar's approximation to the stochastic growth rate (Fieberg & Ellner 2001). This calculation should only be based on ergodic matrix models, as calculations utilize the dominant eigenvalue, which can only be properly defined for ergodic models.

Transient population dynamics are gaining increased attention from researchers. Methods for calculating transients are many and varied, and the impacts of reducibility and ergodicity of matrices on transient analyses will vary according to analyses used. For methods that implicate matrix eigenvalues in their calculation (e.g. Fox & Gurevitch 2000; Yearsley 2004), reducible matrices (whether ergodic or non-ergodic) should be avoided, as the eigenvalues of the matrix are constrained by the model structure. For methods that do not utilize matrix eigenvalues (e.g. Koons, Holmes, & Grand 2007; Townley & Hodgson 2008; Tenhumberg, Tyre, & Rebarber 2009), a general rule would be to avoid reducible–non-

ergodic matrices: many analyses relate transient measures to asymptotic growth (Koons, Holmes, & Grand 2007; Townley & Hodgson 2008) and so the model used requires a robust definition of asymptotic growth. That said, in some cases (as exemplified in the *Pinus* example above), empirical calculation of population growth rates over the transient period may not be adversely affected by a non-ergodic model.

CONCLUSIONS

With reducible models so abundant in the literature, it is important for population biologists to know of the issues concerning their use, be able to identify whether a matrix is irreducible, reducible–ergodic or reducible–non-ergodic, and take the necessary precautions to alleviate potential problems associated with these model structures, either by redefining model structure if possible or by choosing the right analytical methods pertaining to the use of that matrix. The methods and models presented here should help to inform on these processes. Although biologists now have the necessary mathematical, statistical and computational tools at their disposal to conduct highly complex analyses, it is important not to forget about the foundations of PPM models and to remember to consider the basic life cycle model and matrix structure very carefully.
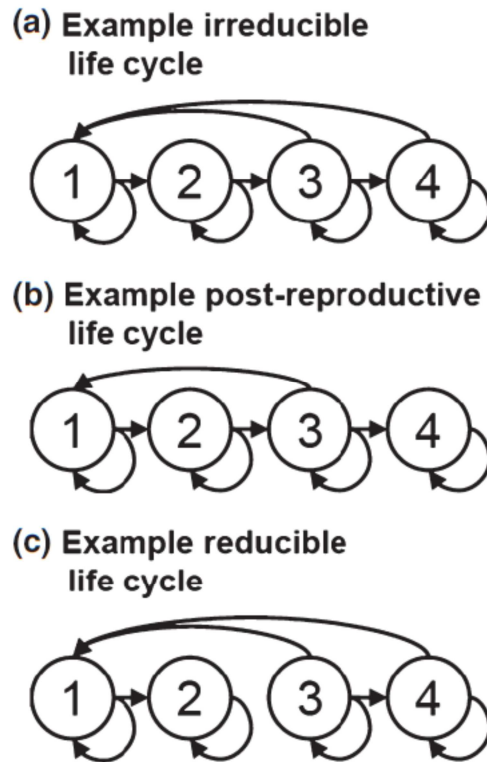
FIG. 3.1: Example stage-structured life cycles. **(a)** An irreducible life cycle. Every stage is connected to every other stage via at least one pathway. **(b)** A reducible, post-reproductive life cycle. Sufficient transitions to facilitate pathways from every stage to every other stage are lacking: once in stage 4, there are no connections to the rest of the life cycle. Such a life cycle, although reducible, is biologically plausible. **(c)** A reducible life cycle that is missing a necessary transition rate. Sufficient transitions to facilitate pathways from every stage to every other stage are lacking: once in stages 1 and 2, an individual cannot then contribute to stages 3 and 4. Such a model clearly defies biological rationale, with portions of the life cycle isolated from the rest of the cycle.

(a) Irreducible matrix

	1	2	3	4	5	6
1	0·5	0·01	0·75	1	1·25	1·5
2	0·1	0·525	0·01			
3		0·08	0·55	0·01		
4			0·06	0·575	0·01	
5				0·04	0·6	0·01
6					0·02	0·625
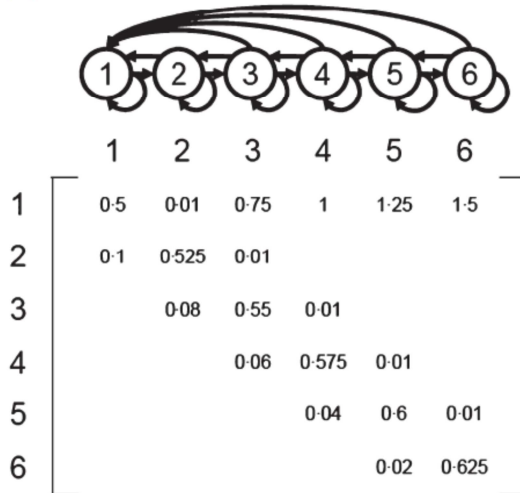
(b) 2-block reducible matrix
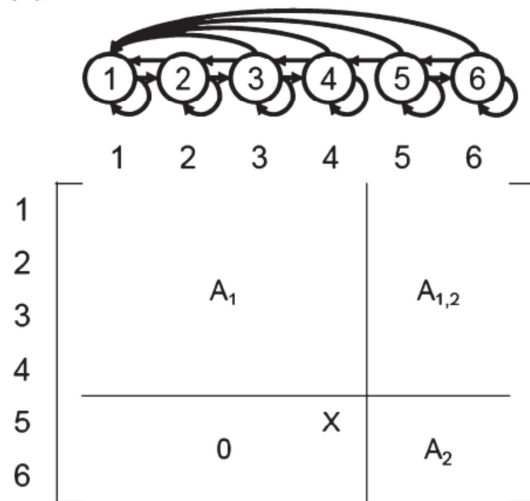
(c) 3-block reducible matrix
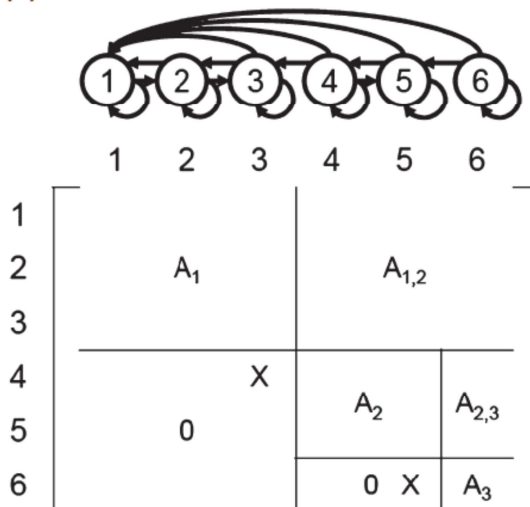
FIG. 3.2: The matrices used for modelling. In each case, the life cycle described by the matrix is also shown for clarity. **(a)** The irreducible projection matrix upon which the reducible matrices are based. This is similar to one that may be parameterized for a tree species: fecundity and survival with stasis increase with size, whilst survival with growth decreases with size. Each stage also has a small probability of regression. (b) The two-block reducible matrix in block-permuted form. An $\times$ indicates the 'knocking-out' of transition $a_{5,4}$ from the irreducible matrix and its replacement with a zero value in order to create the reducible matrix. The matrix may be subdivided with irreducible blocks A_1 and A_2 on the diagonal as indicated. '0' indicates a zero block (i.e. all elements of the block are zero). (c) The three-block reducible matrix in block-permuted form. An $\times$ indicates the 'knocking-out' of transitions $a_{4,3}$ and $a_{6,5}$ from the irreducible matrix and their replacement with zero values in order to create the reducible matrix. The matrix may be subdivided with irreducible blocks on the diagonal as indicated. Again, '0' indicates a zero block. Note: in all cases, only irreducible blocks on the diagonal are important in the modelling process. Henceforth in this study, blocks $A_{1,2}$ and $A_{2,3}$ can be disregarded.
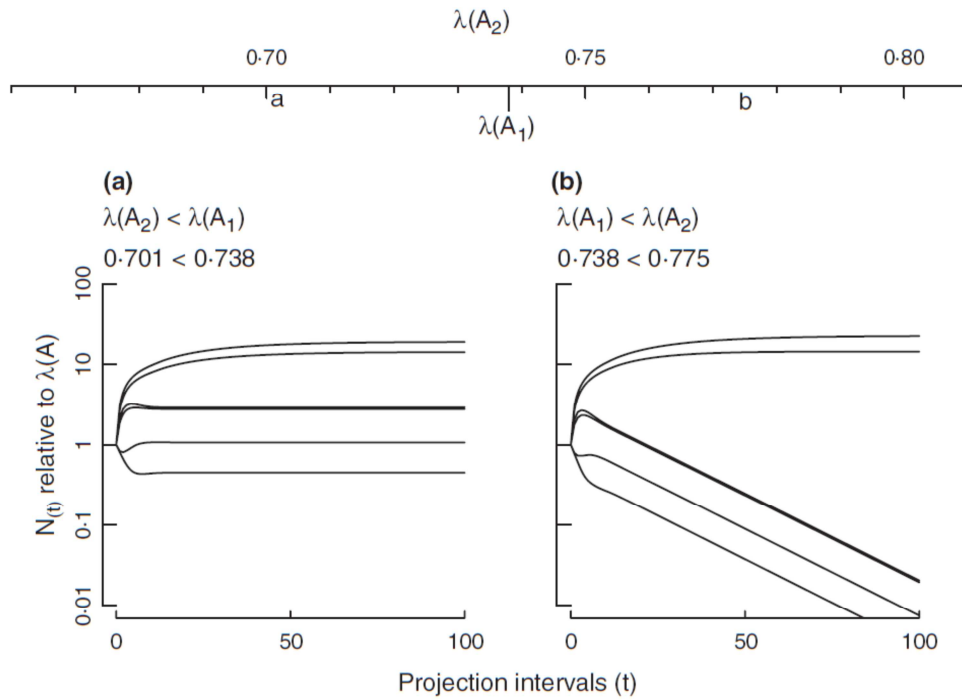
FIG. 3.3: Axes at the top of the graph show the modelling process for the simple two-block reducible matrix. $\lambda(A_1)$ is fixed (=0.738) and $\lambda(A_2)$ varies. Relative positions of $\lambda(A_1)$ and graphs (a) and (b) are indicated on the scale at the top of the figure. The y-axes of graphs (a) and (b) follow a log scale. Population size [$N_{(t)}$] is standardized by $\lambda(A)$ to clearly indicate differences in growth rates, therefore stages that follow $\lambda(A)$ converge to horizontal lines on the graph. The number of different asymptotic growth rates that may be achieved by the model depends on the relative magnitudes of the dominant eigenvalues of its constituent blocks: **(a)** $\lambda(A_2) < \lambda(A_1)$, therefore all stages follow $\lambda(A) = \lambda(A_1) = 0.738$. **(b)** $\lambda(A_1) < \lambda(A_2)$, therefore stages 5 and 6 follow $\lambda(A) = \lambda(A_2) = 0.775$. Stages 1–4 continue to follow $\lambda(A_1) = 0.738$.
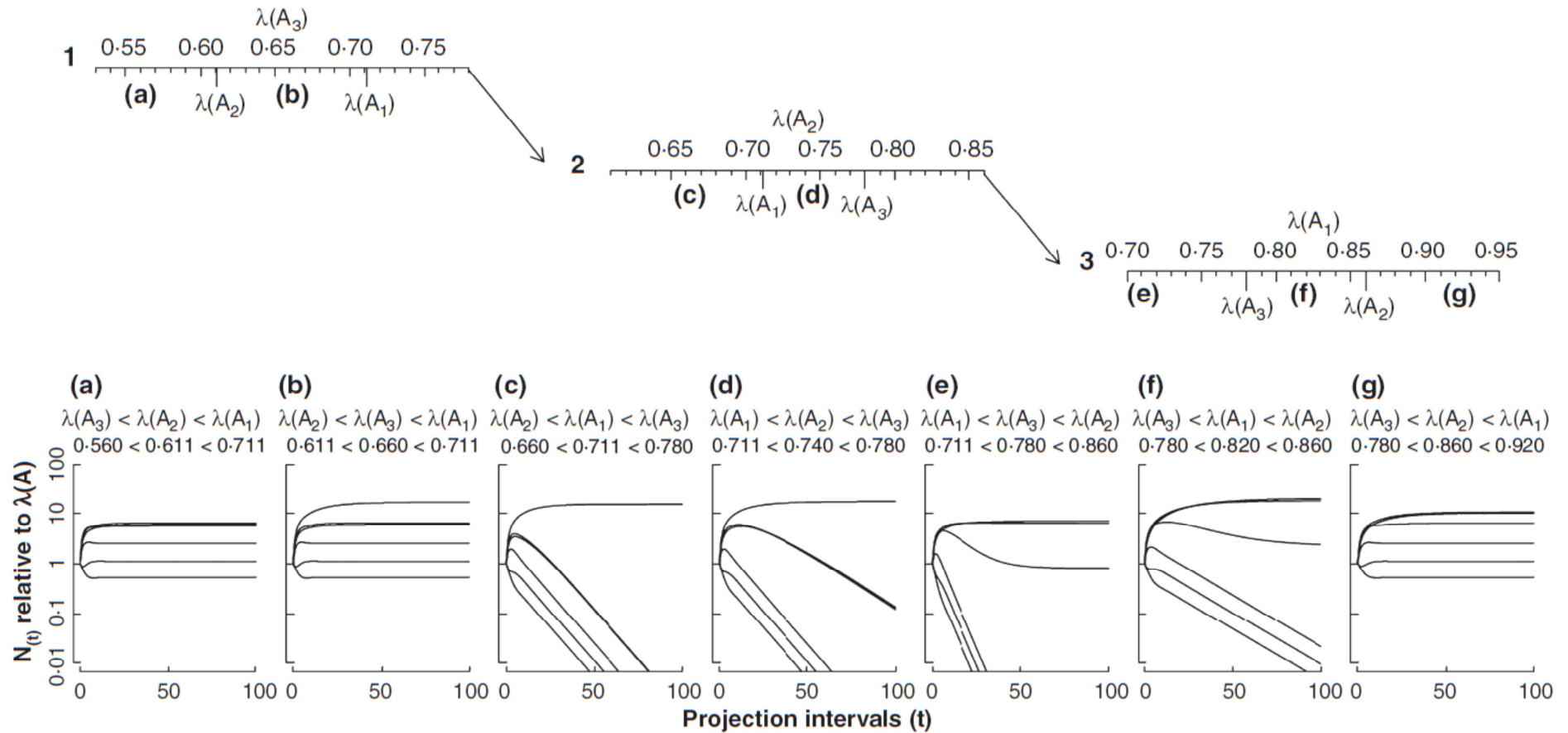
FIG. 3.4:

Axes at the top of the graph show the modelling process for the three-block reducible matrix. In part 1, $\lambda(A_2)$ and $\lambda(A_1)$ are fixed (=0.611 and 0.711 respectively) and $\lambda(A_3)$ varies. In part 2, $\lambda(A_1)$ and $\lambda(A_3)$ are fixed (=0.711 and 0.780 respectively) and $\lambda(A_2)$ varies. In part 3, $\lambda(A_3)$ and $\lambda(A_2)$ are fixed (=0.780 and 0.860

respectively) and $\lambda(A_1)$ varies. In all cases, relative positions of block-specific eigenvalues and of graphs (a)–(g) are indicated where appropriate on the axes at the top of the figure. The y-axes of graphs (a)–(g) follow a log scale. Population size $[N_{(t)}]$ is standardized by $\lambda(\mathbf{A})$ to clearly indicate differences in growth rates, therefore stages that follow $\lambda(\mathbf{A})$ converge to horizontal lines on the graph. The number of different asymptotic growth rates that may be achieved by the model depends on the relative magnitudes of the dominant eigenvalues of its constituent blocks: **(a)** $\lambda(A_3) < \lambda(A_2) < \lambda(A_1)$, therefore all stages follow $\lambda(\mathbf{A}) = \lambda(A_1) = 0.711$. **(b)** $\lambda(A_2) < \lambda(A_3) < \lambda(A_1)$, therefore all stages follow $\lambda(\mathbf{A}) = \lambda(A_{1)} = 0.711$. **(c)** $\lambda(A_2) < \lambda(A_1) < \lambda(A_3)$, therefore stage 6 follows $\lambda(\mathbf{A}) = \lambda(A_3) = 0.780$, while stages 1–5 follow $\lambda(A_1) = 0.711$. **(d)** $\lambda(A_1) < \lambda(A_2) < \lambda(A_3)$, therefore stage 6 follows $\lambda(\mathbf{A}) = \lambda(A_3) = 0.780$, while stages 4 and 5 follow $\lambda(A_2) = 0.740$ and stages 1–3 follow $\lambda(A_1) = 0.711$. **(e)** $\lambda(A_1) < \lambda(A_3) < \lambda(A_2)$, therefore stages 4–6 follow $\lambda(A) = \lambda(A_2) = 0.860$, while stages 1–3 follow $\lambda(A_1) = 0.711$. **(f)** $\lambda(A_3) < \lambda(A_1) < \lambda(A_2)$, therefore stages 4–6 follow $\lambda(\mathbf{A}) = \lambda(A_2) = 0.860$, while stages 1–3 follow $\lambda(A_1) = 0.820$. **(g)** The model is returned to its original state of $\lambda(A_3) < \lambda(A_2) < \lambda(A_1)$, and all stages follow $\lambda(\mathbf{A}) = \lambda(A_1) = 0.920$.
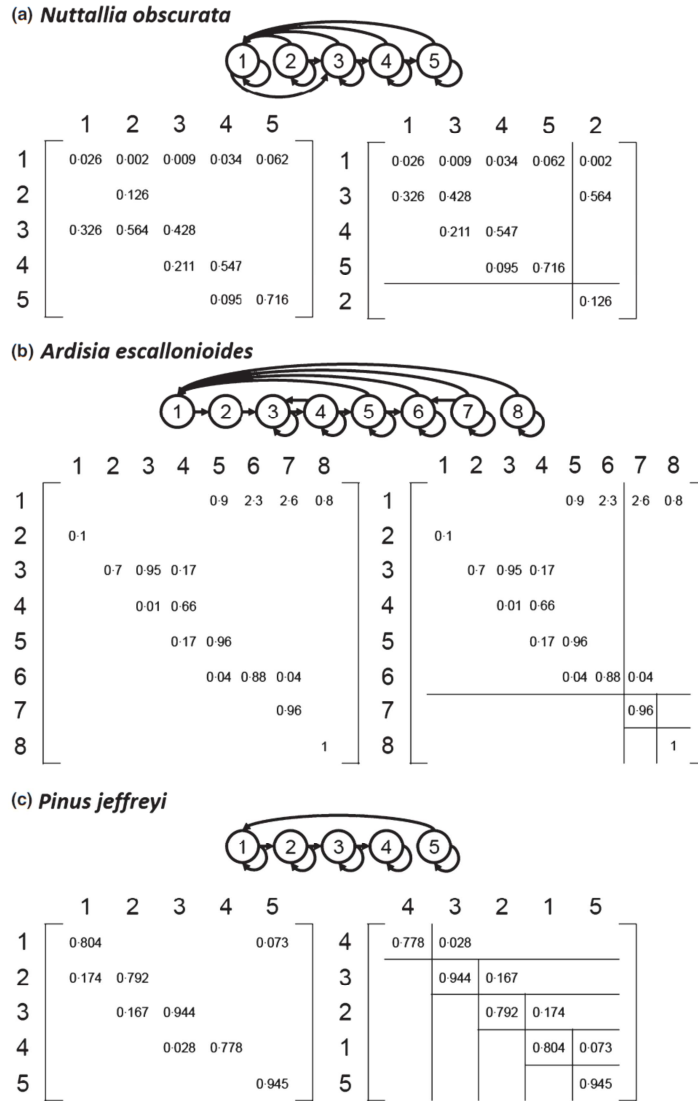
FIG. 3.5: Empirical examples of reducible matrices with varying numbers of asymptotic growth rates that may be achieved (see Fig. 3.6). Each matrix is shown in its original (left) and block-permuted (right) form. In each case, the life cycle described by the matrix is also shown for clarity. **(a)** Left: PPM parameterized for the Robber's passage population of varnish clams *Nuttallia obscurata* (Dudas, Dower, & Anholt 2007). Right: the block-permuted matrix, with two irreducible blocks on the diagonal. **(b)** Left: PPM parameterized for marlberry *Ardisia escallonoides* (Pascarella & Horvitz 1998) under a 5% open canopy. Right: the block-permuted matrix, with three irreducible blocks on the diagonal. **(c)** Left: PPM parameterized for the Jeffrey Pine *Pinus jeffreyi* (van Mantgem & Stephenson 2005). Right: the block-permuted matrix, with five irreducible blocks on the diagonal.
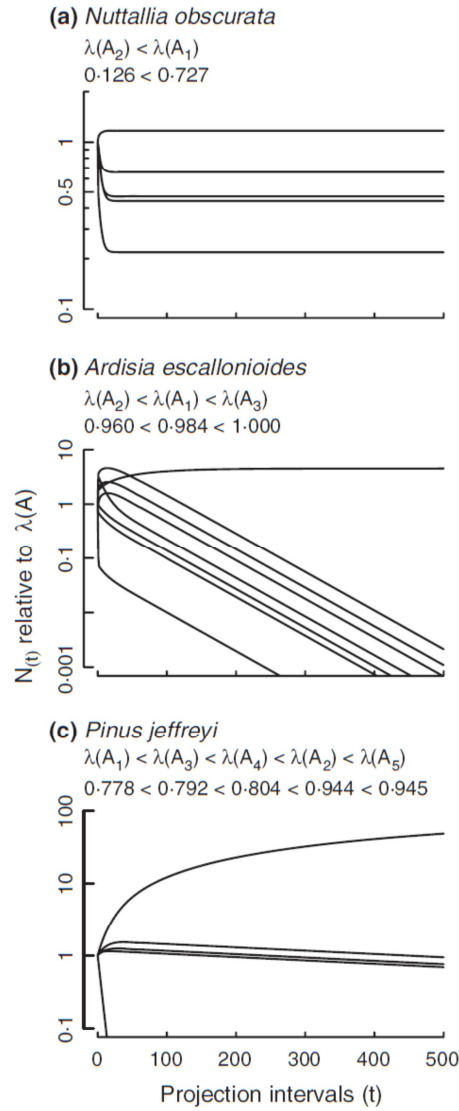
FIG. 3.6: Projections of the example empirical reducible matrices from stage-biased initial populations. In all cases, y-axes follow a log scale and population size [$N_{(t)}$] is standardized by $\lambda(\mathbf{A})$ to clearly indicate differences in growth rates; therefore, stages that follow $\lambda(\mathbf{A})$ converge to horizontal lines on the graph. In agreement with the illustrative models, the number of different asymptotic growth rates that may be achieved by the model (and therefore the ergodicity of the model) depends on the relative magnitudes of the dominant eigenvalues of its constituent blocks: **(a)** The *Nuttallia obscurata* model exhibits ergodicity, as $\lambda(A_2) < \lambda(A_1)$, therefore all stages follow $\lambda(\mathbf{A}) = \lambda(A_1) = 0.727$. **(b)** The *Ardisia escallonioides* model exhibits two different asymptotic growth rates, as $\lambda(A_2) < \lambda(A_1) < \lambda(A_3)$. Stage 8 follows $\lambda(\mathbf{A}) = \lambda(A_3) = 1$, whereas stages 1–7 follow $\lambda(A_1) = 0.984$. **(c)** The *Pinus jeffreyi* model exhibits three different growth rates, as $\lambda(A_1) < \lambda(A_3) < \lambda(A_4) < \lambda(A_2) < \lambda(A_5)$. Stage 5 follows $\lambda(\mathbf{A}) = \lambda(A_5) = 0.945$ [although this projection does not completely converge within the 500 projection intervals plotted, it goes on to converge to $\lambda(\mathbf{A})$], stages 1–3 follow $\lambda(A_2) = 0.944$ and stage 4 follows $\lambda(A_1) = 0.778$.

CHAPTER 4

– – – – – – – – – – – – – –

Ecologists and evolutionary biologists are increasingly required to be computer programmers to implement the mathematical and statistical models necessary for research. Open-source software packages have been an integral part of this revolution: they make complex methods freely available to everyone, whilst the efforts of third-party developers ensure they are continually expanded and kept up-to-date. R is perhaps the most widely-used open source programming language in ecology and evolution, and is the language used to implement all analytical methods that contributed to this thesis. Making these methods freely available by compiling them into an R package was the logical next step to encourage their wider use. Chapter 4 is the fifth paper published as part this thesis, and provides a user's guide to software tools for the methods presented in the first three chapters. These are freely available as part of the R package `popdemo`.

Chapter 4:

Stott, I., Hodgson, D.J. & Townley, S. (2012) `popdemo`: an R package for population demography using projection matrix analysis. *Methods in Ecology and Evolution*.
doi: 10.1111/j.2041-210X.2012.00222.x

POPDEMO: AN R PACKAGE FOR POPULATION DEMOGRAPHY USING PROJECTION MATRIX ANALYSIS

ABSTRACT

1. Effective population management requires accurate predictions of future population dynamics and how they may be manipulated to achieve management goals.

2. The R package `popdemo` provides software tools for novel analytical methods that aim to enhance the predictive power of basic population projection matrix models. These include indices of transient population dynamics and transfer function analyses.

3. We use a case study to demonstrate the use and importance of these methods for population management and briefly discuss their potential application outside population ecology.

INTRODUCTION

`popdemo` is an R package (available at http://cran.R-project. org) that provides novel analytical methods for basic population projection matrix (PPM) models. These add to the more traditional approaches available in the package `popbio` (Stubben & Milligan 2007). In this study, we highlight key methods covered by `popdemo` and use a PPM case study to show how these may be used for population management. For detailed information, we point the reader in the direction of package demos that provide comprehensive coverage of functionality. Finally, we discuss how the tools in this package could find use outside population ecology.

POPULATION PROJECTION MATRIX MODELS

Population projection matrix models are an important tool in ecological and evolutionary demography, for population management (Kareiva, Marvier & McClure 2000), comparative ecology (Buckley *et al.* 2010) and life history theory (Åberg *et al.* 2009). Many studies rely on basic density-independent, non-stochastic (linear, time-invariant) PPM models (e.g. Linkie *et al.* 2007), as data required by more complex density-dependent and stochastic models (e.g. Jensen 1996; Fieberg & Ellner 2001) are often difficult to provide. Our examples use a PPM for medium-fecundity desert tortoise (*Gopherus agassizii*) with eight size classes (Doak, Kareiva & Klepetka 1994). Once `popdemo` is installed and loaded, the matrix is created by running `data(Tort):`

	1	2	3	4	5	6	7	8
1	0	0	0	0	0	1.300	1.980	2.570
2	0.716	0.567	0	0	0	0	0	0
3	0	0.149	0.567	0	0	0	0	0
4	0	0	0.149	0.604	0	0	0	0
5	0	0	0	0.235	0.560	0	0	0
6	0	0	0	0	0.225	0.678	0	0
7	0	0	0	0	0	0.249	0.851	0
8	0	0	0	0	0	0	0.016	0.860

Basic PPM models take the form $n_t = A^t n_0$, where A is the PPM describing the stage-structured life cycle of the organism, and n_0 and n_t are vectors containing numbers or densities of individuals in each stage class (the demographic structure) of the current population and the population at time t in the future, respectively (see Caswell 2001). Projecting and graphing population dynamics using this equation is often the first step towards understanding the model. popdemo's function project enables this [Fig. 4.1; see demo(projection)]:

```
n0 <- c(1,1,2,3,5,8,13,21)
pr1 <- project(Tort, vector=n0, time=50)
plot(pr1)
```

MEASURING POPULATION DYNAMICS

Traditionally, analysis of basic PPM models has focussed on long-term (asymptotic) population dynamics. Assuming density-independence and a constant environment, any population is predicted to eventually settle to a stable state, with a stable demographic structure equal to the dominant right eigenvector w of the PPM, and a stable geometric growth rate equal to the dominant eigenvalue λ_{max} of the PPM (Caswell 2001). The stable growth rate is often used as an indicator of population viability and fitness: $\lambda_{max} > 1$ predicts long-term population increase, whereas $\lambda_{max} < 1$ predicts long-term decline. The desert tortoise PPM declines in the long term, with $\lambda_{max} = 0.958$ (Fig. 4.1; Appendix 4.1).

MODEL ASSUMPTIONS

Ideally, most PPMs should be *primitive*, like the desert tortoise PPM, with asymptotic dynamics conforming to the aforementioned description. In contrast, *imprimitive* PPMs exhibit periodic life cycle transitions (Otto & Day 2007), which cause cyclic long-term population dynamics rather than stable geometric growth. Imprimitive PPMs may also be *reducible* and *nonergodic*:

such models can be decomposed into two or more parts, yielding several different potential long-term growth rates that depend on demographic structure (Stott *et al.* 2010b [Chapter 3]). Many analyses assume primitivity, irreducibility and/or ergodicity, so it is important to check these properties to ensure analyses are appropriate to the model. The functions `is.matrix_primitive`, `is.matrix_irreducible` and `is.matrix_ergodic` facilitate these checks [Appendix 4.1; see `demo(matrixtools)`].

TRANSIENT DYNAMICS

Even if a model is primitive, analysing only long-term dynamics has significant drawbacks. Asymptotic analyses ignore *transient dynamics* of the population. Populations are frequently subject to environmental disturbances, so are rarely at stable state. Consequently, long-term growth rate is often a poor predictor of real-world population dynamics (Bierzychudek 1999). Short-term (transient) dynamics may differ drastically from long-term trends because of discrepancies between the current and stable demographic distributions. In the short term, populations may increase faster than their stable growth rate (amplify) if reproductive adults are overrepresented in the population (as is the case in Fig. 4.1). Alternatively, they may grow more slowly than their stable growth rate (attenuate) if immature juveniles are overrepresented.

`popdemo` includes functions to calculate three key pairs of indices that measure transient dynamics. Reactivity (`reactivity`) and first-timestep attenuation (`firststepatt`) represent immediate amplification/attenuation in the first timestep, respectively. Maximum amplification (`maxamp`) and maximum attenuation (`maxatt`) represent the largest/smallest possible amplification/attenuation, respectively (Townley & Hodgson 2008). Upper and lower inertia (`inertia`) represent fixed long-term amplification/attenuation, respectively (Koons, Holmes & Grand 2007). These indices are standardised to remove effects of asymptotic dynamics and to assume a total initial population density of 1, so they can be compared both amongst and within models where these may differ, thus offering advantages over analysing simulated dynamics (see Stott, Townley & Hodgson 2011 [Chapter 1]). Each index therefore describes how much larger or smaller the non-stable population is at a certain point along the population projection, relative to the density of an equivalent population initiated at stable stage structure. Indices of amplification are >1, whilst indices of attenuation are <1, with the exact value of the index giving the magnitude of amplification or attenuation.

The desert tortoise population amplifies if adults are overrepresented:

```
n0.amp <- c(1,1,2,3,5,8,13,21)
reactivity(Tort, vector=n0.amp)
maxamp(Tort, vector=n0.amp)
inertia(Tort, vector=n0.amp)
```

This population amplifies (reactivity equals 2.6) and, because of this, settles to a density over four times that predicted by stable growth (inertia equals 4.1; Fig. 4.2a). As asymptotic analysis indicates population decline, basing management decisions on that alone could result in poor strategies that ignore the potential for transient population amplification.

The population attenuates if juveniles are overrepresented:

```
n0.att <- c(21,13,8,5,3,2,1,1)
firststepatt(Tort, vector=n0.att)
maxatt(Tort, vector=n0.att)
inertia(Tort, vector=n0.att)
```

This population attenuates (first-timestep attenuation equals 0.92) and settles to a density below that predicted by stable growth (inertia equals 0.91; Fig. 4.2a). In this case, asymptotic analysis would underestimate the severity of short-term decline, so that management efforts may fail to achieve desired goals.

Transient dynamics depend strongly on population structure. If population structure is not known, then transient bounds inform on the potential range of transient dynamics (Townley & Hodgson 2008; Stott, Townley & Hodgson 2011 [Chapter 1]). Transient bounds on indices of amplification represent the largest possible values that those indices may take, whilst bounds on indices of attenuation represent the smallest possible values that those indices may take. These extreme values of amplification and attenuation result from projections of stage-biased demographic vectors (Townley & Hodgson 2008). A stage-biased vector contains 100% of individuals in a single-stage class, and there is one stage-biased vector for each stage of the life cycle (Fig. 4.2b). For example, a 3×3 matrix has a set of stage-biased vectors [1 0 0]; [0 1 0]; [0 0 1]. When using the aforementioned functions for generating transient indices, the relevant transient bound is returned if a demographic vector is not specified:

```
reactivity(Tort)
firststepatt(Tort)
maxamp(Tort)
maxatt(Tort)
inertia(Tort, bound='upper')
inertia(Tort, bound='lower')
```

For the desert tortoise, a bias towards the largest individuals results in amplification bounds, whilst a bias towards yearlings results in attenuation bounds (Fig. 4.2b). The population can grow to an absolute maximum of almost seven times its current size (maximum amplification bound equals 6.82) and an absolute minimum of 12% its current size (maximum attenuation bound equals 0.12; Fig. 4.2b). The information provided by these transient bounds therefore provides best- or worst-case scenarios. There are further indices of transient density available in `popdemo`, and the functions described here have extra utilities [see `demo(transient)`]. `popdemo` also contains functions for transient indices that deal with

model convergence [see `demo(convergence)` and Stott, Townley & Hodgson 2011 [Chapter 1] for a discussion on convergence indices].

PERTURBATION ANALYSES

For population management, it is important to know how population dynamics may be changed to achieve management goals. Perturbation analyses assess how changes to vital rates of the life cycle such as survival, fecundity or growth affect population dynamics. A classical approach is to conduct sensitivity analysis of the stable growth rate (asymptotic sensitivity analysis). This provides a linear estimate of the effect of perturbations on long-term population growth (Caswell 2001). Asymptotic sensitivity analyses have been used to prioritise potential management practises (e.g. Ratsirarson, Silander & Richard 1996) and analyse prospective population dynamics under varying environmental conditions (e.g. Abe, Nakashizuka & Tanaka 1998). Asymptotic sensitivity analysis of the desert tortoise PPM suggests that promoting growth of young adults (element [8,7] of the matrix) is an efficient way to encourage long-term population growth (Appendix 4.1). This could perhaps be achieved through protection and/or supplementary feeding of those individuals. Sensitivity analyses for transient dynamics also exist and provide a linear estimate of the effect of perturbations on short-term population density or growth (e.g. Caswell 2007).

TRANSFER FUNCTION ANALYSES

The linear relationships described by sensitivity analysis are tangents to more complicated nonlinear functions (Fig. 4.3). Because of this, sensitivity analyses may poorly describe the effect of larger perturbations on population dynamics. *Transfer function analyses* can model the exact nonlinear relationship between a perturbation and resulting population dynamics and require no more information than sensitivity analyses.

The function `tfa` models the transfer function of asymptotic growth (Hodgson & Townley 2004), and `inertia.tfa` models the transfer function of population inertia, providing a good indication of the effect of perturbation on transient dynamics (Stott, Hodgson & Townley 2012b [Chapter 2]). Three parameters are required for these functions: the PPM, a perturbation structure and a range of perturbation magnitude. The perturbation structure is given with two vectors: `d` picks out the rows to be perturbed, and `e` picks out the columns to be perturbed. For example, to perturb element [3,2] of a 3×3 matrix, input `d=c(0,0,1)` and `e=c(0,1,0)` into the functions. The perturbation magnitude is a range of values that specifies how much to change the vital rate(s) by, and is given by a variable called `prange`. `inertia.tfa` also needs to either be given the demographic structure with which to calculate inertia, or be instructed to calculate the upper or lower bound on inertia. The transfer function

relating asymptotic growth to growth rate of young adult tortoises (element [8,7]) is modelled using the following code:

```
tf1 <- tfa(Tort, d=c(0,0,0,0,0,0,0,1), e=c(0,0,0,0,0,0,1,0),
           prange=seq(0,0.25,0.01))
plot(tf1)
```

Sensitivity analysis of asymptotic growth underestimates the effort needed to reverse long-term population decline (Fig. 4.3a): sensitivity (dashed line) suggests that increasing growth of young adults by approximately 0.12 would achieve $\lambda_{max} = 1$, whereas the transfer function (solid line) indicates that an increase of approximately 0.25 is required. As this would bring the overall survival rate of young adults to above 1 $(0.851 + 0.016 + 0.25 = 1.117)$, it is a biologically unrealistic solution.

For the same perturbation, the transfer function for inertia of a specified demographic structure is modelled using:

```
n0 <- c(1,1,2,3,5,8,13,21)
tf2 <- inertia.tfa(Tort, vector=n0, d=c(0,0,0,0,0,0,0,1),
                   e=c(0,0,0,0,0,0,1,0),
                   prange=seq(0,0.25,0.01))
plot(tf2)
```

Sensitivity analysis of inertia overestimates the negative effect of larger perturbations (Fig. 4.3b): sensitivity predicts a decline in inertia with an increase in perturbation (dashed line), but the transfer function demonstrates a dramatic shift to increasing inertia at larger perturbation magnitudes (solid line). Nonlinear effects such as these highlight that management strategies based on sensitivity analyses may be ecologically and/or economically inefficient at achieving desired goals.

Deciding on potential management regimes can be difficult. To aid this process, `popdemo` provides functions to perform transfer function analyses across the whole life cycle. The functions `tfamatrix` and `inertia.tfamatrix` generate multiplots of transfer functions, one for every life cycle transition. These plots are laid out in the same way as the PPM, so that the position of each panel in the multiplot indicates which PPM element it corresponds to. Analysing such plots by eye gives an impression of which vital rates are best to target. We provide an example here for `inertia.tfamatrix` using the desert tortoise PPM:

```
tfmat <- inertia.tfamatrix(Tort, vector=n0)
plot(tfmat)
```

Overall, it seems that increasing fecundity may be the best way to promote population amplification (Fig. 4.4, top row). The plot also shows that most perturbations have a highly nonlinear effect on transient population dynamics.

Another key advantage of using transfer functions is that they can model complex perturbation structures, including simultaneous perturbation to multiple vital rates, different

perturbation magnitudes for different vital rates and life cycle trade-offs (Hodgson & Townley 2004; Stott, Hodgson & Townley 2012b [Chapter 2]). This means that transfer functions can accurately model the effect of complicated management regimes [see `demo(transfer)`].

CONCLUSIONS

The tools provided in `popdemo` facilitate the use of novel analytical methods for basic PPM models. Used alongside traditional analytical approaches, these enable more comprehensive and more predictive analyses of population dynamics, without demand for extra data. The software tools showcased here will likely be of most use for informing population management for relatively data-deficient species. They are also likely to be of use in comparative ecology (Stott *et al.* 2010a [Chapter 5]). They have potential application in studying life history evolution: for example, transient dynamics can be used as a measure of resilience (Neubert & Caswell 1997) and transfer functions could be used to model life cycle trade-offs. Lastly, these methods could find application in modelling stage-structured ecological or evolutionary systems other than populations.

For a full index of functions available in `popdemo` and links to their documentation, run `?popdemo`.

FIGURES
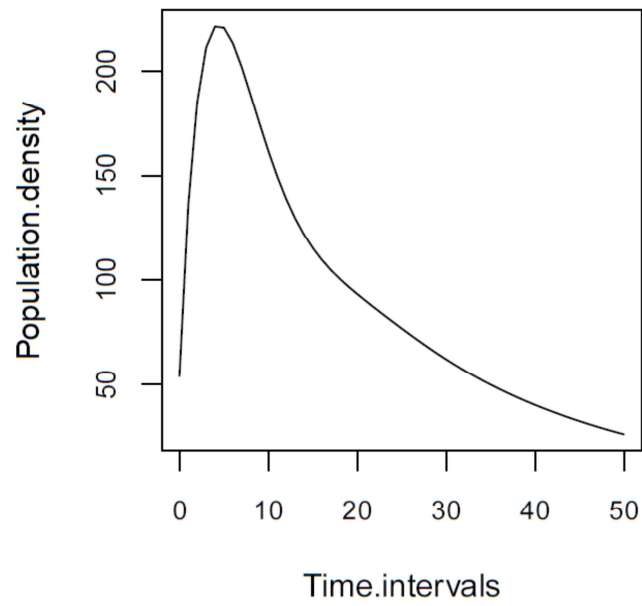
FIG. 4.1: Population projection for the desert tortoise population projection matrix, generated using the `project` function (Appendix 4.1).
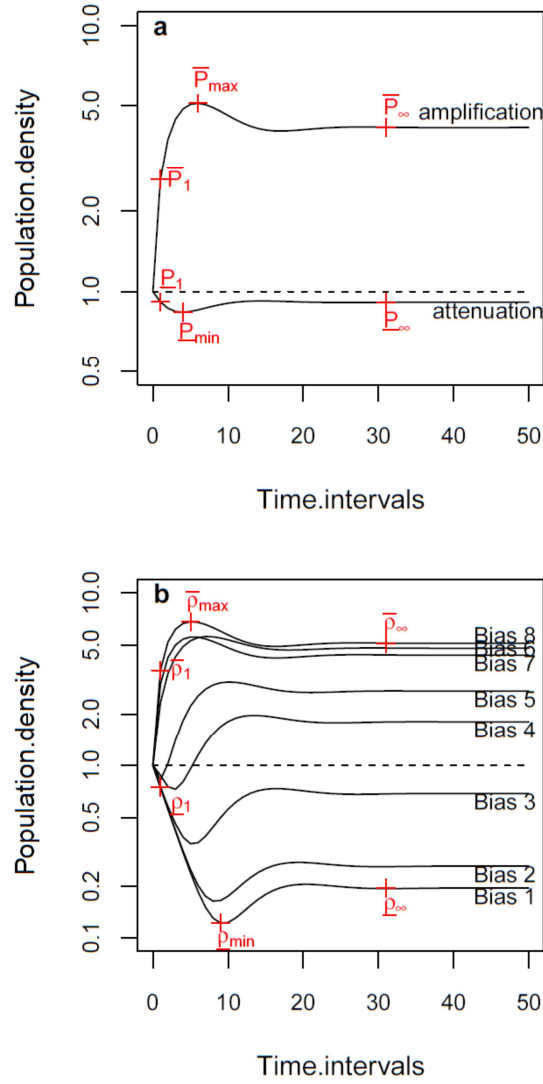
FIG. 4.2: Transient dynamics of the desert tortoise population projection matrix. Plots are generated using the project function (Appendix 4.1) and are standardised to remove asymptotic dynamics and to assume an initial overall density of 1. Transient indices and bounds are added to plots in red. **(a)** A population where adults are overrepresented amplifies: reactivity ($\overline{P}_1$) = 2.63; maximum amplification ($\overline{P}_{max}$) = 5.11; inertia ($\overline{P}_\infty$) = 4.14, whilst a population where juveniles are overrepresented attenuates: first-timestep attenuation ($\underline{P}_1$) = 0.92; maximum attenuation ($\underline{P}_{min}$) = 0.84; inertia ($\underline{P}_\infty$) = 0.91. **(b)** Transient bounds result from stage-biased population projections: reactivity ($\overline{\rho}_1$) = 3.58; first-timestep attenuation ($\underline{\rho}_1$) = 0.75; maximum amplification ($\overline{\rho}_{max}$) = 6.83; maximum attenuation ($\underline{\rho}_{min}$) = 0.12; upper inertia ($\overline{\rho}_\infty$) = 5.12; lower inertia ($\underline{\rho}_\infty$) = 0.20.
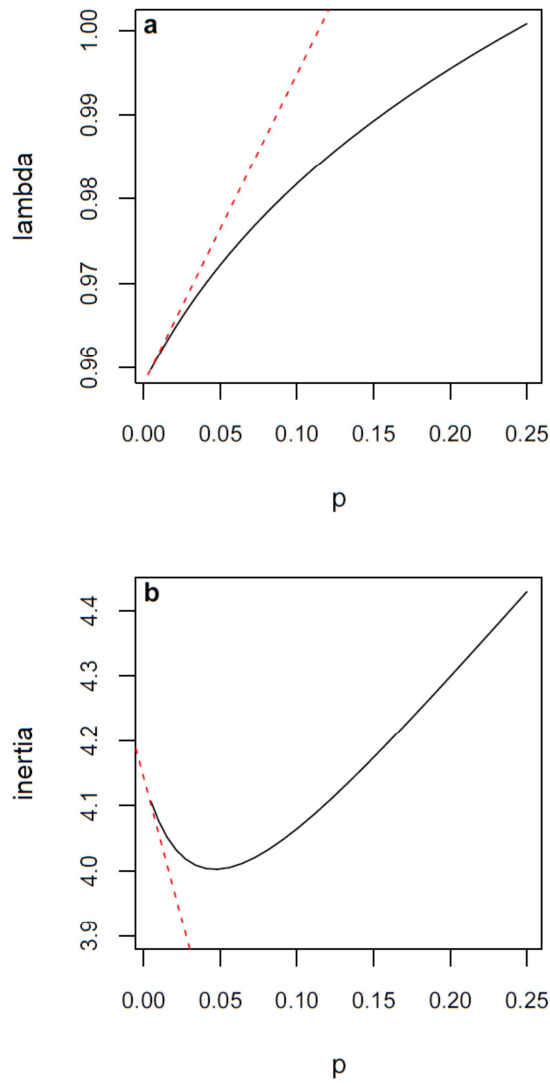
FIG. 4.3: Transfer functions generated by the `tfa` and `inertia.tfa` functions (Appendix 4.1). Perturbation affects element [8,7] of the desert tortoise population projection matrix. Sensitivity slopes are added to the plots in red. **(a)** Transfer function of asymptotic growth generated using `tfa`, showing the how perturbation magnitude (p) affects asymptotic population growth (lambda). **(b)** Transfer function of population inertia generated using `inertia.tfa`, showing how perturbation magnitude (p) affects population inertia.
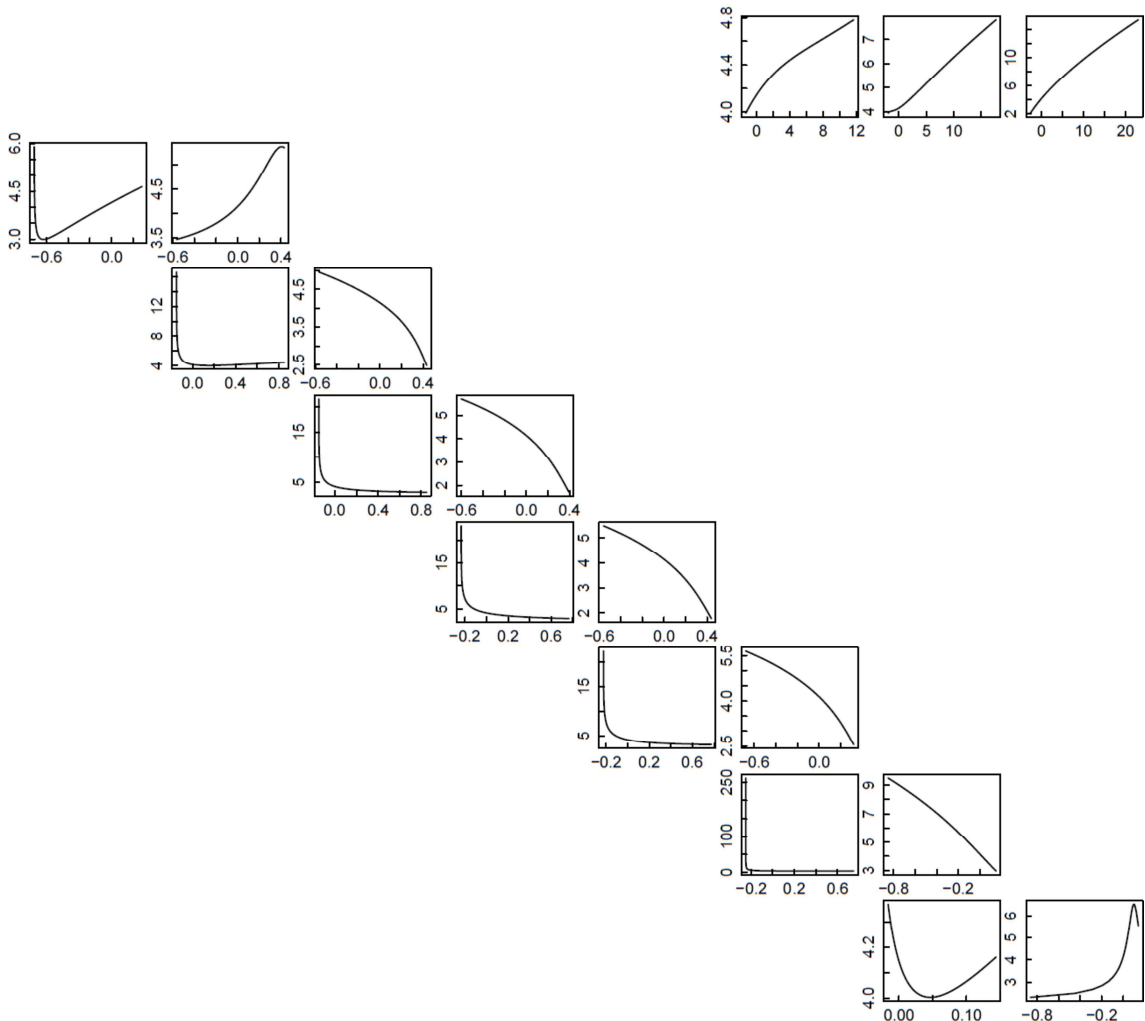
FIG. 4.4: A multiplot of transfer functions for inertia of the desert tortoise population projection matrix, generated using the `inertia.tfamatrix` function (Appendix 4.1). Perturbation magnitude is on the x axis, inertia is on the y axis. The layout of the multiplot corresponds with the layout of the PPM. Similar plots can be generated for the transfer function of asymptotic growth using the function `tfamatrix`.

CHAPTER 5

— — — — — — — — — — — — — —

Having synthesised and developed methods for the analysis of transient dynamics, and written code for their implementation, we wished to use these to answer interesting ecological and evolutionary questions. To do this, we exploit a large database of PPM models for plant species. Chapter 5 is the first paper published as part of this thesis, and is (to our knowledge) the first large-scale comparative analysis of transient population dynamics ever done. With transient theory in its infancy, the importance of transient dynamics in ecological systems is poorly understood. In this chapter we explore patterns in the potential range of transient dynamics that may be exhibited by populations. We seek patterns according to life form, and phylogenetic relatedness. Alongside this, we test the effect of model parameters on indices of transient dynamics. Because this was the first study published, the methods used are perhaps somewhat different to what we might choose now: we make use of the Kreiss bound rather than population inertia, and would perhaps choose differently from the more diverse range of methods for comparative study. However, the tools available to us at the time enabled us to uncover some interesting results.

Chapter 5:

Stott, I., Franco, M., Carslake, D., Townley, S. & Hodgson, D.J. (2010) Boom or bust? A comparative analysis of transient population dynamics in plants. *Journal of Ecology*, **98**, 302-311. doi: 10.1111/j.1365-2745.2009.01632.x

BOOM OR BUST? A COMPARATIVE ANALYSIS OF TRANSIENT POPULATION DYNAMICS IN PLANTS

ABSTRACT

1. Population dynamics often defy predictions based on empirical models, and explanations for noisy dynamics have ranged from deterministic chaos to environmental stochasticity. Transient (short-term) dynamics following disturbance or perturbation have recently gained empirical attention from researchers as further possible effectors of complicated dynamics.

2. Previously published methods of transient analysis have tended to require knowledge of initial population structure. However, this has been overcome by the recent development of the parametric Kreiss bound (which describes how large a population must become before reaching its maximum possible transient amplification following a disturbance) and the extension of this and other transient indices to simultaneously describe both amplified and attenuated transient dynamics.

3. We apply the Kreiss bound and other transient indices to a data base of matrix models from 108 plant species, in an attempt to detect ecological and mathematical patterns in the transient dynamical properties of plant populations.

4. We describe how life history influences the transient dynamics of plant populations: species at opposite ends of the scale of ecological succession have the highest potential for transient amplification and attenuation, whereas species with intermediate life history complexity have the lowest potential.

5. We find ecological relationships between transients and asymptotic dynamics: faster-growing populations tend to have greater potential magnitudes of transient amplification and attenuation, which could suggest that short- and long-term dynamics are similarly influenced by demographic parameters or vital rates.

6. We describe a strong dependence of transient amplification and attenuation on matrix dimension: perhaps signifying a potentially worrying artefact of basic model parameterization.

7. *Synthesis*. Transient indices describe how big or how small plant populations can get, en route to long-term stable rates of increase or decline. The patterns we found in the potential for transient dynamics, across many species of plants, suggest a combination of ecological and modelling strategy influences. This better understanding of transients should guide the formulation of management and conservation strategies for all plant populations that suffer disturbances away from stable equilibria.

INTRODUCTION

The dynamics of natural systems are highly complex and as such often prove difficult to predict. Yet, it is in the interest of ecologists to be able to predict the natural dynamics of ecological systems. Populations have received perhaps the most attention in the ecological modelling literature, with population projection matrices (PPMs) emerging as a prevailing modelling tool. This is hardly surprising, considering their wide application in pest control (Smith & Trout 1994; Shea & Kelly 1998; Hastings, Hall & Taylor 2006; Dudas, Dower & Anholt 2007), harvesting (Cropper & DiResta 1999; Souza & Martins 2006) and conservation (Price & Kelly 1994; Esparza-Olguín, Valverde & Vilchis-Anaya 2002; Linares *et al.* 2007), and although there is an increasing interest in habitat- and ecosystem-level practice (Harding *et al.* 2001), the population still remains a popular target for management. Often population dynamics defy simple model predictions, and current explanations for fluctuations in dynamics of populations range from deterministic chaos (Hastings *et al.* 1993) to environmental stochasticity (Dennis & Costantino 1988) and various combinations of these (Dennis *et al.* 1997, 2001; Bjørnstad & Grenfell 2001).

Transient dynamics have recently emerged as a further explanation for unpredictable population behaviour (Hastings 2001). Typically, ecological systems are not at equilibrium, and disturbances are integral to ecosystem function (Wallington, Hobbs & Moore 2005). As such, populations may be subject to frequent exogenous disturbances to stage structure (Koons *et al.* 2005; Townley *et al.* 2007; Townley & Hodgson 2008), such as weather events, disease, human impacts, invasive species or migration. Following a disturbance, short-term transient dynamics often prove to be radically different from long-term trajectories (Caswell 2007). Thus, in reality, population dynamics are likely to be dominated by transient responses to exogenous disturbances (Townley *et al.* 2007) – deterministic reactions to largely stochastic events. Additional complications arise because studies of plant demography usually last only a few years (Jongejans *et al.* 2010), and short-term goals are often the norm in management strategies (Hastings 2004).

With only a relatively recent interest in transients and their quantification, PPM models have commonly undergone asymptotic analyses (but see Hastings 2004; Koons *et al.* 2005; Townley *et al.* 2007; Townley & Hodgson 2008; Maron, Horvitz & Williams 2010) – eigendata of matrices, used to describe such long-term trends, have proven analytically tractable and conceptually simple (Caswell 2001). Studies have considered the asymptotic responses of plant populations to disturbances such as fire (Hoffmann 1999), grazing (O'Connor 1993) and hurricanes (Batista, Platt & Macchiavelli 1998). In addition to this, there are established means of analysing the contributions of demographic parameters to long-term growth rates in the forms of sensitivity and elasticity analyses (Caswell 2001) and, more recently, transfer function analysis (Hodgson & Townley 2004). Many studies have utilized such analyses, with results often advocated for use in informing policy and management of species (e.g. Fiedler

1987; Menges 1990; Nault & Gagnon 1993). Larger comparative analyses have found general patterns according to life history (Silvertown *et al.* 1993; Franco & Silvertown 2004; Burns *et al.*2010). But, if transients do dominate ecological systems, then policy, management and conservation decisions based on asymptotic analyses may be severely limited, risking the waste of resources on suboptimal population management strategies. Indeed, in plants, there is evidence that long-term (asymptotic) trends in population models can provide very poor predictions of the true long-term behaviour of populations over time (Bierzychudek 1999).

Transients and their sensitivities, however, have proven to be difficult to quantify. Published methods of transient analysis have often either lacked applicability to every PPM model (Neubert & Caswell 1997) have needed large amounts of demographic information (Fox & Gurevitch 2000) or have required intensive computation (Yearsley 2004; Caswell 2007). The largest drawback of published methods of transient analysis is that none have truly managed to divorce the need for knowledge of initial population structure – something that asymptotic analysis benefits hugely from. Population ecologists have hence been ill-equipped to utilize transient analysis to inform management and conservation strategies. Thus, although now gaining greater attention in the literature (e.g. Drake 2005; Koons *et al.*2005), transients have yet to gain wide popularity in practice.

However, Townley & Hodgson (2008) recently developed a computationally simple new set of indices that builds in part on the work of Neubert & Caswell (1997), aimed at providing a means of calculating best- and worst-case scenarios following disturbance. These included the Kreiss bound, a flexible parametric index that may be calculated independently of initial population structure. They also extended transient measurements to include both population amplification (transient increase in population size or density) and attenuation (transient decrease in population size or density) following disturbance events. It is these indices that we employ in this study. We have chosen not to analyse other established indices of transient population size or density, such as population momentum and inertia (the long-term population amplification following perturbations to demographic rates; see Koons, Holmes & Grand 2007). These differ from our indices primarily in that they measure responses to specified disturbances or perturbations – here, we focus instead on indices of maximal transient amplification and attenuation as measures of the overall transient dynamical properties of populations.

This article reports the first large-scale analysis of global patterns in transient dynamical properties of populations. We scrutinize a data base of models for 108 plant species with the aim of detecting deterministic biological and mathematical signals in patterns of transient dynamics. With relevance to plant ecology, we describe how life history influences the transient dynamical properties of populations. Our results also indicate relationships between magnitudes of transient departure from long-term growth and long-term growth itself, perhaps suggesting that short- and long-term dynamics are similarly influenced by the vital rates (e.g. survival,

growth, fecundity) of members of populations. In an attempt to further inform the building of more predictive models and reliable analyses, we describe dependence of transients on matrix dimension and explore the influence of matrix structure on transients.

MATERIALS AND METHODS

DATA BASE

Population projection matrices were collected from the literature, with the current data base of plant PPMs at the time of analysis numbering 500 matrices for 113 plant species of 11 different Subclasses and 52 Families. The taxonomy for each species was found using Tudge (2000) for the taxonomic level of Order and above and Systema Naturae 2000 (Brands 1989–2005) for taxonomic levels below Order.

One matrix was chosen for each species for use in analyses. This 'species reference matrix' was, where possible, an average of a number of subpopulation matrices of spatial and/or temporal replication. Where it was not biologically justifiable to take an average, the selected species reference matrix was chosen as the matrix for the (sub)population subject to conditions that most closely resembled the species' ecological 'norm' (e.g. before, rather than after, hurricane disturbance). Matrices with redundant seed stages (the 'seeds' problem, highlighted in Caswell 2001, pp. 60–62) were corrected in the appropriate manner.

Each matrix was tested for reducibility using the argument that a square matrix $\mathbf{A}$ is irreducible if, and only if, $(\mathbf{I} + \mathbf{A})^{s-1}$ is positive (i.e. every element of the new matrix is greater than zero), where $\mathbf{I}$ is the identity matrix of same dimension as $\mathbf{A}$, and s represents the dimension (number of columns or rows) in the matrix (Caswell 2001). Reducible matrices were not used in analyses because they often represent biologically implausible life cycles and defy asymptotic analysis. One hundred and eight species reference matrices remained after reducible matrices were removed (see Appendix 7 for a full list).

INDICES OF TRANSIENT DYNAMICS

The indices of transient dynamics used were measures described by Townley & Hodgson (2008). The method of calculation uses theoretical stage-biased disturbances to initial population structure (i.e. with all individuals in a single stage class and a density of 1), thus modelling extreme transient dynamics of populations in response to such disturbances. We studied transient amplification and attenuation of each population relative to the long-term growth or decline predicted by the dominant eigenvalue of its PPM. This avoided the problem of there not being any upper bounds on the transient growth of an asymptotically growing population, or any lower bounds on the transient attenuation of an asymptotically declining population. Hence, all our transient indices describe how much bigger or smaller a population

could get, relative to how big it would be if it started out at stable stage structure. This is equivalent to measuring the dynamics of a geometrically weighted population $\lambda^{-t}N_{(t)}$, where $N_{(t)}$ is the population size or density at time t. In practice, we did this by measuring transient indices, not of the PPM **A** itself, but of the 'standardized' PPM **Â** (equal to **A** divided by its dominant eigenvalue λ). This standardized λ of all **Â** to be 1, allowing direct comparison of both amplified and attenuated dynamics across all populations (Fig. 5.1). This particular method also has the advantage of removing the effect of the dominant eigenvalue on the indices that we measure, allowing us to infer relationships between those indices and the asymptotic growth rate of the population as predicted by the PPM **A**.

Six indices were calculated for each PPM, with three indices describing amplified dynamics and three analogous indices describing attenuated dynamics. Figure 5.1 illustrates the indices graphically with respect to the matrix projections. Table 5.1 provides formulae for calculation and biological interpretations of each index. In brief, our amplification indices are *reactivity* (the largest possible population density achieved in one timestep after disturbance), *maximum amplification* (the largest possible population density achieved in any timestep after disturbance) and the *upper Kreiss bound* (an analytical lower bound for maximum amplification). These are partnered by indices of attenuation, which are *first-timestep attenuation*, *maximum attenuation* and the *lower Kreiss bound*, respectively. Code to calculate the 6 indices is available in the R package `popdemo`. Table 5.2 is a correlation matrix of the indices, which shows that by nature, these indices are interrelated. To account for this non-independence, we conducted a principal components analysis (PCA) on the six indices.

PRINCIPAL COMPONENTS ANALYSIS

Principal components analysis distils variation in a large number of correlated (i.e. non-independent) variables into just one or two uncorrelated measurements, called principal components. In our case, this means that the variation held in the six indices of transient dynamics can potentially be described instead by just one or two measurements, thus simplifying the analytical process and reducing the probability of type I statistical errors by accounting for the high correlates between indices.

The PCA was conducted on $\log_{10}$-transformed indices, as this describes more accurately the multiplicative nature of these transient dynamics. Hence, amplified transients become positive, whereas attenuated transients become negative. Detailed results for the PCA are presented in Appendix 5.1. These results suggest that more than 90% of the variance can be accounted for by principal components 1 and 2. Each index has an associated 'loading', which is the coefficient associated with that index in the principal component's linear function. In our case, for principal component 1 (PC1), amplified transients have a positive loading and attenuated transients have a negative loading. For principal component 2 (PC2), both amplified and attenuated transients have a positive loading. This means that PC1 describes the overall

tendency of the population to produce transients of large magnitude (i.e. a large PC1 corresponds to a population with both amplified and attenuated transients of large magnitude, and a small PC1 corresponds to a population with both amplified and attenuated dynamics of small magnitude). PC2 describes the tendency of the population to be biased towards either relatively larger amplified dynamics or relatively larger attenuated dynamics (i.e. a large PC2 corresponds to a population with amplified dynamics that are large relative to its attenuated dynamics, and a small PC2 corresponds to a population with attenuated dynamics that are large relative to its amplified dynamics).

STATISTICAL MODELS

To find ecological and model parameterization patterns in the observed variation in transient dynamics, we regressed PC1 and PC2 against four different explanatory variables using general linear modelling. The *life history* of a plant is a categorical variable equivalent to those described in Franco & Silvertown (2004): monocarpic (semelparous) plants from open and/or disturbed habitats, perennial (iteroparous) herbs from open and/or disturbed habitats, perennial herbs from forest habitats, shrubs and trees. The long-term (asymptotic) intrinsic population growth rate r is equal to $\ln(\lambda)$, where λ is the dominant eigenvalue of PPM **A.** The *dimension* of the matrix is equal to the number of matrix columns or rows, and is equivalent to the number of stage-classes in the life cycle model. Last, the *matrix type* is distinguished by the position of non-zero data in the matrix and represents a qualitative description of the complexity of the demographic model. Our descriptions are consistent with Carslake, Townley & Hodgson (2009b). *Leslie+* matrices are traditional Leslie matrices (Leslie 1945) incorporating growth and fecundity but also allowing for stasis of the last stage class, therefore containing positive data in the first row, the first subdiagonal and the last entry. These are usually age-structured models, in which 'old' individuals are grouped into a single stage class whose members die at a fixed rate per projection interval. *Progression* matrices are like Leslie+ matrices, but additionally incorporate stasis of all stage classes (individuals can remain within a stage-class between projection intervals; e.g. where stages are determined by the size of the individual) and therefore contain data in the first row, the first subdiagonal and the diagonal. *Growth* matrices are like progression matrices, but allow for skipped stage classes and therefore may include additional data anywhere in the lower triangle of the matrix. *Lefkovitch* matrices (after Lefkovitch 1965) represent a generalized, stage-structured life cycle which can contain data anywhere in the matrix, including regression through the life cycle: individuals can, e.g. get smaller, undergo fission or produce smaller vegetative offspring.

Statistical models considered the effects of all explanatory variables simultaneously on a single principal component, although interactions between explanatory variables were not considered. We used general linear models with Gaussian error structure, identity link function and stepwise model simplification from the maximal model, in order of least significance,

using F-test analysis of deviance model comparisons and a significance threshold of $p = 0.05$, until a minimal adequate model was achieved (i.e. one where only significant effects remain). One clear outlier was removed in all analyses that involved r as an explanatory variable (*Digitalis purpurea*, $\lambda = 11.8$; $r = 2.5$). All minimal adequate models were checked for normality of standardized residuals and homoscedasticity.

All analyses were conducted in a TIPS framework, where every species is treated as an independent data point (Silvertown & Dodd 1996; the name of the analysis refers to using the data from the 'tips' of the phylogenetic tree). However, previous statistical analyses that were conducted on the raw transient indices employed both TIPS and phylogenetically independent contrasts (PICs), where the degree of relatedness between species is controlled for (Felsenstein 1985; Freckleton 2000). Each included matrix dimension as a covariate (cf. Salguero-Gómez & Casper 2010). The results from PIC analyses corroborated those of TIPS analyses, although they are not presented here. Phylogeny was obtained using Phylomatic, using taxonomic groups recognized by the Angiosperm Phylogeny Group (2003).

All mathematical and statistical modelling was performed using R version 2.8.0 (R Development Core Team 2008).

RESULTS

EFFECTS OF LIFE HISTORY

Plants with different life histories exhibit different potential magnitudes of transient amplification and attenuation. Analyses showed there to be a significant relationship between life history and PC1 ($F_{4,100} = 3.6$, $p = 0.009$; Fig. 5.2), however, there was no significant relationship between life history and PC2 ($F_{4,100} = 0.5$, $p = 0.72$). Monocarpic plants and trees are probably to exhibit both amplified and attenuated transients of greater magnitude than perennial, iteroparous herbs from open habitats and shrubs, which in turn are probably to exhibit amplified and attenuated transients of greater magnitude than perennial, iteroparous herbs from forest habitats. There is no bias towards either relatively larger amplification or relatively larger attenuation. Statistically, life histories can be grouped as indicated in Fig. 5.2 with perennials (both open and forest) and shrubs having similar transients, being lower in magnitude than those of monocarps. Trees can be grouped with either monocarps or perennials and shrubs, having transients of a lower magnitude than monocarps but of a higher magnitude than perennials and shrubs.

RELATIONSHIPS BETWEEN TRANSIENTS AND ASYMPTOTIC GROWTH

Populations that grow faster in the long term show both amplified and attenuated transients of a greater magnitude than those that are slower-growing or declining (significant positive

relationship between r and PC1; $F_{1,100} = 4.2$, $p = 0.042$; Fig. 5.3), with no bias towards either relatively larger amplification or relatively larger attenuation (no significant relationship between r and PC2; $F_{1,99} = 0.04$, $p = 0.83$).

INFLUENCE OF MATRIX STRUCTURE

Matrices with a greater dimension are probably to exhibit both amplified and attenuated transients of a greater magnitude than matrices with a smaller dimension (significant positive relationship between matrix dimension and PC1; $F_{1,100} = 36.2$, $p < 0.001$; Fig. 5.4), with no bias towards either relatively larger amplification or relatively larger attenuation (no significant effect of dimension on PC2; $F_{1,104} = 0.3$, $p = 0.60$).

Matrix type was not influential in determining the transient dynamical properties of the PPM models: it had no significant effect on PC1 ($F_{1,99} = 0.52$, $p = 0.47$) or PC2 ($F_{1,105} = 2.1$, $p = 0.15$).

DISCUSSION

RELATIONSHIPS BETWEEN TRANSIENTS AND LIFE HISTORY

Analyses showed there to be a U-shaped relationship between life-history strategy, defined along a continuum of ecological succession, and the magnitude of both amplified and attenuated transient dynamics. Monocarpic plants (a grouping of annuals and monocarpic perennials) and trees, representing opposite ends of a scale of ecological succession, generally have amplified and attenuated transients of greater magnitude than shrubs and iteroparous perennials. This is an intriguing observation – the expected relationship might be one of monotonic decline with increasing life history complexity, at least for amplified dynamics: several studies have shown that annuals and species of early succession have greater reproductive allocation than perennials and species of later succession (Gleeson & Tilman 1990; Aarssen & Taylor 1992; Silvertown & Dodd 1996; Fenner 2000).

Selective environmental pressures acting on life-history trade-offs may account for our findings. Early-successional species inhabiting open habitats will benefit from a quick pre-emption of abundant resources. For trees, gaps in the forest are ephemeral and may be filled by a few individuals at most. In both situations, under models of 'lottery' recruitment, where successful establishment of juveniles is random and indiscriminate (Chesson & Warner 1981; Chesson 1991; Turnbull, Crawley & Rees 2000), producing many viable offspring may give the best chance of successful colonization (which increases the potential for transient amplification). Due to subsequent space constraints and/or competition for resources, juvenile mortality would be high (which increases the potential for transient attenuation). This would account for the boom-and-bust transient properties exhibited by these life histories. Perennials

104

in forest habitats, in contrast, experience a relatively constant environment, where colonization opportunities are more predictable. Therefore, whilst still experiencing space and resource constraints once established, they might be less exposed to the pressure of 'lottery' colonization. Thus, their best strategy may be to weigh the costs of (unnecessary) reproduction against the benefits of survival and vice versa, resulting in decreased fecundity and increased juvenile survival (and therefore more stable transient properties as a result). There is ample evidence for trade-offs such as these in plants (Mitchell-Olds 1996a,b; Ehrlén & van Groenendael 1998 and citations therein). It is worth bearing timescale in mind when considering this: tree populations are slow-growing, and their 'transient state' will therefore probably last far longer than that of an annual. Transient dynamics can be just as extreme for both, but over entirely different timescales.

The discrepancy between our findings and results for reproductive allocation theory (Silvertown & Dodd 1996) perhaps reflect the differences between studying individual demographic traits and demographics (the size, structure and dynamics of populations) *per se*. The number of offspring produced is a product not only of reproductive allocation, but of many vital rates. For example, trees may allocate comparatively less resources to reproduction than annuals, but given increased pollination success, greater number of seeds produced or greater seed set, a tree may produce as many individual offspring in a single year, and hence have the capacity to exhibit the same magnitude of transient amplification. Indeed, seed size (and therefore number) is not necessarily proportional to individual size across species, and shows great variation across taxa and life histories (Moles *et al.* 2005). In addition, measures of reproductive allocation do not account for adult survival: increased adult survival in trees will probably contribute to greater population amplification.

Further analysis of how life history and transient dynamics are related is needed. Sensitivity, elasticity and/or transfer function analyses of transient indices would inform on whether, as for asymptotic elasticity (Silvertown *et al.* 1993; Silvertown, Franco & Menges 1996; Franco & Silvertown 2004), specific life histories show individual patterns in their responses to perturbation. Such results would equip population managers with the information on the ability of populations of certain species to amplify and/or attenuate.

RELATIONSHIPS BETWEEN TRANSIENTS AND LONG-TERM DYNAMICS

Populations with rapid asymptotic growth (greater *r*) are likely to harbour the potential for greater magnitudes of both transient amplification and attenuation.

For transient amplification, this relationship is relatively intuitive: vital rates such as survival and fecundity that contribute to long-term population growth also contribute greatly to transient amplification. However, the relationship with transient attenuation is less intuitive, since attenuation is associated with low sub-adult survival, and low or zero fecundity. Again, given trade-offs in allocation of resources to survival and reproduction, a plant that has high

adult survival (hence increasing asymptotic growth rates and the potential for transient amplification) may invest less in sub-adult survival (hence simultaneously increasing the potential for transient attenuation). Our discovery of positive relationships between long-term rates of growth and the magnitude of short-term population amplification and attenuation may suggest that all of these are similarly influenced by vital rates of members of the population, which in turn will be determined by evolutionary history or environmental resources and stressors. We explore this possibility by relating our results to reported patterns in both asymptotic and transient sensitivities and elasticities.

The popularity of asymptotic analyses is accompanied by an abundance of literature on sensitivities of long-term population dynamics to vital rates of plants. Comparative studies utilizing empirical models have explored patterns in elasticity of asymptotic growth to both compound transition rate elasticities (Silvertown *et al.* 1993; Silvertown, Franco & Menges 1996; Crone 2001) and vital rate elasticities (Franco & Silvertown 2004; Burns *et al.* 2010). Simulation studies have also explored relationships between elasticities of matrix elements (Carslake, Townley & Hodgson 2009b). In the vast majority of these cases, it has been reported that elasticity of asymptotic growth to survival is greater than elasticity to fecundity. As outlined earlier, we might intuitively expect transient amplification to respond to adult survival (as well as fecundity), but attenuation to respond to sub-adult survival.

Despite the wealth of studies of sensitivities of asymptotic growth rates to vital rates, there is a dearth of similar studies for the sensitivity of transient dynamics to recruitment, survival and growth in plants. Perhaps, the only investigation into patterns of sensitivity in transient dynamics was made by Koons *et al.* (2005). They considered three bird and three mammal species at various points on the fast–slow life-history continuum. They found that for populations close to stable stage structure, transient sensitivities showed a greater dependence on sub-adult survival than on fecundity (which is similar to results for asymptotic elasticity in mammals and birds – see Heppell, Caswell & Crowder 2000 and Sæther & Bakke 2000). Conversely, for populations disturbed away from stable stage structure, transient sensitivities showed a greater dependence on fecundity and adult survival than on sub-adult survival. Our indices utilize initial structures that represent significant departures from stable structure, and as such they would be more likely to exhibit this second pattern. This agrees with expectations as outlined above for amplified dynamics, but not with expectations for attenuated dynamics. It is noteworthy that Koons *et al.*'s results are not directly comparable with those described for asymptotic dynamics as one is a measure of sensitivity and the other is a measure of elasticity (for formal definitions see Caswell 2001). However, it appears that, for animals at least, transient sensitivities do not conform to the neat, global patterns of asymptotics and are far more attuned to variation in initial conditions.

It is difficult to infer how vital rates may determine the transient dynamics of plant populations using studies of asymptotic dynamics in plant populations or transient dynamics in

animal populations. However, patterns of transient sensitivity in plants could be complex, and amplified and attenuated dynamics might show differing responses to variation in vital rates. A study explicitly concerning transient sensitivity, elasticity and/or transfer function analyses in plants needs to be performed to infer these relationships. For now, we are left with the intriguing observation that plant populations predicted to grow faster in the long term tend to exhibit the potential for larger magnitudes of transient amplification and attenuation than (asymptotically) slower-growing or declining populations.

EFFECTS OF MATRIX STRUCTURE ON TRANSIENT INDICES

Both amplified and attenuated dynamics increase in magnitude with increasing matrix dimension.

One explanation for this is that it is an artefact of model design. A larger matrix (i.e. one with a larger number of stages in the life cycle model) will house comparatively more demographic transition rates and hence will capture peak rates of fecundity and mortality more efficiently. A small (low-dimension) matrix used to describe the same life cycle will effectively average out variation in fecundity and mortality rates, so that peak rates of a small matrix will always be of lesser magnitude than those of a large matrix for the same population. This 'averaging effect' is a parsimonious explanation for an increase in transient magnitude with increasing matrix dimension, since maximum (and minimum) column sums of a larger matrix are likely to be larger (and smaller) than for an averaged, smaller matrix. This is an important consideration, because it highlights that populations may amplify or attenuate beyond bounds predicted by simplified models.

However, if the number of stages chosen is a true reflection of the life cycle, then this should not be the case – modelled transient dynamics would be indicative of the true transient dynamical properties of the population. An organism with greater stage specificity (i.e. greater heterogeneity in demographic rates across the life cycle) will require a life cycle model with more stages (and hence a larger projection matrix) to capture that heterogeneity. In this case, our finding that magnitudes of transient dynamics increase with increasing matrix dimension would indicate that organisms with greater stage specificity exhibit more extreme transient dynamics.

As a comparative study, ours does not control for stage specificity and as such we cannot reliably distinguish between these two explanations. However, a recent study by Tenhumberg, Tyre & Rebarber (2009) provides some support for the former. They collected demographic data from the pea aphid, *Acyrthosiphon pisum*, and used it to create matrices of differing dimension. They then compared model predictions from these matrices to empirical dynamics of laboratory populations. They found that larger matrices modelled greater transient growth rates and captured observed transient growth rates more effectively than smaller matrices. This further supports our hypothesis that magnitudes of transient dynamics increase with increasing matrix dimension.

Approaches to parameterizing matrix models are often based upon data availability (Vandermeer 1978; Moloney 1986) or are taxon-specific (e.g. Noon & Sauer 1992), whilst reviews of methods for modelling complex factors such as environmental stochasticity (Fieberg & Ellner 2001) or spatial heterogeneity (Day & Possingham 1995) reveal a diversity of approaches. Matrix dimension is known to have a significant effect on the elasticities of matrix elements (Enright, Franco & Silvertown 1995). However, its effect on population size, density or growth rate has not often been studied (but see de Matos & Silva Matos 1998; Lamar & McGraw 2005; Ramula & Lehtilä 2005; Tenhumberg, Tyre & Rebarber 2009) and is less often controlled for in demographic analyses. Our results indicate that it could have consequences for these measures and hence for management strategies based upon them. Perhaps there is a need for more stringent rules in matrix parameterization to assure that models are predictive and comparative. Enright, Franco & Silvertown (1995) suggested that matrix dimension should either be a function of longevity or equal for different models that require comparison (see also Salguero-Gómez & Casper 2010 for homogenizing matrix dimension across models). Our results indicate that either solution could have an effect on transient dynamics depending on the population under study. We also note that the discretization of infinite-dimensional integral projection matrices (see Ellner & Rees 2006), for numerical analysis, should consider the impacts of dimensionality not just on asymptotic predictions, but also on the transient properties of the discretized model.

Matrix type did not show a significant relationship with transient magnitude and so appears to have no effect on the transient dynamics of the model. This may be because real-world populations do not conform rigidly to the definite boundaries of classification used to describe empirical models. For example, inclusion of just one extra stasis parameter in a Leslie+ matrix changes it into a growth matrix. However, this single parameter is unlikely to have huge effects on the model output. Whilst it is a good idea to incorporate possible model effects in analyses, perhaps a more robust definition of matrix 'type' is required.

CONCLUSIONS

The indices of transient dynamics that we employ here should prove to be useful in many scenarios. In the fields of *in situ* conservation and pest control, measures such as reactivity and first-timestep attenuation would allow demographers to calculate 'best-case' and 'worst-case' scenarios, so establishing the ability of disturbance to cause population booms and crashes in the very near term, and enabling attempts to design 'quick fixes' to buffer against population disturbances. In the contrasting fields of *ex situ* population management (including species reintroduction) and harvesting, indices such as maximum amplification and attenuation may enable demographers to utilize population disturbance to their advantage and enable population managers to maximize population size and viability without compromising costs or harvest

rates. In fundamental research, these indices (and in particular, the Kreiss bounds) are useful in comparative analyses as measures of the overall transient dynamical properties of a population or species. Primarily, however, all of these indices would be of use to anyone who does not have knowledge of initial population structure. Where information on population structure is available, other methods may prove more pertinent. For example, the measures of transient growth employed in Maron, Horvitz & Williams (2010) may be more useful to demographers who have information on current population structure and are interested in population growth rate rather than size (e.g. to identify whether a population is currently undergoing short-term decline or increase). Population momentum and inertia (Koons, Holmes & Grand 2007) may be more useful to demographers who are interested in population size or density but have information on current population structure. In research, measuring transient growth rates or population inertia and/or momentum would be more useful when comparing within, rather than between, species or populations exposed to differing conditions, e.g. as a measure of fitness.

Our results have shown that there are strong correlations between the Kreiss bounds and immediate and maximum measures of population amplification and attenuation. The relationships of these indices with one another, and with other indices of transient dynamics such as population momentum and inertia, warrant further exploration. In addition, we have uncovered several patterns in the transient dynamical properties of populations. First, life history and transient dynamical properties of populations are related. Second, transient and long-term dynamics are positively correlated. To shed more light on both of these findings, a study that looks at the sensitivity of transients to changes in transition rates would be ideal. Last, transient dynamics are sensitive to matrix dimension with consequences for management strategies based upon such models. It is debateable whether this is an artefact of the model or because of larger matrices modelling organisms with greater stage specificity and life cycle complexity. In either case, matrix dimension ought to be controlled for in any transient analysis of population dynamics. Transient analysis is likely to see increased popularity in the near future – these results and further studies of transient population dynamics should aid population managers and conservationists working with wild plant populations.

TABLES

TABLE 5.1: The transient indices used in analyses, accompanied by formulae for calculation, and biological descriptions. After Townley & Hodgson (2008). See also Fig. 5.1. *minCS*, minimum column sum of the matrix. Note that r used in Kreiss bound calculations is different from r used to describe intrinsic population growth rate.

DESCRIPTION	INDICES	BIOLOGICAL MEANING (AMPLIFICATION/ ATTENUATION)	STRENGTHS/ WEAKNESSES	ADDITIONAL INFORMATION
Immediate (first-timestep) transient index	**REACTIVITY** $$reactivity = \|\widehat{\mathbf{A}}\|_1$$ **FIRST-TIMESTEP ATTENUATION** $$first\ timestep$$ $$attenuation = minCS(\widehat{\mathbf{A}})$$	The largest/smallest possible density (relative to asymptotic dynamics) that may be reached by the population in the first projection interval.	Simple; amenable to perturbation analysis / Does not always capture largest transient.	$\|\widehat{A}\|_1 \leq \overline{\rho}_{max}$ $minCS(\widehat{\mathbf{A}}) \geq \underline{\rho}_{min}$
Kreiss bound	**UPPER KREISS BOUND** $$\overline{K}_\lambda^* = \max_{r>1}\left\{(r-1)\|(r\mathbf{I}-\widehat{\mathbf{A}})^{-1}\|_1\right\}$$ **LOWER KREISS BOUND** $$\underline{K}_\lambda^* = \min_{r>1}\left\{(r-1)minCS(r\mathbf{I}-\widehat{\mathbf{A}})^{-1}\right\}$$	The density a population must amplify/ attenuate to (relative to asymptotic dynamics) before reaching its maximum/minimum overall size; therefore inner bounds on transient amplification/attenuation.	Amenable to perturbation analysis; captures largest transient more effectively / Inner rather than outer bound on transient magnitude.	$\overline{K}_\lambda^* < \overline{\rho}_{max}$ $\underline{K}_\lambda^* > \underline{\rho}_{min}$

Maximum transient index	**MAXIMUM AMPLIFICATION** $$\bar{\rho}_{max} = \max_{t \geq 0}\left\{\left\|\widehat{\mathbf{A}}^t\right\|_1\right\}$$ **MAXIMUM ATTENUATION** $$\underline{\rho}_{min} = \min_{t \geq 0}\left\{minCS(\widehat{\mathbf{A}}^t)\right\}$$	The largest/smallest density (relative to asymptotic dynamics) that may be reached by the population overall.	Captures outer bound, maximum transient / Not amenable to perturbation analysis.	May or may not result from the same stage-bias as $\left\|\widehat{\mathbf{A}}\right\|_1$ / $minCS(\widehat{\mathbf{A}})$

TABLE 5.2: Spearman's rank correlation matrix for the $\log_{10}$-transformed transient indices used in analyses. Values reported are Spearman's ρ values. All $p < 0.001$.

	$\overline{\rho}_{max}$	$\overline{K}^*_\lambda$	$\|\hat{\mathbf{A}}\|_1$	$\underline{\rho}_{min}$	$\underline{K}^*_\lambda$
$\overline{K}^*_\lambda$	0.99				
$\|\hat{\mathbf{A}}\|_1$	0.97	0.96			
$\underline{\rho}_{min}$	-0.66	-0.65	-0.65		
$\underline{K}^*_\lambda$	-0.48	-0.49	-0.46	0.92	
$minCS(\hat{\mathbf{A}})$	-0.44	-0.41	-0.56	0.70	0.55

FIGURES
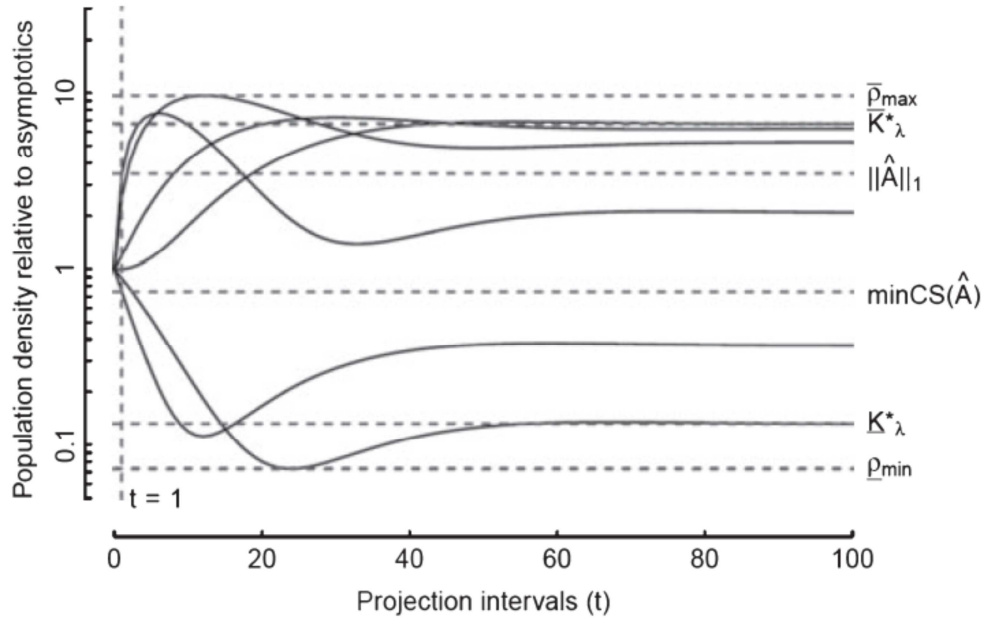
FIG. 5.1: Graphical representation of the indices of transient dynamics used in analyses. Each solid line represents a single stage-biased projection (of the standardized matrix) initiated with a total density of one (i.e. each projection starts with all individuals clustered in a single stage class: a population initiated at stable stage distribution would follow a flat line at $y = 1$). Therefore, in this example from a six-stage PPM, there are six projections. The vertical axis is on a logarithmic scale to illustrate the multiplicative nature of the measurements. Note that maximum amplification $\overline{\rho}_{max}$ and reactivity $\|\hat{\mathbf{A}}\|_1$ may or may not result from the same initial stage structure, which is also true for first-timestep attenuation $minCS(\hat{\mathbf{A}})$ and maximum attenuation $\underline{\rho}_{min}$. $\overline{K}^*_\lambda < \overline{\rho}_{max}$ and $\underline{K}^*_\lambda > \underline{\rho}_{min}$. $\|\hat{\mathbf{A}}\|_1 \leq \overline{\rho}_{max}$ and $minCS(\hat{\mathbf{A}}) \geq \underline{\rho}_{min}$. Example PPM used for projection is for the palm *Iriartea deltoidea* (Pinard 1993).
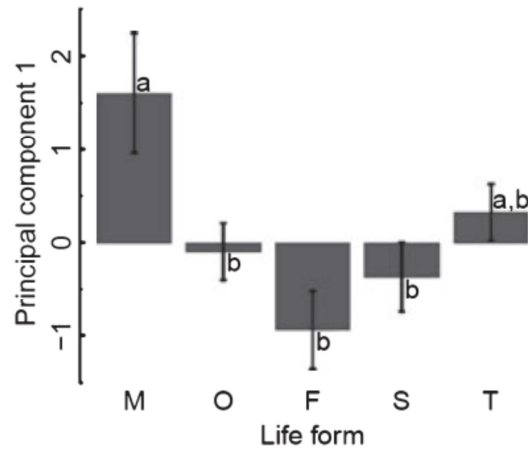
FIG. 5.2: On average, plants at the extremities of life history complexity (i.e. monocarps and trees) tend to have transients of greater magnitude than those of mid-range complexity (i.e. perennial herbs and shrubs). Lowercase letters signify groupings of life history by statistical significance. M = monocarpic plants from open and/or disturbed habitats, O = perennial herbs from open and/or disturbed habitats, F = perennial herbs from forest habitats, S = shrubs, T =trees. Means and SD are plotted for an average matrix dimension and average r where relevant, using the minimum adequate model.
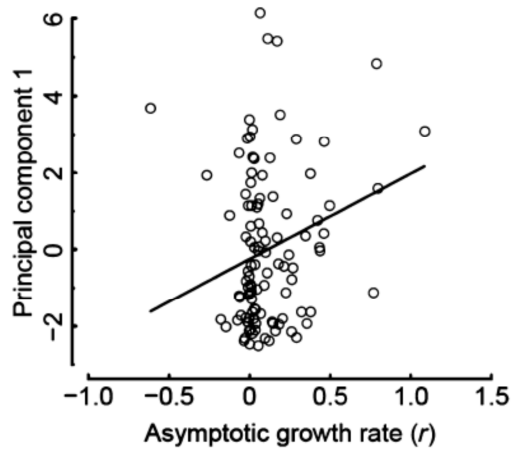
FIG. 5.3: The potential magnitudes of transient dynamics (both amplified and attenuated measures) have a positive association with r, the measure of long-term population growth or decline, although there is a lot of scatter in the relationship, as is evident from the graph.

The fitted line is plotted for an average matrix dimension using the minimal adequate model (but excluding life history because of the difficulty of calculating an 'average' value for this parameter).
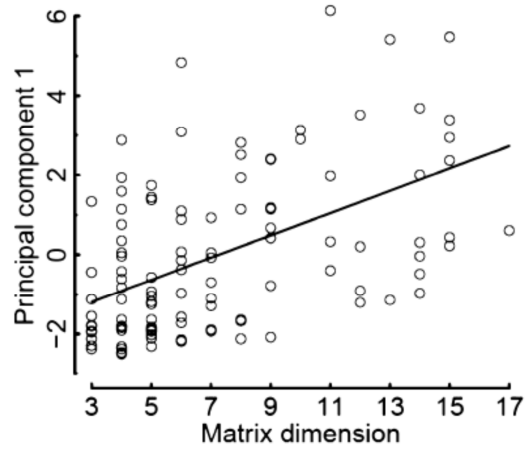
FIG. 5.4: The dimension of the matrix model (equal to the number of stages chosen in the life cycle model) shows a positive relationship with the potential magnitudes of transient dynamics (both amplified and attenuated transient measures). Fitted curves are plotted for average r where relevant, using the minimum adequate model (but excluding life history due to the difficulty of calculating an 'average' value for this parameter).

CHAPTER 6

– – – – – – – – – – – – – –

Exploring patterns of the range of transient dynamics naturally led to questions regarding the probability of models exhibiting certain transient dynamics over others. Chapter 6 is the one unpublished chapter of this thesis. As the last chapter written, it improves on the methods used in chapter 5. We choose to analyse population inertia given its strength and tractability as an index of transient dynamics. We make use of the innovative MCMCglmm analysis framework, which uses Bayesian inference to fit complex models to data, most importantly enabling an accurate modelling of phylogenetic signal. We explore whether populations tend to amplify or attenuate following disturbance, and nudge transients into the realms of evolutionary biology by linking our results to life history theory. The results presented in this chapter suggest that transient dynamics may not just be important to our understanding of ecological dynamics, but also to our understanding of how life histories may evolve over time.

Chapter 6:

Stott, I., Townley, S. Franco, M., Matsikis, I., Carslake, D.J., & Hodgson, D.J. (2012) Stage-structured life cycles favour demographic resilience of plant populations. In prep.

STAGE-STRUCTURED LIFE CYCLES FAVOUR DEMOGRAPHIC RESILIENCE OF PLANT POPULATIONS

ABSTRACT

The importance of incorporating environmental variation into demographic studies is well-recognised. However, little is understood about the short-term responses of populations to demographic disturbance events, which act over short periods of time to directly alter population size and structure, but have little effect on the longer-term vital rates of the population. Recent interest in transient dynamics of populations has enabled study of the response of populations to disturbance. Using novel transient analyses, we show that populations have a remarkable tendency to boom in response to disturbance by exhibiting short-term increase in population density. This is true both across the entire range of possible disturbances and for disturbances that have been recorded in the field. We uncover patterns in this booming behaviour, according to life history and phylogeny. We argue that this demographic resilience to disturbance should be an evolved property of populations living in disturbed environments, and tentatively suggest a link between tendency towards amplification and the evolution of stage-structuring in natural life cycles.

INTRODUCTION

Natural populations are subject to an ever-changing environment. Sources of heterogeneity that may influence a population's vital rates and structure include variation in abiotic factors such as temperature (Egley 1990) or light availability (Ballantine & Forde 1960), biotic factors such as disease (Tompkins, White & Boots 2003) or competition (Connell 1983), and anthropogenic factors such as harvesting (Pinard 1993) or habitat destruction (Tilman *et al.* 1994). Changes in a population's vital rates and structure translate over time into changes in its dynamics: consequently the environment influences population density and growth (Savage *et al.* 2004). Population density and growth are key components of fitness (Hunt & Hodgson 2010), therefore environmental variation imposes an important selection pressure on populations.

The importance of modelling environmental variation in population dynamic and evolutionary studies is well-recognised. Stochastic models of demography are established in population ecology (Fieberg & Ellner 2001), and stochastic measures of fitness have long been used in evolutionary ecology (Gillespie 1974). Stochastic models usually incorporate environmentally-induced variation in survival, fecundity, growth or regression, termed *perturbations* to life cycle rates. An alternative (although less common) approach to stochastic analysis is to model *disturbance* to population structure. In this case, stochastic variation is not

forced through changes in matrix entries, but through changes in the population vector (Stott, Townley & Hodgson 2011 [Chapter 1]). Hence, in a model with perturbation, population dynamics are dictated by a changing schedule of vital rates that slowly mould structure and density over time. On the other hand, population dynamics of a model with disturbance follow the schedule of an unchanging set of vital rates, punctuated by sudden changes in structure and density. While it might be possible to model demographic disturbances via perturbations to vital rates (e.g. a disease epidemic will cause a sudden increase in mortality; the ploughing of a field will cause a sudden increase in seed bank germination), we suggest there is value in modelling such events as disturbances to demographic structure. From a modelling perspective, it may be more revealing to disturb the state rather than to perturb the system.

Whichever form a stochastic model takes, analyses usually focus on long-term dynamics: mean and variance in long-term population growth and density (Fieberg & Ellner 2001). In the long term, expected growth rate is independent of the population's current structure. However, patterns of short-term growth can prove to be very different to expected long-term trends, and are highly dependent on the current structure of the population (Townley *et al.* 2007; Townley & Hodgson 2008). These 'transient' dynamics have seen increased research interest in recent years, both as a means of increasing accuracy of models for population management (Stott, Hodgson & Townley 2012b [Chapter 2]), and as a means of explaining the complicated time series of population dynamics in nature (Koons *et al.* 2005a; Stott *et al.* 2010a [Chapter 5]; Maron, Horvitz & Williams 2010). Although some methods explore transient response to perturbation (Neubert and Cawell 1997), studying transient dynamics in the context of disturbance has proven more tractable and meaningful. Hence, the vast majority of transient analyses consider population response to disturbance (Fox & Gurevitch 2001; Yearsley 2004; Koons *et al.* 2007; Caswell 2007; Townley *et al.* 2007; Townley & Hodgson 2008; Stott, Townley & Hodgson 2011 [Chapter 1]).

Transient response of populations to disturbance will matter from an evolutionary perspective: a population that can boom in response to disturbance, thus quickly rebounding from reduced density, will have significant competitive advantage over a population that busts in response to disturbance. Evolutionary studies often use measures of long-term growth as surrogates for fitness (Hunt & Hodgson 2010). Theoretically however, populations in disturbed environments should evolve to maximise not only this long-term growth, but also their ability to rebound from disturbance in the short term. This observation yields the notion of *demographic resilience*, which we define as the ability of a population to bounce back from disturbance in the short term by booming in density. This definition differs importantly from many established concepts of ecological 'resilience': such measures more commonly estimate the rate of return to stability or the time taken to reach stability, following disturbance or perturbation (Gunderson 2000). The concept of demographic resilience is complementary to these ideals: we don't look to redefine the concept of ecological resilience, but to extend the concept of resilience to the

study of transient demography (Neubert & Caswell 1997). We study demographic resilience in the very short term as the propensity to be *reactive* (Neubert & Caswell 1997): in other words the probability of growing faster than the stable rate of increase following disturbance. We study demographic resilience in the longer term as the propensity to have positive *inertia* (Koons 2007): in other words the probability of ending up larger than a stable population, following disturbance. These measures fit with the general concept of resilience: the former measures the instant rate at which a disturbed population bounces back (towards carrying capacity or to regain numerical advantage); the latter measures whether this 'rate of return' advantage can be maintained through time. A life history that can achieve quicker numerical replacement following disturbance and maintain high density in the longer term will, all else being equal, dominate a disturbed system. As high demographic resilience to disturbance will infer superior competitive advantage, it might be expected that rates of high demographic resilience should be found in nature.

In this study, we explore patterns of demographic resilience in natural populations of angiosperm plants. First of all, we merely seek to measure rates and distributions of demographic resilience in populations. Second, we explore how patterns of demographic resilience change according to shared ancestry and life history. We employ a recently-established framework for measuring transient dynamics (Stott, Townley & Hodgson 2011 [Chapter 1]), as well as introducing novel statistical sampling procedures for studying transient dynamics in the context of demographic resilience. We explore rates and distributions of demographic resilience using simple but robust statistical methods, and extend this exploration into patterns according to phylogeny and life history using cutting-edge Bayesian generalised linear mixed models (Hadfield 2010).

Our results indicate that populations show remarkably high rates of demographic resilience to disturbance. Patterns in these rates are linked to both phylogenetic history and life form. We argue that this emergent property of populations is highly likely to be an evolved response to a disturbed environment. We analytically link high demographic resilience to the stage-structuring of life cycles, including delayed reproduction and asymmetry in juvenile and adult survival, and discuss how the differences in disturbance regimes experienced by different species may shape differences in their patterns of demographic resilience. Last, we speculate on how transient dynamics may contribute to understanding fitness of populations in stochastic environments.

MATERIALS AND METHODS

DATABASE

We use a database of 620 population projection matrix (PPM) models for 147 angiosperm species representing 57 different families. These models have been collected from the published literature, and for some species include within-species replicates (multiple populations per species) and/or within-population replicates (multiple PPM models per population, measured at different times). We found 133 of the models in the database to be reducible. Reducible models present problems for analysis as they often represent biologically implausible life cycles, and may be non-ergodic, thus violating certain assumptions of many PPM analyses (Stott *et al.* 2010b [Chapter 3]). In all analyses, we excluded reducible models, leaving 487 irreducible PPM models for 143 species representing 56 different families. To these remaining models, we applied the 'seeds' correction (Caswell 2001 p.60-62) to matrices with redundant seed stages, which are sometimes a by-product of incorrect modelling of fast germination rates.

Only a portion of our database contained information on the current demographic structure of populations, which is a necessary prerequisite for some of our analyses. This subset numbers 215 irreducible PPM models for 70 species representing 36 different families. Some demographic vectors excluded measures of certain life stages (usually seeds and early life stages): in this case we took the conservative approach of fixing densities of those stages at their stable-stage density and combining these with the recorded demographic densities of other life stages. All demographic vectors were scaled to sum to 1 in analyses.

Appendix 7 contains the database of PPM models and associated information.

BASIC PPM MODELS

We study the dynamics of density-independent, non-stochastic (i.e. linear, time-invariant) population projection matrix models, which are discrete-time models that take the form $\mathbf{n_t}=\mathbf{A}^t\mathbf{n_0}$. In this equation, $\mathbf{n_t}$ and $\mathbf{n_0}$ are the demographic vectors at time t and time 0 respectively, containing numbers or densities of individuals in each stage class. $\mathbf{A}$ is a square, nonnegative matrix representing the life cycle of the organism, incorporating measures of survival, growth, retrogression and fecundity. If $\mathbf{A}$ is primitive (which should usually be the case), then whatever its demographic structure, the population is predicted to settle to a *stable state*, with long-term (asymptotic) stable rate of growth or decline equal to the dominant eigenvalue λ_{max} of the PPM, and stable demographic structure with ratios of stages equal to the dominant right eigenvector $\mathbf{w}$ of the PPM (Caswell 2001). The relative reproductive value of each stage is embodied in the dominant left eigenvector $\mathbf{v}$ of the PPM.

TRANSIENT DYNAMICS

Population projections of linear, time-invariant models are a combination of both the long-term asymptotic dynamics described above, and short-term *transient dynamics*. Transient dynamics can differ dramatically from long-term trends (Townley & Hodgson 2008): in the short term, populations may either boom by growing faster than their stable rate of growth (amplify) or bust by growing slower than their stable rate of growth (attenuate). Hence, a population that amplifies becomes larger in size/density than an equivalent stable population, and a population that attenuates becomes smaller (Townley & Hodgson 2008; Stott, Townley & Hodgson 2011 [Chapter 1]). Whether a population amplifies or attenuates is dictated by its demographic structure. In this study we introduce the notion of 'demographic resilience': a population that amplifies in response to a disturbance is considered to be resilient in the short-term to that disturbance, whilst a population that attenuates is considered to be non-resilient.

We employ two measures of transient amplification and attenuation, following Stott, Townley & Hodgson (2011) [Chapter 1]. These measures use the standardised matrix $\hat{\mathbf{A}}$ (equal to $\mathbf{A}$ scaled by λ_{max}) and the standardised vector $\hat{\mathbf{n}}_0$ (equal to $\mathbf{n_0}$ scaled to sum to 1) in their calculation. Thus, they remove any confounding effects of differing asymptotic growth and differing initial density to give transient indices that are comparable both among and within models. These standardisations mean that the indices we employ measure the transient density of a non-stable population projection, relative to the density of an equivalent population projection initiated with stable stage structure. As a result of this, indices with values greater than 1 indicate population amplification whereas indices with values less than 1 indicate population attenuation.

The first index, reactivity, measures the transient amplification or attenuation of the population in the first timestep (note that Stott, Townley & Hodgson 2011 [Chapter 1] distinguish between 'reactivity' being amplification in the first timestep and 'first-timestep attenuation' being attenuation in the first-timestep: for ease, here we use reactivity as a catch-all term for first-timestep response). Reactivity is measured as:

$$reactivity = \mathrm{P}_1 = \left\| \hat{\mathbf{A}}\, \hat{\mathbf{n}}_\mathbf{0} \right\|_1 .$$

The second index we employ is population inertia. As a result of transient dynamics, a non-stable population will settle at a density above or below its predicted stable density when it reaches stable state. Inertia is the measure of this long-term population amplification or attenuation and is measured as:

$$inertia = \mathrm{P}_\infty = \frac{\mathbf{v}^\mathrm{T}\hat{\mathbf{n}}_\mathbf{0}\|\mathbf{w}\|_1}{\mathbf{v}^\mathrm{T}\mathbf{w}} .$$

By using both reactivity and inertia, we are able to assess first whether populations are resilient to disturbance in the very near term, and second whether they maintain that resilience in the long term.

DATA SIMULATION

We explore demographic resilience in two settings: first, we measure 'general demographic resilience' to all possible disturbances. Second, we measure 'specific demographic resilience' to recorded disturbances in the field.

GENERAL DEMOGRAPHIC RESILIENCE: We consider the general demographic resilience of the population to be the probability of amplification across all possible disturbances. We compute this by calculating the reactivity and inertia of the population for randomly generated demographic structures that cover the entire range of possible population structures. We achieve this unbiased sampling of demographic vectors by drawing population structures from the Dirichlet distribution. The Dirichlet is a multivariate generalisation of the beta distribution, and is parameterised by a vector of shape parameters $\boldsymbol{\alpha}$. The distribution concentrates on this vector, with the degree of concentration modelled by a scaling factor: increasing the scale of $\boldsymbol{\alpha}$ increases the probability of sampling near $\boldsymbol{\alpha}$. Hence, when all α_i are equal, the distribution is symmetric, and when all α_i equal one, the Dirichlet is equal to the multivariate uniform [0,1] distribution.

We calculated a mean PPM per species (using all irreducible PPM models), and drew one million random demographic distributions from the symmetric Dirichlet with all α_i equal to one for each mean matrix. We then calculated both reactivity and inertia for each matrix-vector pair, giving 1 million measures each of reactivity and inertia for every mean species matrix. From these one million samples we were then able to calculate the probability of immediate amplification $p(P_1>1)$ and the probability of long-term amplification $p(P_\infty>1)$ for each species.

These measures of general resilience were calculated using the preactivity and pinertia functions in the R package popdemo (Stott, Hodgson & Townley 2012a [Chapter 4]).

SPECIFIC DEMOGRAPHIC RESILIENCE: We consider the specific demographic resilience of the population to be the transient response of the population to a specific, observed demographic disturbance. Observed demographic disturbance is modelled using the recorded non-stable structure of the population. We calculated reactivity and inertia for each population (using all irreducible PPM models with recorded demographic structures), and from this data, calculated a mean reactivity and a mean inertia per species.

Reactivity and inertia were calculated using the reactivity, firststepatt and inertia functions in the R package popdemo (Stott, Hodgson & Townley 2012a [Chapter 4]).

STATISTICAL METHODS

Our first question is simply: in the short term, how resilient are species to disturbance?

EXACT BINOMIAL TESTS: We initially explore this question non-parametrically, and conservatively, with exact binomial tests. For general demographic resilience, we binary-transformed probabilities of reactivity and inertia by assigning a 0 if there was higher probability of attenuation (i.e. if $p(P_1>1)$ or $p(P_\infty>1)$ were <0.5), or assigning a 1 if there was higher probability of amplification (i.e. if $p(P_1>1)$ or $p(P_\infty>1)$ were >0.5). We conducted an exact binomial test on this data against a null value of 0.5, representing a null hypothesis that each case occurs with equal probability. For specific demographic resilience, we binary-transformed measures of reactivity and inertia by assigning a value of 0 if the population attenuated (i.e. if P_1 or P_∞ were <1) or a value of 1 if the population amplified (i.e. if P_1 or P_∞ were >1). We conducted an exact binomial test on this data against a null value of 0.5, again representing a null hypothesis that amplification and attenuation are equally likely to occur.

BOOTSTRAP T TESTS: Second, we explore this question parametrically using two-tailed, one-sample bootstrap t-tests. For general demographic resilience, we tested mean probability of amplification in reactivity and inertia against the null hypothesis that amplification and attenuation are equally likely overall (i.e. we tested $E[p(P_1>1)]$ and $E[p(P_\infty>1)]$ against a null mean value of 0.5). For specific demographic resilience we log-transformed reactivity and inertia (as this better represents the multiplicative nature of the indices for parametric statistical analysis, and yields values >0 for amplification and <0 for attenuation), and tested these against a null hypothesis that populations are equally likely to amplify or attenuate to the same magnitude overall (i.e. we tested $E[\log(P_1)]$ and $E[\log(P_\infty)]$ against a null mean value of 0). Significance was determined by assessing whether confidence intervals calculated from t-distributions overlapped with null mean values.

Our second question is, does demographic resilience show relationships with shared ancestry or life history?

MCMCglmm: To address this question, we employ generalised linear mixed models (glmm) that use Markov Chain Monte Carlo (MCMC) algorithms in a Bayesian inference framework, using the R package MCMCglmm (Hadfield 2010).

Random effects: We constructed a phylogeny including branch lengths for all species, using phylomatic (http://phylodiversity.net/phylomatic) to find topology down to family level, phylocom (Webb, Ackerly & Kembel 2008) to calculate branch lengths down to family level, and then taxonomic literature to find topology and branch lengths for remaining within-family polytomies. This yielded an almost fully-resolved phylogeny, with just 2 remaining polytomies. Phylogeny was modelled as a random effect in MCMCglmm models, in each analysis trimming species from the tree that did not appear in the data for that analysis. The final phylogeny and full details on its inference can be found in Appendix 6.1.

Fixed effects: We assigned each species a life form of either monocarpic (M), perennial herb in open habitat (O), perennial herb in forest habitat (F), shrub (S) or tree (T) following

Franco & Silvertown (2004). This was modelled as a 5-level, categorical, fixed effect in MCMCglmm models.

Model structure: For both general and specific demographic resilience measures, we assessed the following 4 models: including both phylogeny and life form, including phylogeny but excluding life form, excluding phylogeny but including life form, and excluding both phylogeny and life form. Support for phylogeny and life form were assessed using the deviance information criterion (DIC), with lowest DIC indicating the most informative model. For general demographic resilience, we logit-transformed per-species measures of $p(P_1>1)$ and $p(P_\infty>1)$, converting any values of 1 to $1-10^{-6}$ as probabilities of 1 cannot be modelled by the logit distribution. We analysed both logit$\{p(P_1>1)\}$ and logit$\{p(P_\infty>1)\}$ simultaneously in a bivariate gaussian glmm, allowing interactions between the two responses and fixed effects, and full variance-covariance between the two responses when estimating random and residual variance. We used default uninformative priors for fixed effects, and specified parameter-expanded uninformative priors for random and residual variance, which gave relatively good chain mixing. Our number of iterations was 300000, with a 10% burnin and a thinning interval of 100, which achieved low autocorrelation in fixed effect posteriors and high repeatability of results. For specific demographic resilience, we binary-transformed reactivity and inertia by assigning a value of 0 if the population attenuated (i.e. if P_1 or $P_\infty <1$) and a value of 1 if reactivity or inertia were >1(i.e. if P_1 or $P_\infty >1$). The two binary responses were analysed separately in univariate binomial glmms, therefore modelling the probability of amplification in response to recorded disturbance. We specified an uninformative prior on the probability scale for fixed effects, parameter-expanded uninformative priors for random effects, and fixed residual variance at 1, which gave relatively good chain mixing for scaled posteriors. The number of iterations was also 300000, with 10% burnin and a thinning interval of 100, which again achieved low autocorrelation of fixed-effect solutions and high repeatability of results.

For more information on all statistical models, and especially detailed explanations and justifications of MCMCglmm model structure, prior choice and model fit, please see Appendix 6.2.

RESULTS

HOW RESILIENT ARE SPECIES TO DISTURBANCE?

Populations show remarkable demographic resilience, with the large majority amplifying in response to disturbance, and maintaining amplification in the long term.

EXACT BINOMIAL TESTS: Exact binomial tests were highly significant in all cases ($p<0.001$ for all tests), which indicates a higher probability of amplification in all data. For general demographic resilience, this means that greater probability of amplification across all

possible demographic structures is significantly more likely both in the immediate and long term (i.e. $p(P_1{>}1) > 0.5$ and $p(P_\infty{>}1) > 0.5$ occur significantly more often than $p(P_1{>}1) < 0.5$ and $p(P_\infty{>}1) < 0.5$ respectively). For specific demographic resilience, this means that amplification in response to recorded disturbance is significantly more likely both in the immediate and long term (i.e. $P_1 > 1$ and $P_\infty > 1$ occur significantly more often than $P_1 < 1$ and $P_\infty < 1$ respectively).

BOOTSTRAP T TESTS: Bootstrap t tests showed that this result also holds parametrically ($p{<}0.01$ for all tests), which again indicates a higher probability of amplification in all cases. For general demographic resilience, this means that the average probability of amplification is significantly greater than 0.5, both in the immediate and the long term (i.e. $E[p(P_1{>}1)] > 0.5$ and $E[p(P_\infty{>}1)] > 0.5$ Figs. 6.1a & 6.1b). For specific demographic resilience, this means that the average magnitude of log-transformed immediate and long-term transient dynamics are both significantly greater than 0 (i.e. $E[\log(P_1)] > 0$ and $E[\log(P_\infty)] > 0$ Fig. 6.1c, Fig. 6.1d).

DOES DEMOGRAPHIC RESILIENCE SHOW RELATIONSHIPS WITH SHARED ANCESTRY OR LIFE HISTORY?

Populations show patterns of general demographic resilience according to both phylogeny and life history, but we identified no such patterns for specific demographic resilience.

MCMCglmm: Analyses of general demographic resilience indicated interesting relationships with both phylogeny and life form. DIC indicated that the inclusion of life form was supported over its exclusion (Table 6.1). Parameter estimates show a U-shaped relationship along the axis of ecological succession (M-O-F-S-T) for probability of both reactivity and inertia (Figs. 6.2a & 6.2b). Thus, monocarps and trees show the highest probabilities of amplification in the immediate and long term, whilst perennials and shrubs have relatively lower probabilities of amplification. However, the model with lowest DIC was the phylogeny-only model (Table 6.1), which indicates that this relationship is better explained through modelling longitudinal shared ancestry than through cross-sectional categories of life form, pointing to a degree of conservation of transient demography within clades. MCMCglmm analyses for specific demographic resilience indicated that there was no support for inclusion of either phylogeny or life form in the model (Table 6.1). Parameter estimates for different life forms were very similar (Figs. 6.2c & 6.2d), and the lack of support for phylogeny indicates that response of species to disturbances experienced in the field is not conserved within clades.

DISCUSSION

Populations show a remarkable tendency towards amplification in response to disturbance. When assessing population response to every conceivable disturbance, we found that the overwhelming majority of species are significantly more likely to amplify rather than attenuate,

both in the immediate and long term. We also found that populations show a high tendency towards both immediate and long-term amplification in response to real-world disturbances. At the least, this represents an interesting ecological phenomenon. However we also link this result to life history theory: we argue that amplification in response to disturbance should be an emergent, evolved property of natural populations, and present analytical results that suggest our observations can be explained in part by the stage-structuring of life cycles, including asymmetry across the life cycle in rates of survival and reproduction.

LINKING DEMOGRAPHIC RESILIENCE AND LIFE HISTORY

Population dynamics are a consequence of the interaction between an organism's life cycle, and its demographic structure. Hence, the transient response of a population to disturbance is mediated through the life cycle.

It is possible to obtain an analytical solution to the Dirichlet sampling procedures we present here, and we illustrate this geometrically using a 3-stage model for *Carlina vulgaris* (Lofgren *et al.* 2000):

$$
\mathbf{A} = \begin{bmatrix} 0.500 & 0 & 2.800 \\ 0.250 & 0.222 & 0 \\ 0 & 0.667 & 0 \end{bmatrix}, \hat{\mathbf{A}} = \begin{bmatrix} 0.479 & 0 & 2.682 \\ 0.239 & 0.213 & 0 \\ 0 & 0.639 & 0 \end{bmatrix}, \mathbf{w} = \begin{bmatrix} 0.667 \\ 0.203 \\ 0.130 \end{bmatrix}, \mathbf{v} = \begin{bmatrix} 0.686 \\ 1.494 \\ 1.841 \end{bmatrix}^{\mathrm{T}}
$$

Figure 6.3 shows a unit triangle plotted in three-dimensional space. The complete set of relative densities of a three-stage demography lie on its surface. The unit triangle is bisected by another triangle which defines the boundary of amplification versus attenuation. For reactivity, the vertices of the bisecting triangle are defined by the reciprocals of the column sums of the standardised PPM $\hat{\mathbf{A}}$. For inertia, vertices are defined by the reciprocals of the entries of the reproductive value vector $\mathbf{v}$ (after scaling $\mathbf{v}$ and $\mathbf{w}$ so that $\mathbf{v}^{\mathrm{T}}\mathbf{w}$ equals 1 and the sum of $\mathbf{w}$ equals 1). Above the bisection boundary the population amplifies, whilst below the boundary the population attenuates. Therefore the area within the unit triangle above the bisection boundary equals our measure of general demographic resilience: the probability of amplification in response to any conceivable disturbance. This geometric representation generalises to an (n-1)-dimensional unit simplex plotted in n-dimensional hyperspace, bisected by another (n-1)-dimensional simplex whose vertices are defined in the same manner.

We provide the algebraic solution to the three-dimensional case in Appendix 6.3, but the n-dimensional generalisation of this equation is far more difficult to deduce. However, we can speculate on how the entries of $\hat{\mathbf{A}}$ and $\mathbf{v}$ affect the response of the population to disturbance. For a non-stage-structured demography, the vertices of the bisecting simplex would be equal to the vertices of the unit simplex. In this case, no demographic structures achieve either amplification or attenuation. For a stage-structured demography with varying rates of survival, growth, retrogression and fecundity, one or more simplex vertices are greater than 1, and one or

more simplex vertices are less than 1. This means that the unit simplex is bisected into regions of amplification and attenuation. Thus, stage-structuring is a necessary prerequisite for transient dynamics. The position of vertices of the bisecting simplex dictates the amplification-attenuation boundary in the unit simplex. Therefore, the relative column sums of the PPM and the relative reproductive value of each stage determine what proportions of demographic vectors achieve amplification immediately and in the long term respectively. It is evident from figure 6.3 that asymmetry in the vertices of bisecting triangles (i.e. some vertices larger than 1 and some vertices smaller than 1) achieve boundaries giving relatively high probability of amplification for both reactivity and inertia, and we provide algebraic support for this assertion in Appendix 6.3. In the case of *Carlina*, this asymmetry is achieved through delayed reproduction and differential juvenile and adult survival. Conversely, early reproduction and/or reduced asymmetry in survival would result in a life history with decreased probabilities of amplification (as vertices >1 are moved down their axes and/or vertices <1 are moved up their axes). Generalising this geometric interpretation to n-dimensional space is more difficult, as the number of simplex vertices increases. However, the core results that stage-structuring achieves transient dynamics and that asymmetry in the life cycle achieves asymmetric probability of amplification or attenuation will still apply.

It is difficult to determine cause and effect without experimental evidence. A tendency towards amplification may be a desirable side-effect of stage-structured life histories, or it could be a target of selection. It is generally accepted that populations evolve to maximise their rate of numerical increase, and measures of population growth are commonly used to represent genotype 'fitness' (Hodgson & Hunt 2010). Although simple conceptual models might suggest that early reproduction and semelparity should be favoured in life histories (Cole 1954), various different explanations for the evolution of delayed reproduction, iteroparity and structured life cycles have been explored. Early reproduction may be constrained by resource availability (Bell 1980), and iteroparity may be favoured when there is differential juvenile and adult survival (Roff 2002; Charnov & Schaffer 1973). Fitness necessarily depends on the environment, and structured life cycles and delayed reproduction may have evolved as a bet-hedging strategy in stochastic environments (Wilbur & Rudolf 2006; Koons 2008). High demographic resilience may be a beneficial consequence of such evolutionary process that favour structured life cycles. Alternatively, a tendency towards amplification in response to disturbance could be selected for. The environment influences population structure through disturbance, and in the same way that fitness may depend on population sex ratio (Carrillo *et al.* 2012), fitness in a disturbed world may depend on population structure. A life history that is able to achieve high rates of numerical replacement both in the long term and in the short term following disturbance should be fitter than a life history that achieves either one, but not the other.

THE EFFECT OF DISTURBANCE REGIME

The optimal life history for promotion of amplification is obviously going to depend on the disturbance regime that the population experiences. When modelling general demographic resilience of populations, we analysed overall population response to uniform random disturbance. This null disturbance regime may admittedly be unlikely to occur in nature. First, disturbance may be non-uniform: this gives peak(s) in the sampling distribution of demographic structures. For example, populations may be more likely to be disturbed closer to their current demographic structures. Second, disturbance may be non-random: this biases the parameter space that demographic structure is pushed into, changing the slope(s) of the sampling distribution. For example, a hurricane may damage large trees but leave saplings unscathed, so that disturbance is relatively more likely to cause demographic structures with more saplings and less adults. These two caveats present a significant conceptual impasse in our approach: disturbances may be non-uniform and/or non-random, but it is almost impossible to state what distributions of non-uniformity and non-randomness exist in nature. On the one hand, our null approach may be a poor representation of real-world disturbance regimes. On the other hand, by avoiding bias altogether, we avoid the pitfall of biasing distributions in the wrong manner.

Timing of disturbances is also likely to be important, and the interaction between type of disturbance and timing of disturbance should conceptually dictate a population's optimal response. A population that experiences frequent, relatively uniform and relatively random (i.e. relatively unpredictable) disturbances would want to be resilient to a large range of disturbance types. Conversely, a population that experiences infrequent, non-uniform and non-random (i.e. relatively predictable) disturbances might wish to be highly resilient to that particular type of disturbance whilst potentially sacrificing resilience to other disturbance types. Various different optima could exist in between these two extremes. Different disturbance regimes can be modelled by changing the sampling pattern within the unit simplex. It is worth noting that the Dirichlet distribution provides the opportunity to model biased disturbance regimes: asymmetry in the distribution is easily achievable by varying the relative values and scale of α_i shape parameters of the distribution. However, the question still remains as to how non-uniformity and non-randomness should be modelled.

Although it is difficult to say what disturbance regimes populations have experienced historically, we found that populations show a substantial tendency towards amplification in response to observed disturbances, albeit a weaker relationship than for resilience across all possible disturbances. This represents a cross-sectional snapshot of natural disturbance regimes, and so it is difficult to discern whether recorded disturbances are frequent or infrequent, random or non-random, and uniform or non-uniform in their respective systems. However, the observation still remains that populations tend, on the whole, to be resilient to them.

PATTERNS ACCORDING TO PHYLOGENY AND LIFE FORM

If demographic resilience is a target of natural selection, then we may expect to find a relationship between demographic resilience and phylogeny if demographic resilience is phylogenetically constrained. Equally, if disturbance regimes dictate optimum patterns in demographic resilience then we may expect to find a relationship between demographic resilience and life form if different life forms experience different disturbance regimes.

We found that plants exhibit patterns of general demographic resilience according to both phylogeny and life form. Plants show a U-shaped relationship between life history (as defined on a continuum of ecological succession) and probability of amplification across all possible population structures (Fig. 6.2a & 6.2b). This echoes results from Stott *et al.* (2010a) [Chapter 5] that found a U-shaped relationship between life history and potential magnitude of both amplified and attenuated transient dynamics. There are two key differences between this study and our earlier study: first of all, here we consider population response to specific disturbances, whereas in Stott *et al.* (2010a) [Chapter 5] we focussed on transient bounds, which represent the most extreme possible transient dynamics that a population can exhibit. Second, in this study we assess the probability of amplification, whereas in Stott *et al.* (2010a) [Chapter 5] we worked with measures of the magnitude of transient dynamics. Combining both results, we find that monocarps and trees show more extreme transient bounds (i.e. a larger transient envelope), alongside a greater probability of amplification in response to disturbance. On the other hand, perennials and shrubs show a decreased range of potential transient dynamics, alongside a relatively lower probability of amplification in response to disturbance.

We previously linked patterns in transient bounds to patterns of recruitment competition mediated by life history trade-offs. Monocarps and trees may experience relatively greater lottery recruitment competition, as opportunities for seedling establishment are relatively more ephemeral than for perennials and shrubs (Chesson & Warner 1981; Chesson 1991; Turnbull, Crawley & Rees 2000). Thus, monocarps and trees benefit from large magnitude of amplification enabling fast population establishment. The flipside of this is that trade-offs between survival and fecundity (Ehrlén & van Groenendael 1998) mean they are more exposed to greater magnitude of attenuation. Conversely, perennials and shrubs experience relatively more stable environments, so are able to weigh survival against fecundity to achieve optimal fitness without the need for such extreme transient dynamics. In this context, the results we find in this study have two possible interpretations. First, greater probability of amplification for monocarps and trees will aid potential population growth under increased lottery competition: whatever the population structure, populations are able to take advantage of ephemeral resources by having a higher probability of amplifying, and by amplifying to a greater magnitude. Second, increased probability of amplification in monocarps and trees will counteract the potential detrimental impacts of attenuation: if life cycle trade-offs necessarily mean that the population also has the potential to attenuate to a greater magnitude, then having a

life cycle with lower probability of attenuation is one way to deal with this. Conversely, perennials and shrubs can endure a relatively higher probability of attenuation because their magnitude of attenuation is relatively smaller. Alternatively, it may simply be that life histories that favour increased potential range in transient dynamics also necessarily favour increased probability of amplification.

We previously found no relationship between range of transient dynamics and phylogeny, but our analyses here show that a phylogeny-only model best explains variation in probability of amplification. This may be a consequence of different analytical techniques: here we incorporate phylogeny with branch lengths into an MCMCglmm model, which may be more robust to some of the pitfalls of comparative analysis (Freckleton 2009) than our previous method of using comparative contrasts (Freckleton 2000) calculated from a phylogeny without branch lengths. Alternatively, we may have uncovered a true result relating to the conservation of life histories within plant clades. Transient bounds on amplification are dictated by the largest matrix column sum (reactivity) or the largest entry in the reproductive value vector (inertia). However, probability of amplification is affected by the relative sizes of all column sums (reactivity) or all stage-specific reproductive values (inertia). Hence, whilst both metrics will be affected by variation in magnitude of vital rates, probability of amplification is additionally affected by aspects of life cycle structure such as delayed reproduction and ability to skip stages or regress through the life cycle. It may be that life cycle structure is conserved within clades, whilst the sizes of vital rates within that structure are less constrained. There is scant evidence for this, although it has been found that sizes of vital rates are relatively independent of phylogeny, whilst the absolute importance of those vital rates to long-term population growth is more constrained (Burns *et al.* 2010). How these patterns affect transient dynamics is unclear, as broad comparative analyses of response of transient dynamics to perturbation are yet to be conducted. On the whole however, conservation of life history within plant clades is not particularly well-understood, and phylogenetic signal in studies of life history is often lacking (Burns *et al.* 2010; Buckley *et al.* 2011).

Whilst we found patterns according to general demographic resilience, we found no support for a relationship between either phylogeny or life history and specific demographic resilience. Conceptually, this could provide support for the idea that different life forms have found different optimum solutions according to the different disturbance regimes they experience. Therefore, despite the fact that different life forms show different patterns of general demographic resilience, they show the same patterns of response to real-world disturbances. However, this hinges on the assumption that recorded disturbances in our database are a representative sample of the disturbances experienced by plants in nature, and there is no simple way to tell whether this is the case.

DENSITY DEPENDENCE AND STOCHASTICITY

Our use of linear, time-invariant PPM models means that we do not account for either density-dependent effects (Benton & Grant 1996) or environmental stochasticity (Tuljapurkar, Horvitz & Pascarella 2003). Consensus techniques for transient analyses are yet to be extended to these modelling systems, so for the moment at least we are limited to studying transients using basic PPM models. However we note that in any case, most systems lack adequate information on the ways in which density dependence and environmental stochasticity affect populations. Many studies may collect demographic information under varying population densities, and/or varying environmental conditions, yet it is another thing altogether to understand the mechanisms of density-dependent action or possible time series of environmental perturbation, which are crucial to modelling such effects.

A common criticism of comparative analyses that use projection matrices or life tables is that they do not account for density dependence of vital rates (Caughley 1966; Gaillard *et al.* 1994). However, the assumption of density-independence is often the best option in the absence of information on the form and strength of density dependence in each species. Despite this, we can speculate on how transient dynamics may behave in density-dependent systems. Density of all or part of the population may affect overall population growth. The relationship between density and growth may be positive, mediated through Allee effects (Stephens *et al.* 1999). In this case, if disturbance tends to decrease population density then amplification may be the only thing that rescues the population from being pushed over an Allee threshold into a phase of decline. Alternatively, the relationship between density and growth may be negative: for example, intraspecific competition may slow growth of a plant population at high densities (Lewontin & Levins 1989). Below carrying capacity, the benefits of amplification in response to disturbance will still exist: populations that tend to amplify will reach carrying capacity soonest. However, this benefit may change as the population increases and approaches its attractor: close to carrying capacity, populations that amplify may risk overcompensating density dependence (May 1975; Grenfell *et al.* 1992).

Environments are rarely constant, and the importance of modelling environmental heterogeneity in natural systems is widely recognised (Fieberg & Ellner 2001). Stochastic models usually incorporate such environmental stochasticity by modelling variation in vital rates (perturbation) of the population over time. It is well-established that long-term mean stochastic growth rate is lower than asymptotic deterministic growth of a mean population, which is due to variation in per-timestep growth (Tuljapurkar 1990; Lande *et al.* 2003). Transient dynamics are an integral part of this stochasticity: per-timestep growth is deterministic, combining asymptotic growth rate (which is independent of population structure) and transient dynamics (which are dependent on population structure). A propensity for amplification may increase mean per-timestep growth and/or decrease variance in per-timestep growth, in both cases increasing long-term mean stochastic growth rate. Demographic

resilience will certainly be important in stochastic systems that experience relatively constant environments that are punctuated by large disturbance events. For example, coral reefs experience relatively constant environmental conditions, but populations endure heavy disturbance in hurricane years (Mumby, Vitolo & Stephenson 2011). An ability to rebound from such disturbance events will be key to population persistence, by avoiding lethal consequences of reduced population density such as susceptibility to interspecific competition, demographic stochasticity and Allee effects.

CONCLUSIONS

We have shown that plant populations exhibit a remarkable propensity towards amplification in response to demographic disturbance, patterns of which vary according to life form and phylogeny. We strongly believe that this demographic resilience will be a target for natural selection: it ameliorates detrimental effects of disturbance, facilitates successful exploitation of ephemeral opportunities for colonisation, avoids harmful Allee effects associated with reduced population density and may contribute positively to long-term stochastic growth. We have analytically linked demographic resilience to the stage-structuring of life cycles, including delayed reproduction and asymmetry in juvenile and adult survival. However, the intricate mechanisms underpinning the relationship between stage-structured life cycles and a tendency towards amplification are unclear. Additionally, the causal relationship between the two is uncertain: demographic resilience may be a desirable consequence of other selection pressures that favour stage-structuring, or it may be a selection target that has helped to mould stage-structuring in organismal life cycles.

Transient theory is a burgeoning field in ecology. Over time it has gained significant traction in the disciplines of population management and comparative demography, and will doubtless continue to contribute to these fields in the future. But perhaps transient theory also has a significant contribution to make in the study of life history evolution. Evolutionary studies often use demographic measures as fitness surrogates. Just as ecologists are increasingly realising the benefits of thinking in the short-term, it may pay evolutionary biologists to do the same. Effects of population structure on fitness and the different selection pressures acting on short- and long-term demographics could be important to understanding evolutionary processes. Consequently, transient dynamics may provide a new perspective for understanding the complex arrays of life history found in nature.

TABLES

TABLE 6.1: Results of MCMCglmm analyses

Model	Type	Response	Fixed	Random	DIC
General resilience	Bivariate	$p(P_1>1)$ and $p(P_\infty>1)$	Life form	Phylogeny	1391.34
			None	Phylogeny	840.15
			Life form	None	1430.27
			None	None	1453.84
Specific resilience	Univariate	Binary-transformed P_1	Life form	Phylogeny	89.04
			None	Phylogeny	88.50
			Life form	None	88.05
			None	None	87.45
Specific resilience	Univariate	Binary-transformed P_∞	Life form	Phylogeny	96.49
			None	Phylogeny	89.23
			Life form	None	88.41
			None	None	87.44
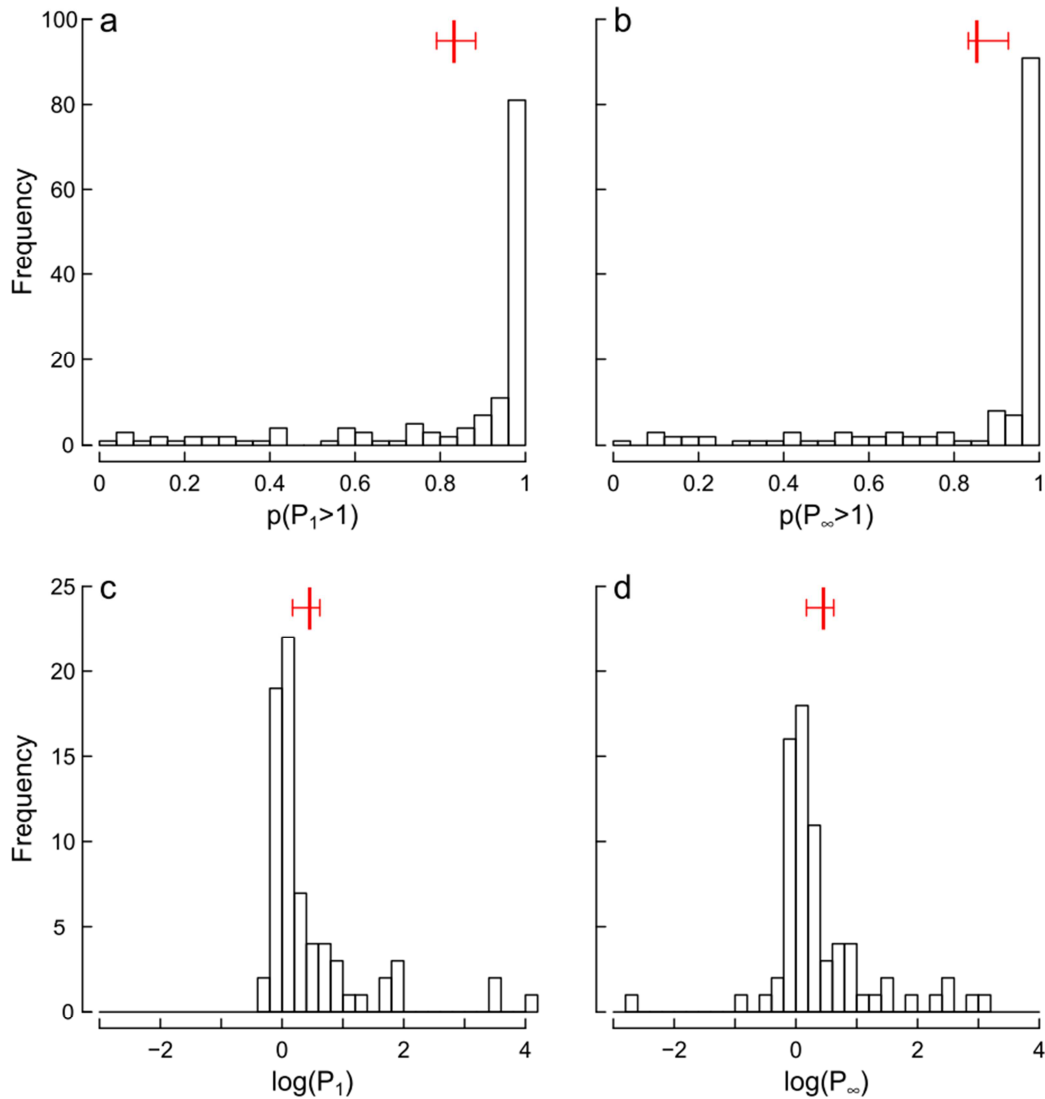
FIG. 6.1: Distributions of measures of demographic resilience. **(a)** the probability of immediate amplification in response to every possible disturbance ($p(P_1>1)$), **(b)** the probability of immediate amplification in response to every possible disturbance ($p(P_\infty>1)$), **(c)** long-transformed immediate transient response (reactivity) of species to recorded disturbances ($\log(P_1)$), **(d)** log-transformed long-term transient response (inertia) of species to recorded disturbances ($\log(P_\infty)$). In each panel, red lines indicate the mean and 95% confidence intervals calculated from bootstrap t-tests. Significance is indicated by the fact that 95% confidence intervals do not overlap with 0.5 in panels a and b, and 0 in panels c and d.
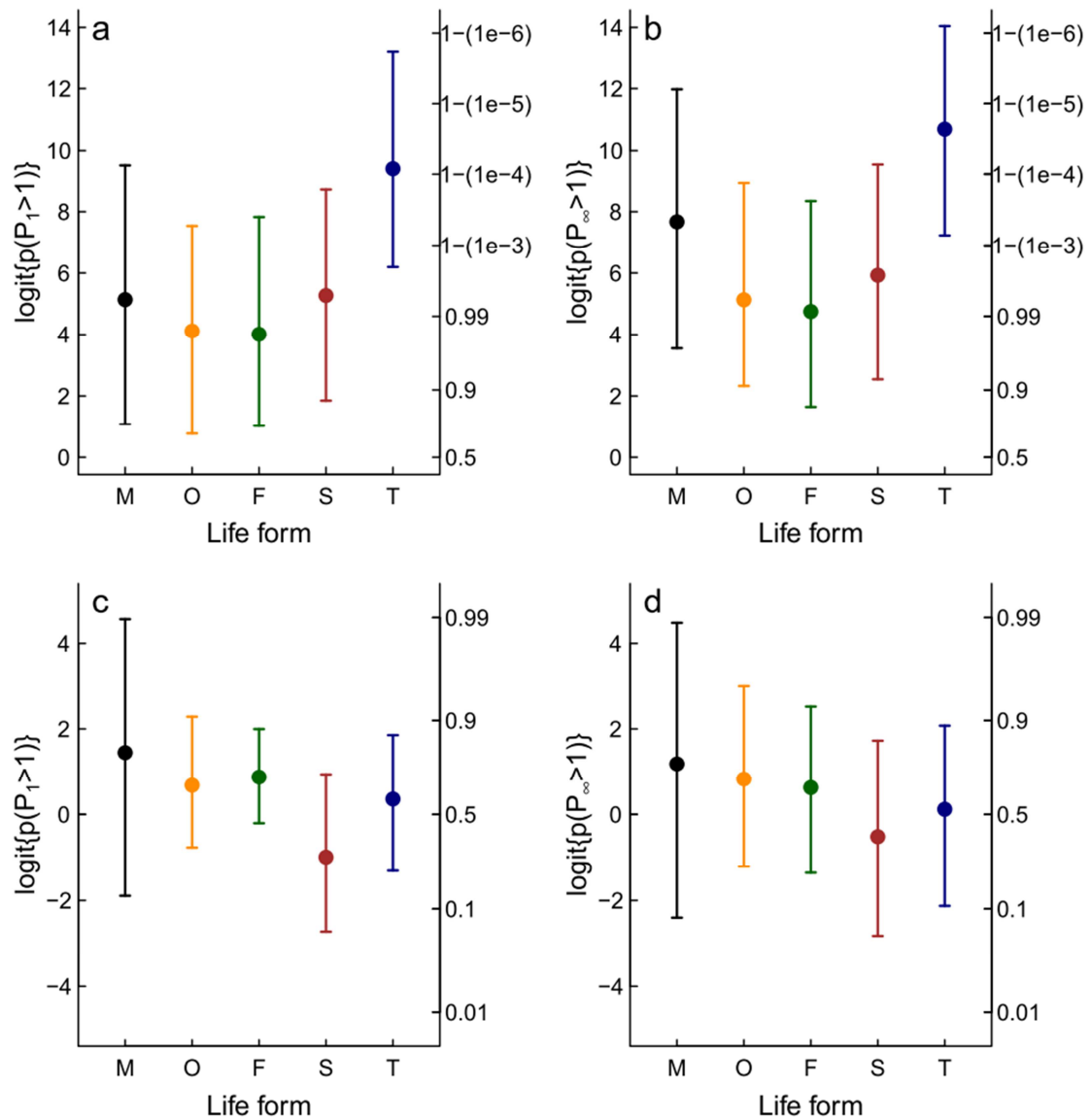
FIG. 6.2: Relationship between life form and demographic resilience. (a) probability of immediate amplification (reactivity) across all possible demographic structures; (b) probability of long-term amplification (inertia) across all possible demographic structures; (c) probability of immediate amplification (reactivity) in response to recorded disturbance; (d) probability of long-term amplification (inertia) in response to recorded disturbance. Inclusion of life form is supported in a and b, but not in c and d. All coefficients are taken from models that include phylogeny. In all cases, probabilities are plotted on a logit scale but the probability scale is shown on the right-hand axis for clarity.
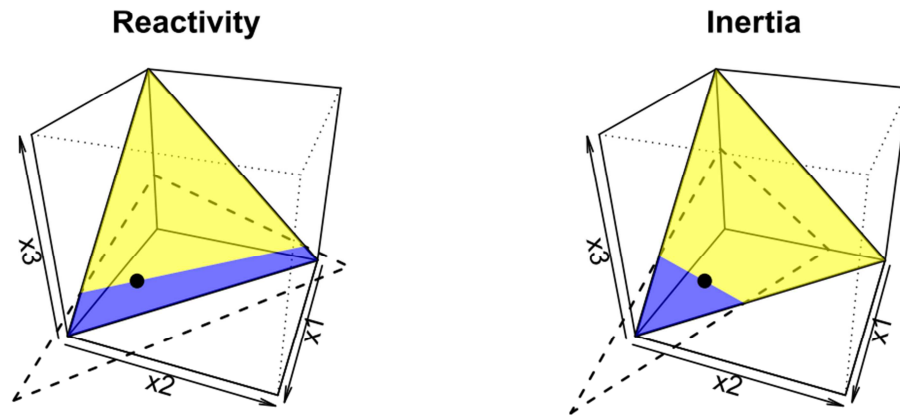
FIGURE 6.3: Geometric representation of general demographic resilience for a 3-stage model for *Carlina vulgaris*. Regions of amplification are shaded yellow, and regions of attenuation are shaded blue.

DISCUSSION

– – – – – – – – – – – – – – –

Thinking in the short term can help demographers understand the ecological and evolutionary processes underpinning population dynamics. Using a framework for studying transient dynamics (Stott, Townley & Hodgson 2011 [Chapter 1]), we have presented methods (Stott, Hodgson & Townley 2012b [Chapter 2]) and software tools (Stott, Hodgson & Townley 2012a [Chapter 4]) that enable demographers to incorporate transient analyses into their work. Using case studies, we have shown that such transient analyses are important for informing population management for conservation and pest control. Using comparative analyses, we have shown that different life forms show different ecological patterns of transient dynamics, and that certain aspects of transient demography may be heritable (Stott *et al.* 2010a [Chapter 5]; Chapter 6). Finally, we have linked transient demography to stage-structuring in life cycles and ventured the possibility that transient dynamics may act as a target for selection (Chapter 6).

Modern ecological paradigms assume a dynamic environment, where systems are constantly subject to factors that force changes in their dynamics (Cuddington 2001). Ecological studies are often conducted over relatively short timescales where such changes in dynamics will be important. Yet even now, analyses of ecological models invariably focus on long-term dynamics (Hastings 2001, 2004). Although transient theory is not a new idea (Kermack & McKendrick 1927), until recently the quantitative analysis of transient dynamics remained somewhat of a black box. New developments in the field of transient demographic analysis, including those presented in this thesis, should help to broaden the use of transient analyses in population management, comparative ecology, and evolution.

The need for more widespread application of transient analyses is not merely conceptual: as we have shown, transient dynamics are important to population management (Stott, Townley & Hodgson 2011 [Chapter 1]; Stott, Hodgson & Townley 2012a [Chapter 3]; Stott, Hodgson & Townley 2012b [Chapter 2]). Ignoring transients in management of populations can be detrimental in many ways: first, management may not identify and deal with patterns of short-term growth or decline that are antagonistic to management goals. Second, management may have detrimental effects on transients, creating short-term dynamics that are detrimental to management goals. Third, management may overlook the opportunity to exploit transient dynamics to achieve management goals in a more ecologically and economically efficient manner. Few applied ecological studies have considered transient dynamics to date (although see McMahon & Metcalf 2008). The methods and software tools presented here should allow that to change, giving population managers and conservationists the opportunity to

conduct analyses that are more predictive of future population dynamics. In many cases, this could result in management schemes that are more ecologically and economically efficient than would otherwise be possible.

We have also shown the methods presented in this thesis to be useful in comparative analyses of transient dynamics (Stott *et al.* 2010a [Chapter 5]; Chapter 6). The prevalence and importance of transients in nature is poorly understood: again, very few studies have explored ecological and evolutionary patterns of transient dynamics (although see Koons *et al.* 2005; Maron, Horvitz & Williams 2010). There is ample evidence, particularly in the plant ecology literature, which show that observed demographic structures differ from predicted stable demographic structures (Bierzychudek 1999; Doak & Morris 1999; Ramula & Lehtilä 2005; Williams *et al.* 2010). However, there is little consensus on whether such deviations tend to be large or small, and whether they have positive or negative consequences for population dynamics. We have shown that observed demographic structures found in natural populations tend to result in amplification, and that this phenomenon extends to the entire range of possible demographic structures a population may take (Chapter 6). This represents early evidence that natural structuring of populations has important consequences for their dynamics. We have shown that these patterns of response to disturbance show links to a plant's life history and ancestry (Chapter 6) and that populations show heterogeneity in the ways in which they can respond to disturbance (Stott *et al.* 2010a [Chapter 5]). This represents early evidence that the dynamical consequences of natural population structuring may induce selection pressures on transients.

These tantalising early results open the door for substantive research into the ecological and evolutionary importance of transient dynamics, and there are many questions yet to be asked. First of all, we need a greater understanding of transients and what influences them. Our understanding of how long-term population dynamics are shaped is comparatively good, as a result of the numerous studies linking long-term growth to life cycles through perturbation analysis. We know that sensitivity of long-term growth to different vital rates depends on an organism's life history. For example, long-term growth is often more sensitive to changes in survival than fecundity (Carslake, Townley & Hodgson 2009b). In plants, long-term growth in tree populations is relatively more sensitive to individual survival, whilst long-term growth in annual plant populations is relatively more sensitive to fecundity (Silvertown *et al.* 1993; Franco & Silvertown 2004). In mammals, age of first reproduction is more important to long-term growth of animal populations than fecundity *per se* (Oli & Dobson 2003). Having identified that patterns of transient dynamics exist amongst different life forms, the logical next step is to identify what most influences those dynamics. Perturbation analyses are the way to answer this. The best method is debateable: sensitivity analyses (Caswell 2007; Stott, Hodgson & Townley 2012b [Chapter 5]) are amenable to statistical study, but pronounced nonlinearity in

perturbation curves of transients may mean that transfer functions (Stott, Hodgson & Townley 2012b [Chapter 2]) are more accurate, if more unwieldy.

We have linked high demographic resilience to the stage-structuring of life cycles (Chapter 6). An important next step is to explore whether there is enough selection pressure on demographic resilience to favour stage-structured life cycles. This will help answer the question as to whether high demographic resilience is a desirable consequence of stage-structured life histories or whether it may have helped to drive the evolution of stage-structuring. To answer such questions using experiments would require a highly tailored study system: an organism that exhibits a stage-structured life cycle, is amenable to tailored population disturbances, and evolves fast enough to detect changes in the life cycle over the course of a single experiment. In the first instance, *in silico* modelling experiments of the same nature may provide a theoretical support for a selection pressure on transient dynamics. A third option may be to conduct invasion experiments that assess whether populations with higher probability and magnitude of transient amplification have competitive advantage. However, this evidence wouldn't be so concrete in its support for transient dynamics as a target for selection, and it would be very hard to delineate effects of transient demography from confounding competitive effects. Perturbation analyses may also help to understand evolutionary patterns of transient dynamics. They could be effective in identifying the main areas of the life cycle that may be targeted by selection: the vital rates that transient dynamics are most sensitive to.

To fully understand how transient dynamics are shaped, our knowledge of transients will have to move beyond density-independent, non-stochastic models. The advances that have been seen in this modelling framework are substantial, and important, and such models may remain the easiest modelling systems with which to study transients. However, transient analyses will need to be migrated to density-dependent and stochastic modelling systems if we are to gain a full appreciation of how transient dynamics can further our understanding of demography. At present, it is unclear how transient dynamics will fit into these systems. In density-dependent models, transient dynamics will still exist in populations that have densities below carrying capacity. However, we might expect that density-dependent effects will dampen transient dynamics as populations approach carrying capacity. Therefore, whilst it may be possible to study near-term transient dynamics, density-dependent systems may not benefit from the existence of an analogue to population inertia.

The study of transient dynamics in stochastic systems raises even more issues. At one level, deterministic transient dynamics are an integral part of stochastic dynamics, as they are a result of the perturbations and disturbances that characterise stochastic systems. However, there may yet be merit in studying stochastic-transient dynamics of systems that experience occasional, significant disturbance events. Disturbances of large enough magnitude may still result in amplification or attenuation that moves population density outside what may be

reasonably expected of 'normal' stochastic effects. In this respect, stochastic systems may exhibit their own transient dynamics at the stochastic level where, for short time periods following disturbance, population growth is significantly larger or smaller than long-term stochastic growth. In such cases, populations could still see stochastic transient amplification and attenuation both immediately and in the long term.

Another future requirement for a fuller understanding of transients is the migration of transient dynamics to other classes of population model. Integral projection models (IPMs) are gaining popularity as alternatives to PPMs in demographic research (Ellner & Rees 2006, 2007). As these are essentially infinite-dimensional PPM models, the migration of transient analyses to IPMs shouldn't present too much of a conceptual problem. Other popular modelling frameworks include individual-based models (van Winkle, Rose & Chambers 1993), difference equation models (May 1975) and metapopulation models (Hanski 1998). Each of these model classes may stand to gain the same kinds of insight that transient dynamics has afforded PPM modelling. The formulation of meaningful indices of transient dynamics for these systems is an important methodological challenge in population biology.

Finally, as mentioned throughout this thesis, there is merit in considering the application of transient theory to other areas of biology. If transient dynamics have proven to be important in stage-structured populations, then theoretically they may be important in other stage-structured biological systems. Biological systems at all levels of organisation may be considered as 'stage-structured', and often very different systems are modelled in very similar ways. For example, at the level of the gene, matrix models are used to represent genetic algorithms (Nix & Vose 1992). At the level of the cell, matrix models are used to represent stoichiometric metabolic networks (Papin *et al.* 2002; Reed *et al.* 2006). At the level of the community they are used to model species distributions (Cherrill *et al.* 1995). At the level of the ecosystem, they are used to represent energy flow (McGinnis *et al.* 1969). It may prove a simple task to apply the sorts of transient analyses developed in matrix population models to these systems. Many other systems may be considered to be stage-structured, even if they are not modelled using matrices: gene expression networks, hormone regulation, models of disease progression, epidemiological models, food webs, speciation models and nutrient cycles are just a few examples. However, once transient analyses are formulated for various model classes (network models, individual-based models, differential equation models, and so on), the application of those analyses between different biological systems could be a relatively easy process.

Transient theory has come a long way in a short time in the field of population ecology. There are a number of challenges that lie ahead, in both methodological development and in exploring the importance of transients in the ecology and evolution of populations. In any case, transients should have a lot more to offer yet in helping to explain the natural variation found in

population dynamics. Results presented in this thesis suggest that transients may even help explain some of the variety found in the life histories of different species. Indeed, if transient analyses are extended beyond demography to other areas of biological research, they may yet help in explaining all sorts of variation found at other levels of biological organisation, across new scales of time and space.

APPENDICES

APPENDIX 1.1

Detailed information on methodology and results of correlation analyses between transient indices and simulated time to convergence (Chapter 1).

We calculated time to convergence as the time taken for the population to settle to within 1% of predicted asymptotic growth. We did this by projecting population size using the population projection matrix (PPM) and randomly generated case-specific initial demographic distribution, and calculating time-dependent growth (λ_t) at each time interval. Once λ_t remained within a window of $(0.99*\lambda_{max}) < \lambda_t < (1.01*\lambda_{max})$ for $10*s$ intervals (where s is the dimension of the PPM) then convergence was deemed to have been reached. So, for example, a 3×3 matrix with $\lambda_{max}=1.05$ would be considered to be converged within 1% of λ_{max} when it exhibits $0.1395 < \lambda_t < 1.0605$ for 30 consecutive time intervals. The value of $10*s$ was used to prevent miscalculation of convergence: some matrices (especially large Leslie-type matrices with similar mortality and fecundity values for each age class) may exhibit 'stable' growth for many consecutive time intervals, when in fact they have not yet converged. Ensuring that our window for stable growth is much larger than s prevents the algorithm from prematurely thinking that such models may have converged. This is additionally preferable than using the same, very large window for every matrix, as it saves on computation time. The same code for calculating convergence time is included in the function `convergence.time` of the R package `popdemo`.

The first figure in this appendix shows relationships between indices of transient population density and time to convergence. The left hand side of the figure shows distributions of Spearman's correlation coefficient between case-specific transient indices (Table 1.2 in Chapter 1) and time to convergence. These were computed by randomly generating an initial demographic distribution for each PPM, computing case-specific transient indices and time to convergence, and correlating this data. This was then repeated 1000 times to find distributions of correlation coefficients for the indices. The right hand side of the figure shows correlations between the transient bounds on population density (Table 1.2 in Chapter 1) and the median time to convergence for each PPM (over 1000 iterations). Neither transient bounds nor case-specific indices show a strong relationship with time to convergence, indicating that larger transient departures from asymptotic growth are not necessarily linked to a longer time to convergence.

The second figure in this appendix shows results for correlations between the damping ratio and median time to convergence for each PPM. Neither the damping ratio nor estimates of time to convergence using the damping ratio show a strong relationship with realised time to convergence, indicating that the damping ratio is not necessarily a good predictor of realised time to convergence.
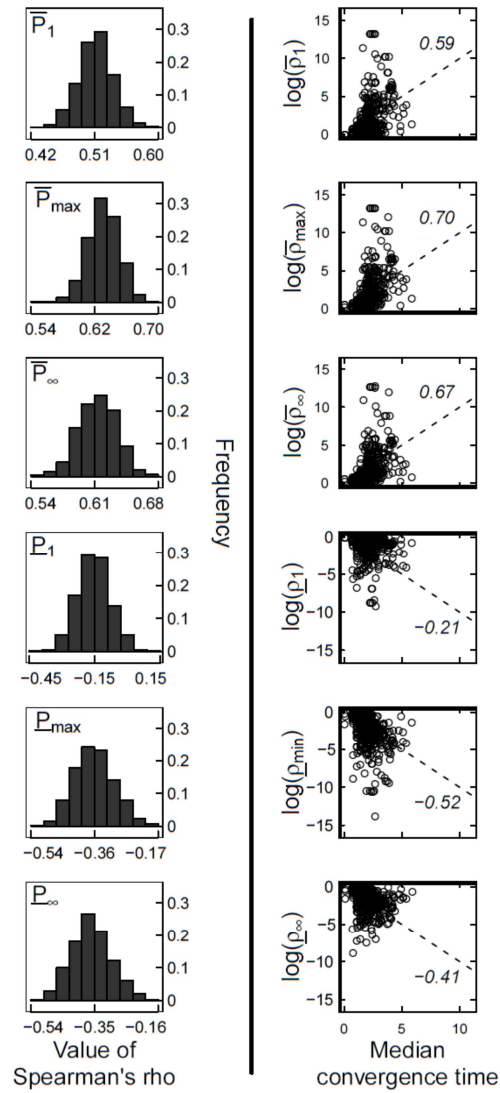
FIG. A1.1.1: Relationships between indices of transient population density and time to convergence.
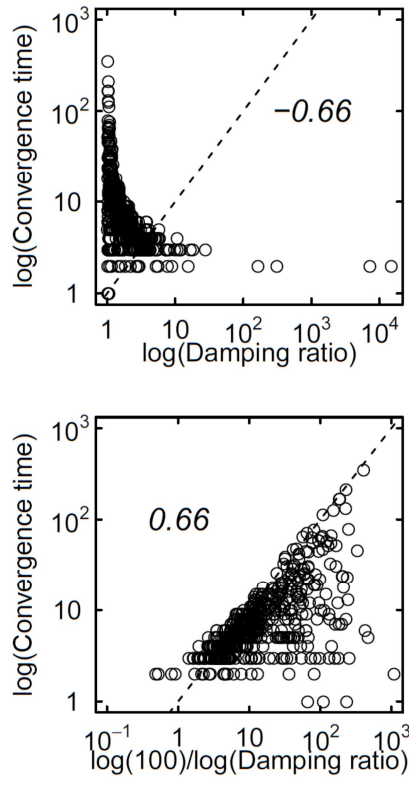
FIG. A1.1.2: Correlations between the damping ratio and median time to convergence.

APPENDIX 1.2

Table of published indices of transient dynamics (Chapter 1).

Some formulae differ slightly to those given in the original articles: we present using a common notation, have simplified some formulae and present some formulae using their analytical solutions. Matrices are presented capitalised, and in bold. Vectors are in small type, and in bold. Numbers and scalars are in normal font. $\|m\|_1$ is the one-norm of m. Where m is a nonnegative vector, this is equal to the sum of all the entries in the vector. Where m is a nonnegative matrix, this is equal to the largest column sum of the matrix. $\mathbf{A}$ represents the population projection matrix; λ_{max} represents 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); represents the current demographic distribution vector of the population. An addition of a hat symbol represents scaling as specified of a vector or matrix.

TRANSIENT INDEX	REFERENCE	FORMULA		NOTES	INTERPRETATION
DAMPING RATIO	Caswell (2001)	Damping ratio $= \dfrac{\|\lambda_{max}\|}{\|\lambda_2\|}$	(1)	Transient bound; measure of convergence rate. λ_2 is the first subdominant eigenvalue of $\mathbf{A}$, including both real and imaginary components where applicable.	The intrinsic resilience of the population to disturbance, excluding the influence of the current demographic distribution.
KEYFITZ'S Δ	Keyfitz (1968)	Keyfitz$'$s $\Delta = \dfrac{1}{2} \|\hat{\mathbf{n}}_0 - \hat{\mathbf{w}}\|_1$	(2)	Distance measure; case-specific. $\hat{\mathbf{n}}_0$ is the current demographic distribution, scaled so that $\|\hat{\mathbf{n}}_0\|_1 = 1$ and $\hat{\mathbf{w}}$ is the stable demographic distribution, where $\hat{\mathbf{w}} = \mathbf{w}/\|\mathbf{w}\|_1$.	The proportional difference between the current and stable demographic distributions, excluding the influence that the PPM has on the path of population projection.

PROJECTION DISTANCE α_0	Haridas & Tuljapurkar (2007)	$\alpha_0 = \hat{\mathbf{v}}^{\mathrm{T}}\mathbf{n_0} - 1$	(3)	Distance measure; case-specific. $\hat{\mathbf{v}}$ is the reproductive value vector scaled so that $\hat{\mathbf{v}}^{\mathrm{T}}\hat{\mathbf{w}} = 1$ with $\hat{\mathbf{w}}$ as in (2).	The difference in the reproductive value of the current and stable demographic distributions.
COHEN'S CUMULATIVE DISTANCE D_1	Cohen (1979)	$D_1 = \left[\left(\mathbf{I} + \hat{\mathbf{w}}\hat{\mathbf{v}}^{\mathrm{T}} - \dfrac{\mathbf{A}}{\lambda_{\max}}\right)^{-1} - \hat{\mathbf{w}}\hat{\mathbf{v}}^{\mathrm{T}}\right]\mathbf{n_0}$	(4)	Distance measure; case-specific. Analytical solution is presented. $\mathbf{I}$ is the identity matrix of same dimension as $\mathbf{A}$; $\hat{\mathbf{v}}$ and $\hat{\mathbf{w}}$ are as in (3).	The distance from current to stable demographic distribution, including the influence that the PPM has on the path of population projection.
POPULATION INERTIA AND MOMENTUM	Koons (2007a); Keyfitz (1971)	$\text{Inertia} = \dfrac{\hat{\mathbf{v}}^{\mathrm{T}}\mathbf{n_0}}{\|\mathbf{n_0}\|_1}$	(5)	Case-specific measure. Simplified formula is presented. $\hat{\mathbf{v}}$ is scaled in the same way as for (3) and (4). Momentum – following the original Keyfitz (1971) definition – is a special case of inertia for a population where $\lambda_{\max} = 1$, following perturbation to vital rates.	The asymptotic density of the population, relative to density that would occur given an initial population with the same overall density but stable demographic distribution.
REACTIVITY	Townley & Hodgson (2008); Neubert & Caswell (1997)	$\text{Reactivity} = \|\hat{\mathbf{A}}\|_1$	(6)	Transient bound. $\hat{\mathbf{A}}$ is the PPM $\mathbf{A}$ scaled by $\lambda_{\max}$.	The maximum overall population density that may be achieved in the first time interval of projection, relative to asymptotic growth and initial population density.

FIRST-TIMESTEP ATTENUATION	Townley & Hodgson (2008)	First timestep attenuation $= \text{minCS}(\widehat{\mathbf{A}})$ (7)	Transient bound. $\widehat{\mathbf{A}}$ is as in (6). minCS denotes the minimum column sum of the matrix.	The minimum overall population density that may be achieved in the first time interval of projection, relative to asymptotic growth and initial population density.
MAXIMUM AMPLIFICATION $\overline{\rho}_{max}$	Townley & Hodgson (2008); Neubert & Caswell (1997)	$\overline{\rho}_{max} = \max_{t>0}\left(\left\|\widehat{\mathbf{A}}^{t}\right\|_{1}\right)$ (8)	Transient bound. $\widehat{\mathbf{A}}$ is as in (6). May be equal to reactivity as defined in (6), and/or $\overline{\rho}_{\infty}$ as defined in (10).	The maximum overall population density that may be achieved, relative to asymptotic growth and initial population density.
MAXIMUM ATTENUATION $\underline{\rho}_{min}$	Townley & Hodgson (2008)	$\underline{\rho}_{min} = \min_{t>0}\left(\text{minCS}(\widehat{\mathbf{A}}^{t})\right)$ (9)	Transient bound. $\widehat{\mathbf{A}}$ and minCS are as in (7). May be equal to first-timestep attenuation as defined in (7) and/or $\underline{\rho}_{\infty}$ as defined in (11).	The minimum overall population density that may be achieved, relative to asymptotic growth and initial population density.
AMPLIFIED ASYMPTOTIC MULTIPLICATION $\overline{\rho}_{\infty}$	Townley & Hodgson (2008)	$\overline{\rho}_{\infty} = \dfrac{v_{max}\|\mathbf{w}\|_{1}}{\mathbf{v}^{T}\mathbf{w}}$ (10)	Transient bound. $\widehat{\mathbf{A}}$ is as in (6). v_{max} is the largest entry of the reproductive value vector $\mathbf{v}$. Equal to population inertia as defined in (5) for the stage-biased demographic vector that achieves $\overline{\rho}_{\infty}$.	The maximum asymptotic population density that may be achieved, relative to asymptotic growth and initial population density.

ATTENUATED ASYMPTOTIC MULTIPLICATION $\underline{\rho}_\infty$	Townley & Hodgson (2008)	$\underline{\rho}_\infty = \dfrac{v_{min}\|\mathbf{w}\|_1}{\mathbf{v}^T\mathbf{w}}$	(11)	Transient bound. $\hat{\mathbf{A}}$ is as in (6). v_{min} is the smallest entry of the reproductive value vector $\mathbf{v}$. Equal to population inertia as defined in (5) for the stage-biased demographic vector that achieves $\underline{\rho}_\infty$.	The minimum asymptotic population density that may be achieved, relative to asymptotic growth and initial population density.
UPPER KREISS BOUND $\overline{K}^*_\lambda$	Townley & Hodgson (2008)	$\overline{K}^*_\lambda = \max_{r>1}(r-1)\left\|(r\mathbf{I}-\hat{\mathbf{A}})^{-1}\right\|_1$	(12)	Transient bound. $\hat{\mathbf{A}}$ is as in (6). $\mathbf{I}$ is the identity matrix with the same dimension as $\mathbf{A}$. Equal to $\overline{\rho}_\infty$ as defined in (10) where maximum occurs at r→1.	The analytical lower bound on maximum amplification as defined in (8).
LOWER KREISS BOUND $\underline{K}^*_\lambda$	Townley & Hodgson (2008)	$\underline{K}^*_\lambda = \min_{r>1}(r-1)\,minCS(r\mathbf{I}-\hat{\mathbf{A}})^{-1}$	(13)	Transient bound. $\hat{\mathbf{A}}$ and minCS are as in (7). $\mathbf{I}$ is as in (12). Equal to $\underline{\rho}_\infty$ as defined in (11) where maximum occurs at r→1.	The analytical upper bound on maximum attenuation as defined in (9).

APPENDIX 2.1

Algebraic proofs of formulae (Chapter 2).

DEFINITION OF TERMS

Throughout, we use a common notation where matrices are presented upper-case bold (e.g. $\mathbf{A}$), vectors are presented lower-case bold (e.g. $\mathbf{a}$), numbers and scalars are presented in normal font (e.g. a) and functions are rendered in italics (e.g. $a(\lambda)$).

A perturbed matrix can be represented as:

$$\mathbf{A}_\delta = \mathbf{A} + \delta\mathbf{d}\mathbf{e}^{\mathrm{T}} \tag{1}$$

where $\mathbf{A}$ is the stage-structured PPM, δ is the perturbation magnitude, and $\mathbf{d}$ and $\mathbf{e}$ are column vectors of the same dimension as $\mathbf{A}$ that determine the perturbation structure. These matrices have some emergent properties relating to asymptotic population dynamics: with respect to $\mathbf{A}$, the dominant eigenvalue λ_{max} represents the long-term (asymptotic) growth of the population, the dominant right eigenvector $\mathbf{w}$ represents the ratio of stages in the stable demographic distribution and the dominant left eigenvector $\mathbf{v}$ represents the reproductive value of each stage. The analogues of these for $\mathbf{A}_\delta$ are termed λ_δ, $\mathbf{w}_\delta$ and $\mathbf{v}_\delta$ respectively.

We use δ to represent a continuous set of perturbation magnitudes:

$$\delta \in \mathbb{R} \,;\, \delta_{\mathrm{min}} \leq \delta \leq \delta_{\mathrm{max}}$$

and λ represents the corresponding set of λ_δ:

$$\lambda \in \mathbb{R} \,;\, 0 < \lambda < \infty \,.$$

TRANSFER FUNCTION OF ASYMPTOTIC GROWTH

If λ is an eigenvalue of $\mathbf{A}_\delta$ then the following is true:

$$1 = \delta\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}$$

therefore,

$$\delta^{-1} = \mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d} \,. \tag{2}$$

This makes it possible to discern the exact relationship between δ and λ.

TRANSFER FUNCTION OF POPULATION INERTIA

Population inertia is calculated using:

$$P_\infty = \frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \|\mathbf{w}\|_1}{\mathbf{v}^T \mathbf{w}} \ . \tag{3}$$

Note that the upper and lower bounds on population inertia ($\bar{\rho}_\infty$ and $\underline{\rho}_\infty$ respectively) are calculated by substituting $\hat{\mathbf{n}}_0$ (the population's demographic distribution, scaled to sum to 1) with $\mathbf{v}_{max}$ or $\mathbf{v}_{min}$, (the standard basis vectors that maximise and minimise population inertia respectively): this is true for all subsequent formulae.

(3) is equivalent to:

$$P_\infty = \frac{\mathbf{v}^T \hat{\mathbf{n}}_0 \mathbf{c}^T \mathbf{w}}{\mathbf{v}^T \mathbf{w}} \tag{4}$$

where $\mathbf{c}$ is a column vector of ones with the same dimension as $\mathbf{A}$. Substituting $\mathbf{v}$ and $\mathbf{w}$ with $\mathbf{v}_\delta$ and $\mathbf{w}_\delta$ respectively will give population inertia of $\mathbf{A}_\delta$. We know that (by definition),

$$\lambda_\delta \mathbf{v}_\delta{}^T = \mathbf{v}_\delta{}^T \mathbf{A}_\delta \ \text{ and } \ \lambda_\delta \mathbf{w}_\delta = \mathbf{A}_\delta \mathbf{w}_\delta \ . \tag{5}$$

Substituting (1) into (5) gives:

$$\lambda_\delta \mathbf{v}_\delta{}^T = \mathbf{v}_\delta{}^T(\mathbf{A} + \delta \mathbf{d} \mathbf{e}^T) \ \text{ and } \ \lambda_\delta \mathbf{w}_\delta = (\mathbf{A} + \delta \mathbf{d} \mathbf{e}^T)\mathbf{w}_\delta \ .$$

Rearranging,

$$\lambda_\delta \mathbf{v}_\delta{}^T - \mathbf{v}_\delta{}^T \mathbf{A} = \delta \mathbf{v}_\delta{}^T \mathbf{d} \mathbf{e}^T \ \text{ and } \ \lambda_\delta \mathbf{w}_\delta - \mathbf{A} \mathbf{w}_\delta = \mathbf{d} \delta \mathbf{e}^T \mathbf{w}_\delta$$

$$\Leftrightarrow \qquad \mathbf{v}_\delta{}^T(\lambda_\delta \mathbf{I} - \mathbf{A}) = \delta \mathbf{v}_\delta{}^T \mathbf{d} \mathbf{e}^T \ \text{ and } \ (\lambda_\delta \mathbf{I} - \mathbf{A})\mathbf{w}_\delta = \mathbf{d} \delta \mathbf{e}^T \mathbf{w}_\delta$$

$$\Leftrightarrow \qquad \mathbf{v}_\delta{}^T = \delta \mathbf{v}_\delta{}^T \mathbf{d} \mathbf{e}^T(\lambda_\delta \mathbf{I} - \mathbf{A})^{-1} \ \text{ and } \ \mathbf{w}_\delta = (\lambda_\delta \mathbf{I} - \mathbf{A})^{-1}\mathbf{d} \delta \mathbf{e}^T \mathbf{w}_\delta \ .$$

Given that $\delta \mathbf{v}_\delta \mathbf{d}$ and $\delta \mathbf{e}^T \mathbf{w}_\delta$ are both non-zero scalars, they can be ignored:

$$\mathbf{v}_\delta{}^T = \mathbf{e}^T(\lambda_\delta \mathbf{I} - \mathbf{A})^{-1} \ \text{ and } \ \mathbf{w}_\delta = (\lambda_\delta \mathbf{I} - \mathbf{A})^{-1}\mathbf{d} \ . \tag{6}$$

Substituting from (6) into (4) and using λ in place of λ_δ gives:

$$P_\infty = \frac{\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\hat{\mathbf{n}}_0\mathbf{c}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\mathbf{d}}{\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\mathbf{d}}.$$ (7)

Hence it is possible to discern the exact relationship between population inertia (whether P_∞, $\overline{\rho}_\infty$ or $\underline{\rho}_\infty$) and λ, and using both (7) and (2) together, it is possible to discern the exact relationship between population inertia and δ.

SENSITIVITY OF POPULATION INERTIA

Using the transfer function method, it is fairly simple to obtain a value for the sensitivity of population inertia through differentiation of the transfer functions themselves. (7) may be represented as:

$$P_\infty = \frac{f_1(\lambda)f_2(\lambda)}{f_3(\lambda)}.$$ (8)

In (8),

$$f_1(\lambda) = \mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\hat{\mathbf{n}}_0 \quad , \quad f_2(\lambda) = \mathbf{c}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\mathbf{d}$$
$$\text{and} \quad f_3(\lambda) = \mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\mathbf{d}.$$ (6)

Differentiating (9) with respect to λ gives:

$$f_1'(\lambda) = -\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\hat{\mathbf{n}}_0 \quad , \quad f_2'(\lambda) = -\mathbf{c}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\mathbf{d}$$
$$\text{and} \quad f_3'(\lambda) = -2\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-3}\mathbf{d}.$$ (7)

Using (9), (10) and the product and quotient rules allows differentiation of (8):

$$\frac{\partial P_\infty}{\partial\lambda} = \lim_{\lambda\to\lambda_{max}}\left\{\frac{f_1'(\lambda)f_2(\lambda)f_3(\lambda) + f_1(\lambda)f_2'(\lambda)f_3(\lambda) - f_1(\lambda)f_2(\lambda)f_3'(\lambda)}{f_3(\lambda)^2}\right\}.$$ (8)

Differentiating (2) with respect to λ and rearranging:

$$0 = \mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\mathbf{d} - \delta\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\mathbf{d}\frac{\partial\lambda}{\partial\delta}$$ (12)

rearranging this,

$$\delta\mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-2}\mathbf{d}\frac{\partial\lambda}{\partial\delta} = \mathbf{e}^T(\lambda\mathbf{I}-\mathbf{A})^{-1}\mathbf{d}$$

so that

$$\frac{\partial \lambda}{\partial \delta} = \frac{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}}{\delta\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-2}\mathbf{d}}.$$

Substituting from (2) gives

$$\frac{\partial \lambda}{\partial \delta} = \frac{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}}{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-2}\mathbf{d}}\,\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}$$

and therefore

$$\frac{\partial \lambda}{\partial \delta} = \lim_{\lambda \to \lambda_{\max}}\left\{\frac{\left(\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-1}\mathbf{d}\right)^2}{\mathbf{e}^{\mathrm{T}}(\lambda\mathbf{I} - \mathbf{A})^{-2}\mathbf{d}}\right\}. \tag{13}$$

In both (11) and (13), the limit as λ approaches $\lambda_{\max}$ must be used to avoid singularity of matrices when $\lambda = \lambda_{\max}$. Finally, the chain rule is used to find the sensitivity of population inertia to δ:

$$\frac{\partial \mathrm{P}_{\infty}}{\partial \delta} = \frac{\partial \mathrm{P}_{\infty}}{\partial \lambda}\frac{\partial \lambda}{\partial \delta}. \tag{14}$$

These formulae are available as part of the R package `popdemo`. The transfer function of inertia can be calculated using the function `inertia.tfa`, and the sensitivity of inertia can be calculated using the function `inertia.tfsens`. The transfer function of asymptotic growth can be calculated using the function `tfa`, and the sensitivity of asymptotic growth can be calculated using `tfsens`.

APPENDIX 2.2

Matrix multi-plots of transfer functions (Chapter 2)

Here we present a series of plots that illustrate the transfer functions of inertia across the cactus (*Neobuxbaumia macrocephala*) and koala (*Phascolarctos cinereus*) life cycles. An individual transfer function is presented for each life cycle transition. Plots are laid out in accordance with the layout of the matrices, so that the position of each plot within the multi-plot indicates which life cycle transition it pertains to. Perturbation ranges are chosen such that fecundity parameters are bounded at a minimum of 0, and a maximum of 5 times the parameter value. Survival/stasis values are bounded at a minimum of 0 and a maximum of either 5 times the parameter value or 1, whichever is smaller. The x axis of each plot is the perturbation value, and the y axis of each plot is the corresponding value of population inertia.
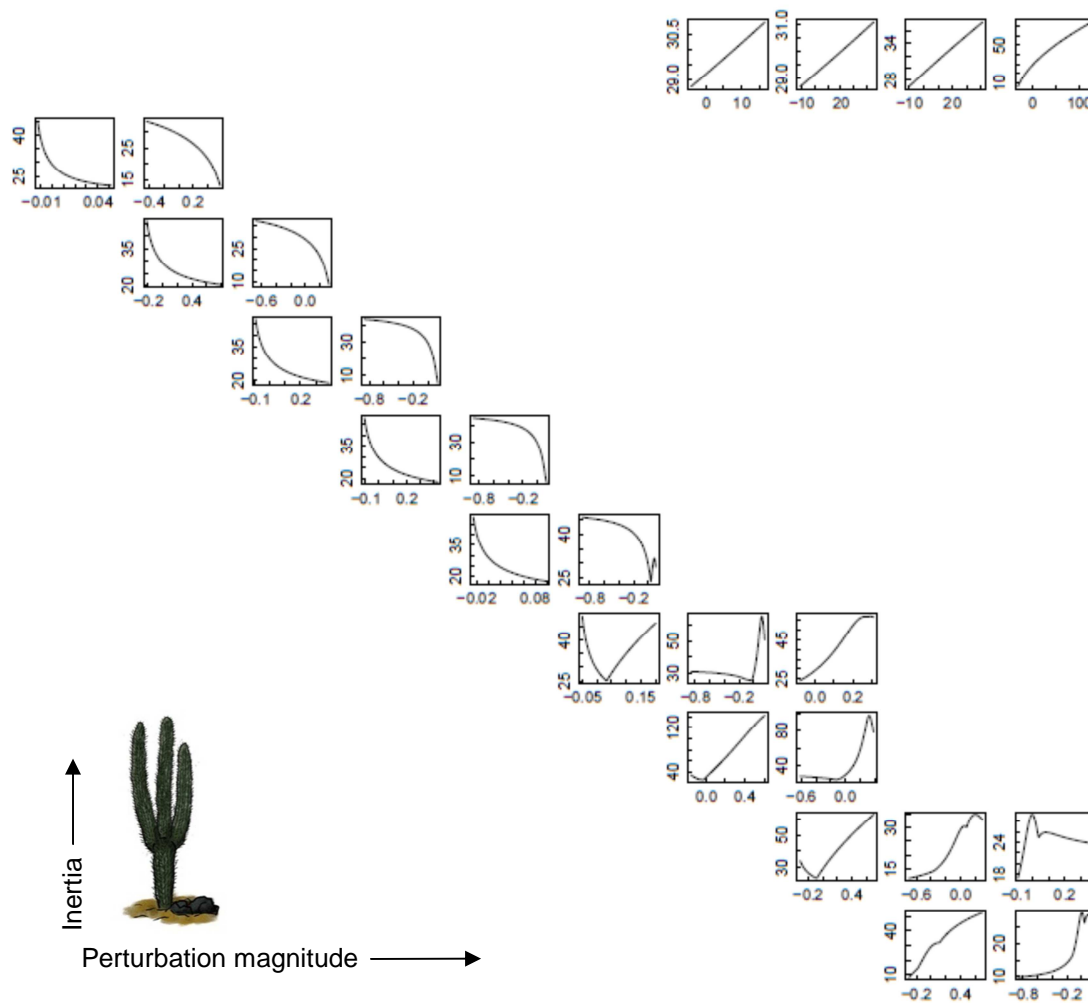
FIG. A2.2.1: Plots for the transfer function of the upper bound on inertia of the cactus model.
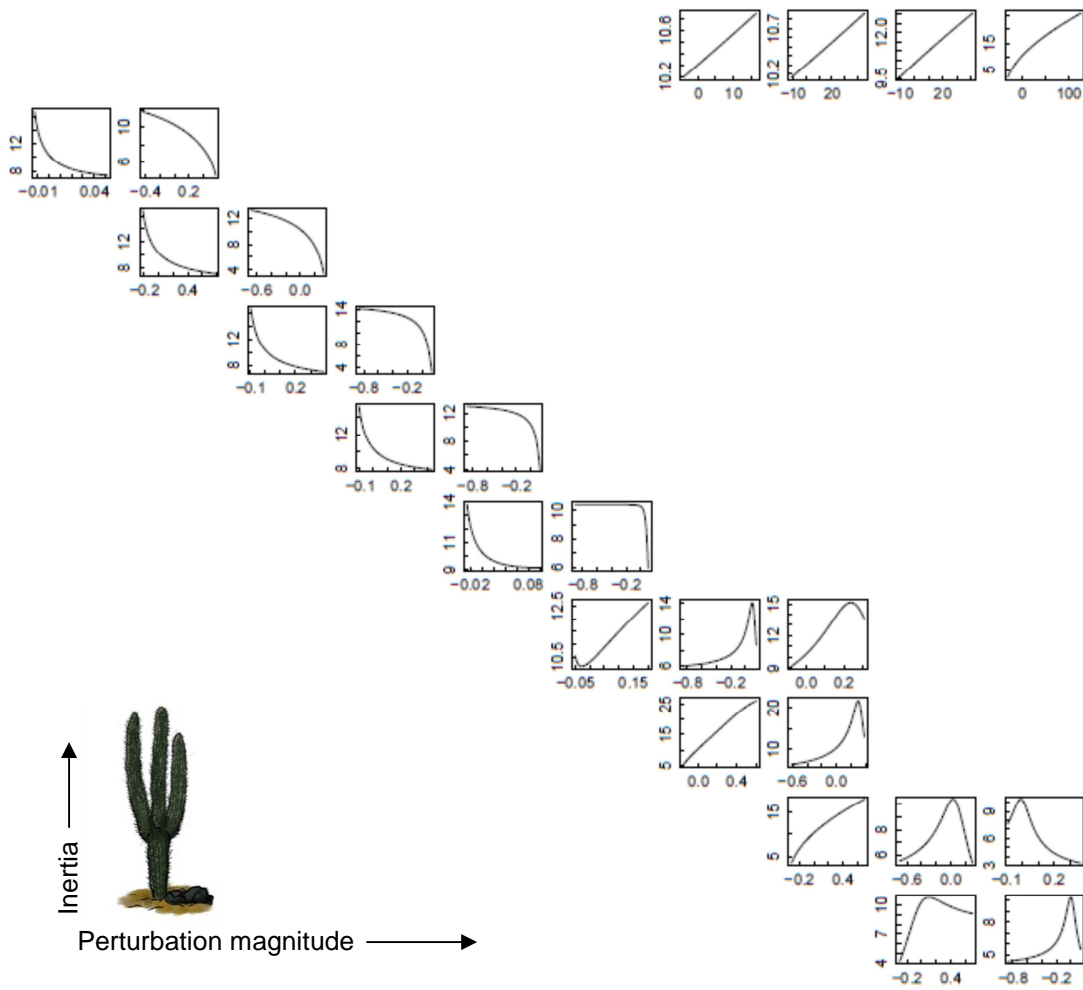
FIG. A2.2.2: Plots for the transfer function of the case-specific inertia of the cactus model for the current population structure.
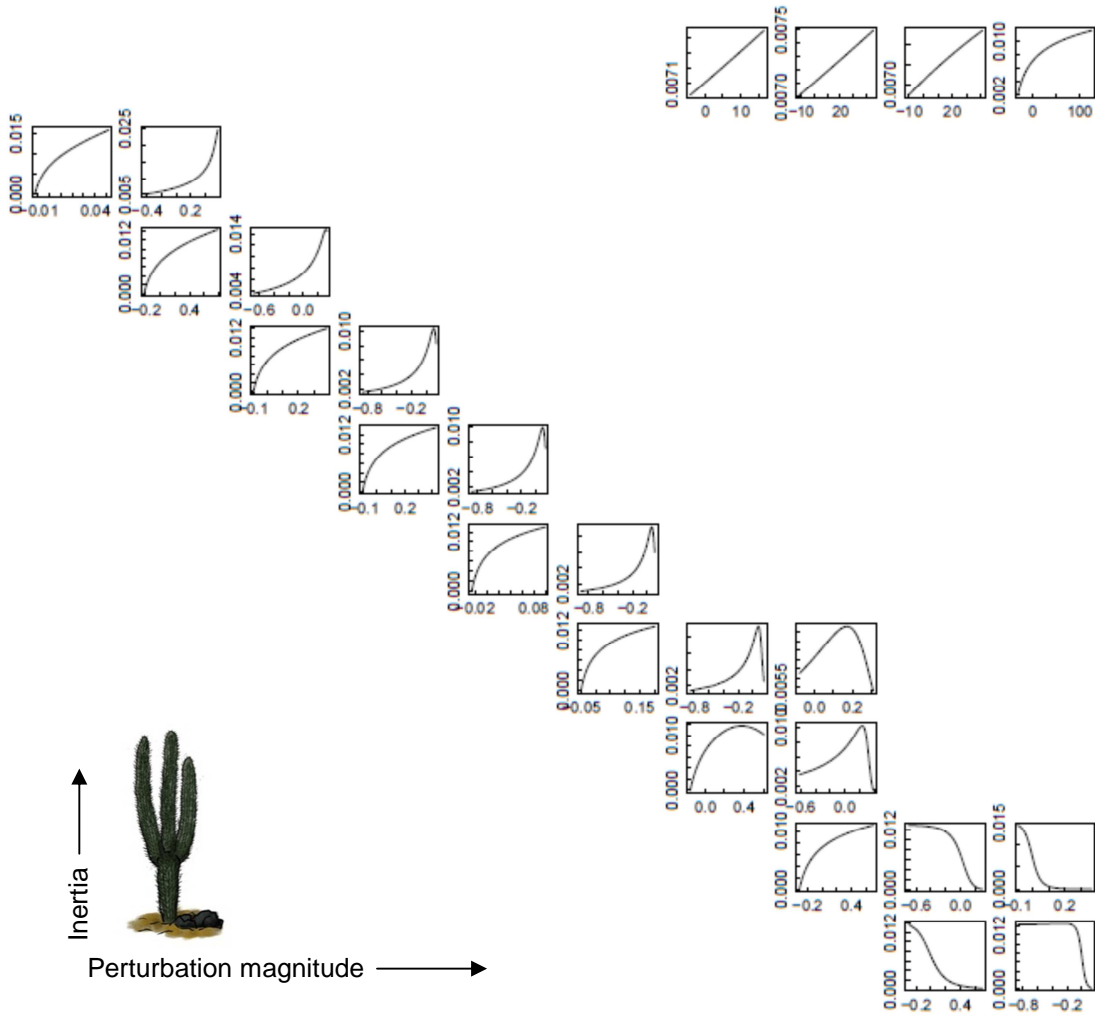
FIG. A2.2.3: Plots for the transfer function of the lower bound on inertia of the cactus model.
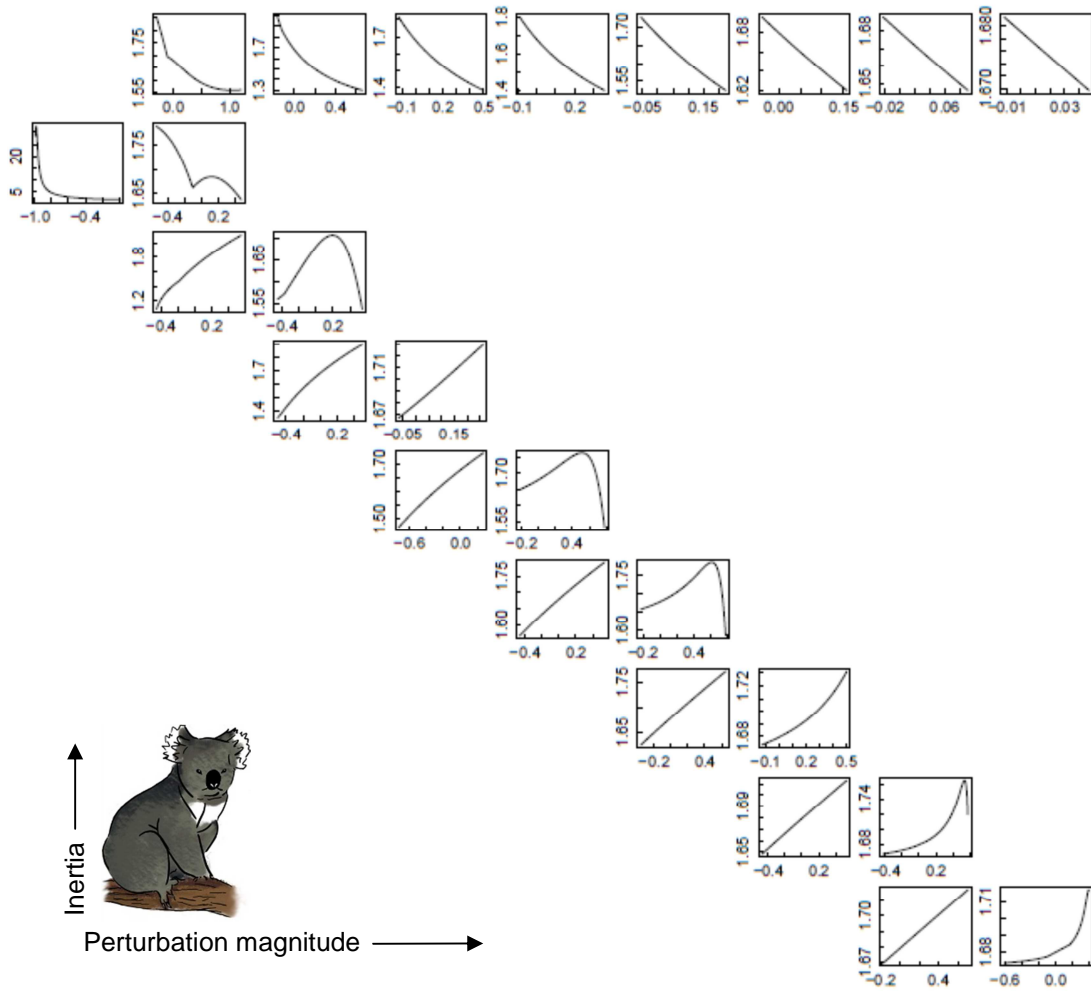
FIG. A2.2.4: Plots for the transfer function of the upper bound on inertia of the koala model.
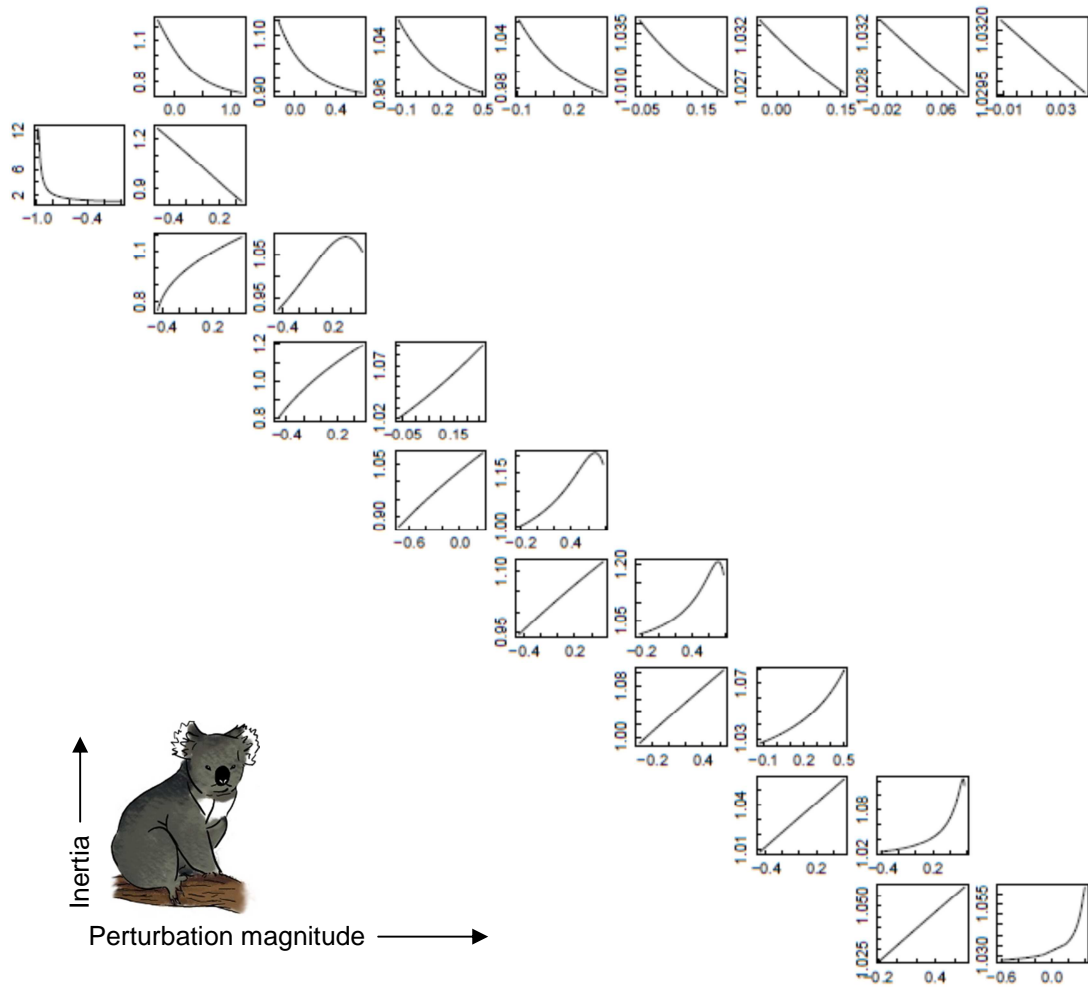
FIG. A2.2.5: Plots for the transfer function of the case-specific inertia of the koala model for the current population structure.
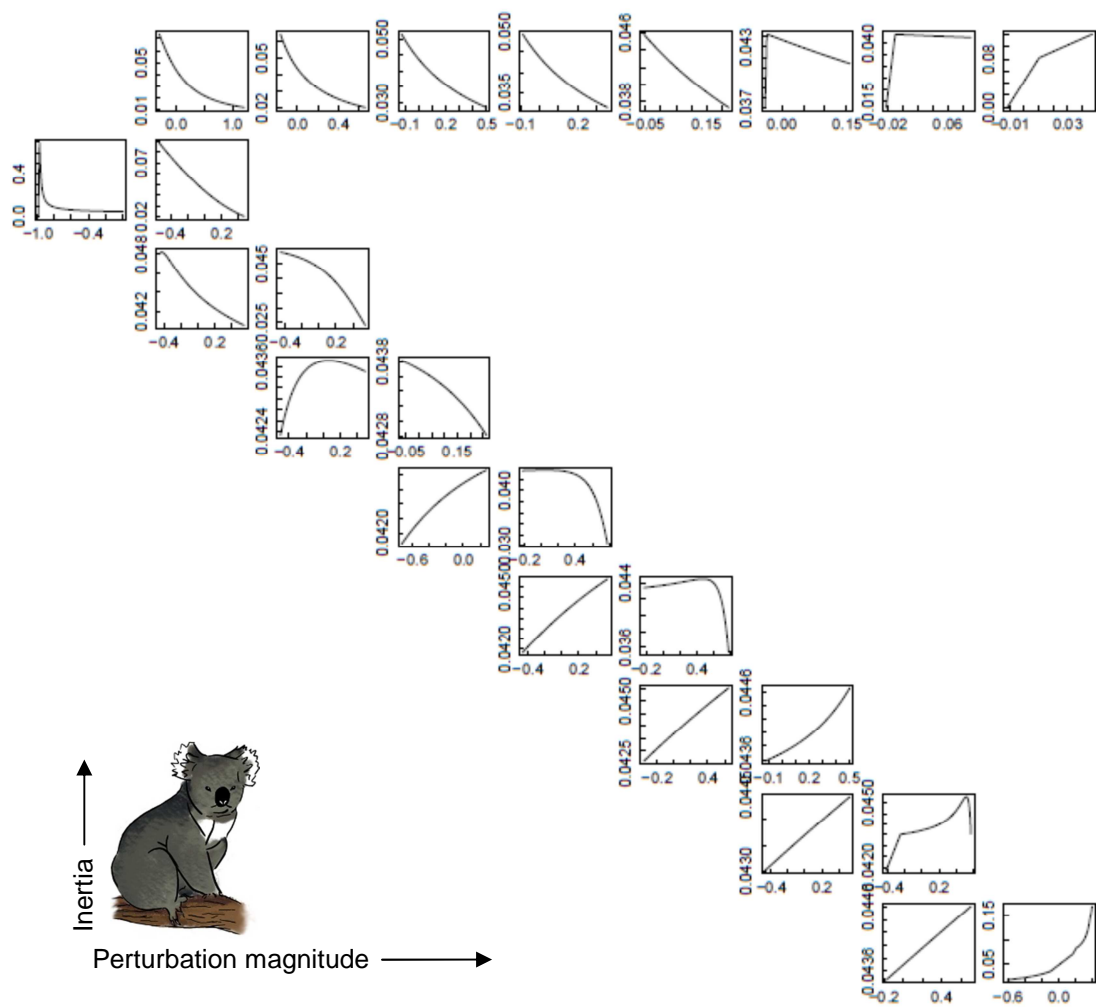
FIG. A2.2.6: Plots for the transfer function of the lower bound on inertia of the koala model.

APPENDIX 3.1

Precise mathematical statement and proof of the ergodicity test (Chapter 3)

A population projection model is ergodic if

$$\lim_{t \to \infty} \left\{ \frac{1}{t} \log(N_t) \right\},$$

i.e. the asymptotic rate of growth of population density is independent of initial population structure. Populations described by irreducible PPMs are ergodic. In many published PPMs, missing transition rates, typically missing growth probabilities caused by lack of observed transitions, lead to reducible population projection matrices. So when is a reducible PPM not ergodic? This non-ergodicity can be detected via long simulation runs by seeking out differences in the asymptotic growth rate of population densities. In fact, we can, as described below, test for ergodicity/non-ergodicity by inspection of the dominant left eigenvector of the PPM.

A reducible PPM **A** will, after permutations of coordinates, take the form

$$\mathbf{A} = \begin{bmatrix} A_1 & U_{12} & \cdots & U_{1q} \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & U_{q-1q} \\ 0 & \cdots & 0 & A_q \end{bmatrix}.$$

Here each A_i is irreducible and typically each column block-matrix

$$U_i = \begin{bmatrix} U_{1i} \\ \vdots \\ U_{i-1i} \end{bmatrix}, \qquad i = 2, \dots, q,$$

formed from the block matrices U_{ij}, contains a non-zero entry. The condition on the U_i means there are no backward hanging chains, i.e. in the decomposition of the life cycle graph of the PPM into sub-graphs determined by the A_i, each sub-graph $i = 2, \dots, q$ is linked by a path back to sub-graph $i = 1$.

In this reducible case, we have observed in our simulation study of the data base of PPMs that the system is ergodic when the dominant eigenvalue of A_1 is the dominant eigenvalue of **A**. To test for such ergodicity, i.e. whether the dominant eigenvalue of A_1 is the dominant eigenvalue of A, we only need to look at the corresponding dominant left eigenvector of **A**.

ERGODICITY TEST

The system is ergodic, i.e. $\lambda(\mathbf{A}) = \lambda(A_1)$, if, and only if, $\mathbf{A}$ has a positive left eigenvector corresponding to the eigenvalue $\lambda(\mathbf{A})$.

PRECISE STATEMENT AND MATHEMATICAL PROOF

Assume that the reducible PPM $\mathbf{A}$ can be mapped via a permutation of coordinates, $x \to \Pi x$, to a form

$$
\mathbf{A_\Pi} = \mathbf{\Pi^{-1}A\Pi} = \begin{bmatrix} A_1 & U_{12} & \cdots & U_{1q} \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & U_{q-1q} \\ 0 & \cdots & 0 & A_q \end{bmatrix},
$$

where

    1. Each A_i, $i = 1,\ldots, q$, is irreducible;

    2. The dominant eigenvalue of $\mathbf{A}$, $\lambda(\mathbf{A})$, is an eigenvalue of only one A_i;

    3. Each column block-matrix

$$
U_i = \begin{bmatrix} U_{1i} \\ \vdots \\ U_{i-1i} \end{bmatrix}, \qquad i = 2, \ldots, q,
$$

        formed from the block matrices U_{ij} , contains a non-zero entry.

Then the dominant eigenvalue of $\mathbf{A}$ is the dominant eigenvalue of A_1 if, and only if, the left eigenvector of $\mathbf{A}$, corresponding to the dominant eigenvalue, is positive.

PROOF

Suppose first that $\lambda(\mathbf{A}) = \lambda(A_1)$. Then by Assumption 1, $\lambda(A_1) > \lambda(A_i)$, for each $i \neq 1$. Using the permuted block form, the left eigenvector equation

$$
\mathbf{v^T A} = \lambda(A_1)\mathbf{v^T}
$$

Becomes

$$
[v_1^T, \ldots, v_q^T] \begin{bmatrix} A_1 & U_{12} & \cdots & U_{1q} \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & U_{q-1q} \\ 0 & \cdots & 0 & A_q \end{bmatrix} = \lambda(A_1)[v_1^T, \ldots, v_q^T]
$$

where

$$\mathbf{v}^T \mathbf{\Pi}^{-1} = \left[v_1^T, \ldots, v_q^T \right].$$

Then

$$v_1^T A_1 = \lambda(A_1) v_1^T$$

and irreducibility of A_1 means that this equation has a positive solution v_1. Then

$$v_1^T U_{12} + v_2^T A_2 = \lambda(A_1) v_2^T$$

and since $\lambda(A_2) < \lambda(A_1)$ we have that

$$v_2^T = v_1^T U_{12}(\lambda(A_1)I - A_2)^{-1}.$$

But

$$v_2^T = v_1^T U_{12}(\lambda(A_1)I - A_2)^{-1} = \frac{1}{\lambda(A_1)} \left(I + \frac{A_2}{\lambda(A_1)} + \left(\frac{A_2}{\lambda(A_1)} \right)^2 + \cdots \right)$$

is positive because of the irreducibility of A_2. Hence

$$v_2^T = v_1^T U_{12}(\lambda(A_1)I - A_2)^{-1}.$$

is positive. Continuing that we have that

$$v_1^T U_{13} + v_2^T U_{23} + v_3^T A_3 = \lambda(A_1) v_3^T.$$

Then

$$v_3^T = \lambda(\mathbf{A}) \mathbf{v}^T = \lambda(A_k) \mathbf{v}^T$$

becomes

$$\left[v_1^T, \ldots, v_q^T \right] \begin{bmatrix} A_1 & U_{12} & \cdots & U_{1q} \\ 0 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & U_{q-1q} \\ 0 & \cdots & 0 & A_q \end{bmatrix} = \lambda(A_k) \left[v_1^T, \ldots, v_q^T \right].$$

165

Then

$$v_1^T A_1 = \lambda(A_k) v_1^T.$$

But $\lambda(A_k)$ is not an eigenvalue of A_1, therefore $v_1 = 0$ and $\mathbf{v}$ is not positive.

Notice that when $\mathbf{A}$ is ergodic in the sense that $\mathbf{A}$ can be permuted to the block form with $\lambda(A_1)$ dominant, then the eigenmode expansion of the solution of

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

is

$$\mathbf{n}_t = \lambda(\mathbf{A})^t \frac{\mathbf{v}^T \mathbf{n}_0}{\mathbf{v}^T \mathbf{w}} \mathbf{w} + other\ terms\,,$$

Where some of the 'other terms' may, if A_1 is imprimitive, grow geometrically like $\lambda(\mathbf{A})^t$ but oscillate with the rest decaying faster than $\lambda(\mathbf{A})^t$, but possibly with oscillations. Importantly, $\mathbf{n}_0$ and $\mathbf{w}$ are non-negative, non-zero vectors, which combined with positivity of $\mathbf{v}$ guarantees that

$$\frac{\mathbf{v}^T \mathbf{n}_0}{\mathbf{v}^T \mathbf{w}}$$

Is positive and finite. It follows that

$$\lim_{t \to \infty} \left\{ \frac{1}{t} \log(N_t) \right\},$$

i.e. the asymptotic rate of growth of population density, is independent of initial population structure.

APPENDIX 3.2

Notes on block-permuting a reducible matrix by hand (Chapter 3)

Here, we provide a step-by-step walkthrough of methods to block-permute a reducible matrix by hand. The method mainly uses the life cycle graph associated with the matrix. The method is illustrated using a reducible matrix based upon the matrix used in our theoretical models. The empirical reducible matrices are shown as further examples. Block-permuting a reducible matrix is sometimes not an easy process – how simple a process it is will depend on the size of the matrix and the number of isolated sections there are in the life cycle. The R package `popdemo` contains a function `blockmatrix` that will block-permute a reducible matrix quickly and easily (with sufficient notes and annotation to allow translation of the code to other programs capable of matrix multiplication).

METHOD

Start with a reducible PPM. For this example, we have taken the PPM used in our theoretical models and eliminated transition rates $a_{4,3}$, and $a_{5,6}$.

	1	2	3	4	5	6
1	0.5	0.01	0.75	1	1.25	1.5
2	0.1	0.525	0.01			
3		0.08	0.55	0.01		
4				0.575	0.01	
5				0.04	0.6	
6					0.02	0.625

Step 1: Draw the life cycle graph associated with this PPM. It's easiest if all arrows that move forwards through the life cycle are drawn below arrows that move backwards through the life cycle.

In this example, the life cycle is:
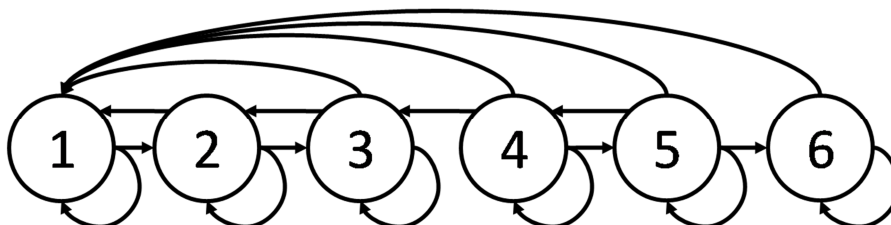
Step 2: Identify groups of stages in the life cycle that communicate fully with one another (i.e. have transitions that link every stage in the group with every other stage in the group). The

easiest way to do this is to find the longest loops in the life cycle. A group may constitute any number of stages (i.e. a 'group' of just one stage is possible).

In this example, there are 3 groups: [1,2,3], [4,5] and [6]. These groups and the life cycle loops associated with them are indicated in red below.
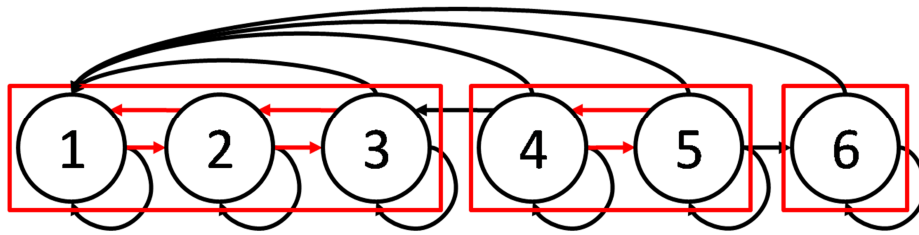
Step 3: Write out a simplified life cycle using these groups instead of individual stages. Arrows indicate which groups contribute to which other groups. There should be no loops in this simplified, group-based life cycle. Again, try to keep arrows moving forwards through the life cycle below arrows moving backward through the life cycle.

In this example, group [4,5] contributes to both other groups, and group [6] contributes to group [1,2,3].
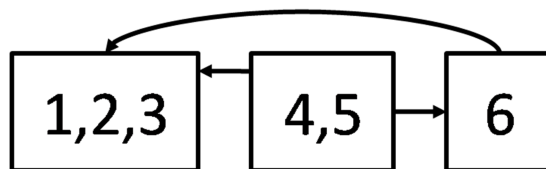
Step 4: Re-write the simplified life cycle so that arrows ONLY face backwards. If steps 1, 2 and 3 have been done correctly then this should be possible. A useful tip is to identify whether the groups have transitions in but not out, out but not in, or both out and in. Groups with transitions in but not out go on the left. Groups that have transitions out but not in go on the right. Groups with transitions both out and in go in the middle. Note that there may be more than one way to do this (see example for *Ardisia escallonioides*, below), and some block-permuted forms are easier to intuitively understand than others.

In this example:
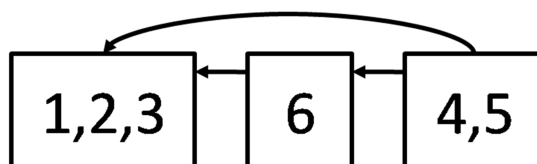
Step 5: Re-write the matrix with the columns and rows in this order. The order of stages within groups does not matter.

So the block-permuted matrix looks something like this:

	1	2	3	6	4	5
1	0.05	0.01	0.75	1.5	1	1.25
2	0.1	0.525	0.01			
3		0.08	0.55		0.01	
6				0.625		0.02
4					0.575	0.01
5					0.04	0.6

EMPIRICAL EXAMPLES

NUTTALLIA OBSCURATA

	1	2	3	4	5
1	0.026	0.002	0.009	0.034	0.062
2		0.126			
3	0.326	0.564	0.428		
4			0.211	0.547	
5				0.095	0.716

Step 1:
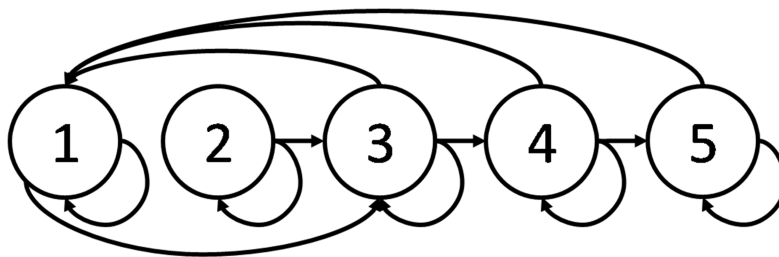
Step 2:
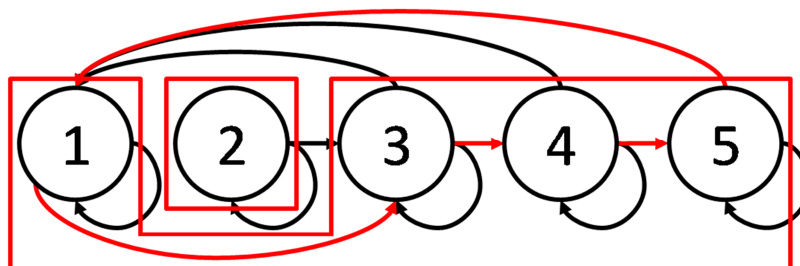
There are 2 groups: [2] and [1,3,4,5].

Step 3:
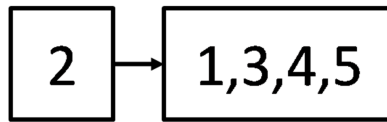
Step 4:
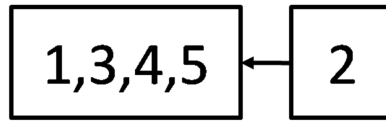
Step 5: The block-permuted matrix is:

	1	3	4	5	2
1	0.026	0.009	0.034	0.062	0.002
3	0.326	0.428			0.564
4		0.211	0.547		
5			0.095	0.716	
2					0.126

ARDISIA ESCALLONIOIDES

	1	2	3	4	5	6	7	8
1					0.9	2.3	2.6	0.8
2	0.1							
3		0.7	0.95	0.17				
4			0.01	0.66				
5				0.17	0.96			
6					0.04	0.88	0.04	
7							0.96	
8								1

Step 1:
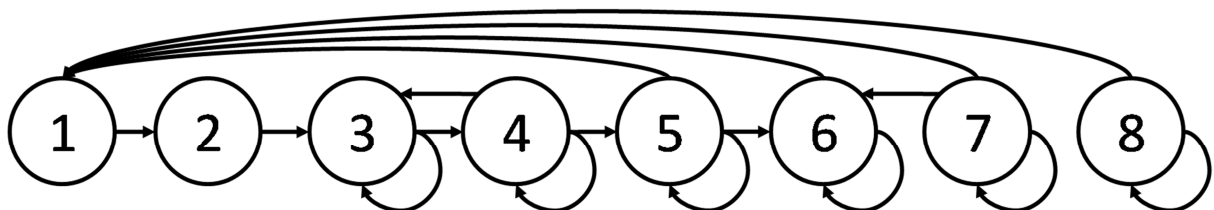
Step 2:
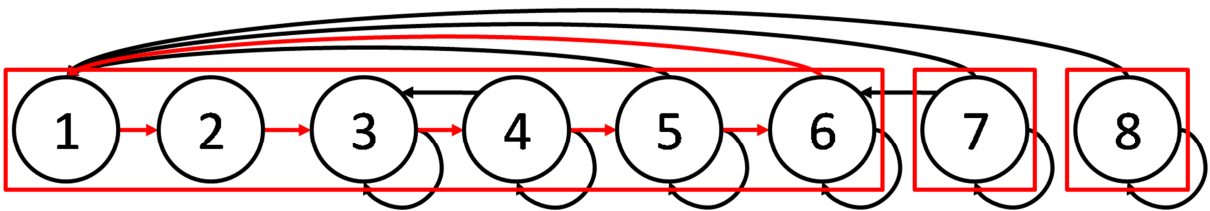
There are 3 groups: [1,2,3,4,5,6], [7] and [8].

Step 3:
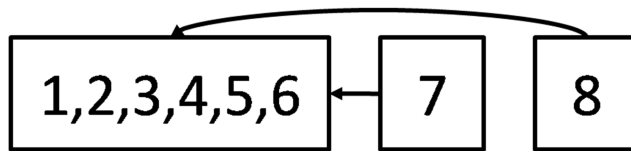
All arrows are facing backwards already. However, in this case, this could also be represented as:
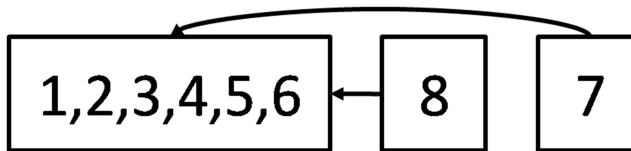
Both of these lead to correct block-permutations of the matrix. As detailed in the manuscript, the situation that results is one where two (or more) submatrices are not fixed relative to one another, therefore their eigenvalues are not dominant relative to one another.

Step 5: The block-permuted matrix is:

	1	2	3	4	5	6	7	8
1					0.9	2.3	2.6	0.8
2	0.1							
3		0.7	0.95	0.17				
4			0.01	0.66				
5				0.17	0.96			
6					0.04	0.88	0.04	
7							0.96	
8								1

Or:

	1	2	3	4	5	6	8	7
1					0.9	2.3	0.8	2.6
2	0.1							
3		0.7	0.95	0.17				
4			0.01	0.66				
5				0.17	0.96			
6					0.04	0.88		0.04
8							1	
7								0.96

PINUS JEFFREYI

	1	2	3	4	5
1	0.804				0.073
2	0.174	0.792			
3		0.167	0.944		
4			0.028	0.778	
5					0.945

Step 1:
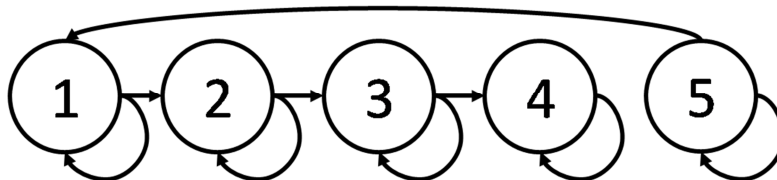
Step 2:
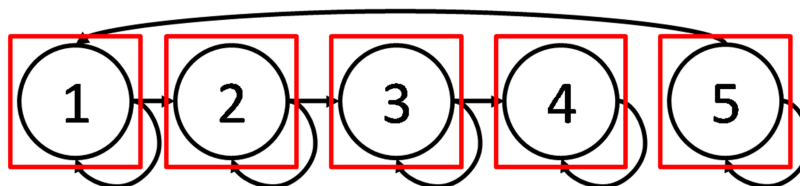
There are 5 groups: [1], [2], [3], [4] and [5].

Step 3:
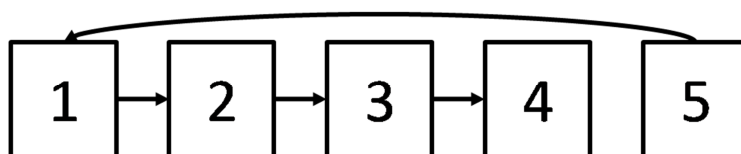
Step 4:
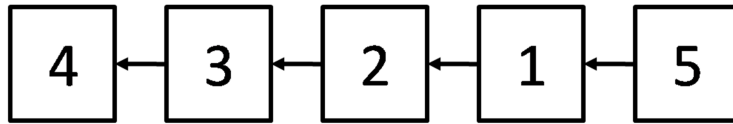
4 ← 3 ← 2 ← 1 ← 5

Step 5: The block-permuted matrix is:

	4	3	2	1	5
4	0.778	0.028			
3		0.994	0.167		
2			0.792	0.174	
1				0.804	0.073
5					0.945

APPENDIX 4.1

R code for figures (Chapter 4)

```
#This appendix provides R code for producing the figures included in the main
#manuscript.
#
#Install the library using install.packages() or by downloading from
#http://cran.R-project.org
#Load the library
library(popdemo)
#
#These figures use a matrix for the desert tortoise Gopherus agassizii:
data(Tort)

#This matrix is size-based, with medium fecundity. The size classes are as
#follows:
#1: Yearling
#2: Juvenile 1
#3: Juvenile 2
#4: Immature 1
#5: Immature 2
#6: Subadult
#7: Adult 1
#8: Adult 2




##########################################################################

#FIGURE 1: POPULATION PROJECTION
#
#This figure is designed to be 3.5" by 3.5"
#(Check size of plot window using 'par(din)').
#
#
#Set margins:
par(mar=c(5,4,1,1))

#Create a population vector.  This one is biased towards adults.
Tortvec<-c(1,1,2,3,5,8,13,21)

#Project the tortoise PPM and population vector.  In this case, we are
#projecting for 50 time intervals.  The torotoise interval is one year, so
#this projection is for 50 years.  We use the function 'project'.
pr1 <- project(Tort, vector=Tortvec, time=50)
```

```
#Plot the projection. This uses an S3 plotting method for projections. For
#info, see '?plot.projection'.
plot(pr1)

#For a primitive matrix (see below), the long-term growth rate is the real
#part of the first dominant eigenvalue of the PPM.
eigs<-eigen(Tort)
lambdamax<-Re(eigs$values[1])
lambdamax

#the dominant right eigenvector is the absolute value of the real part of the
#first eigenvector
w<-abs(Re(eigs$vectors[,1]))
w

#Note that the package popbio provides functions 'lambda' and 'stable.stage'
#that will provide these also.

#For more info on projecting population dynamics, see demo(projection).



##########################################################################

#FIGURE 2: TRANSIENT DYNAMICS

#_____
#
#Fig. 2a: Population-specific transient dynamics
#
#This figure is designed to be 3.5" by 3.5"
#(Check size of plot window using 'par(din)').
#
#Set margins:
par(mar=c(5,4,1,1))

#Create 2 population vectors.  One is adult-biased, and it amplifies.  One is
#juvenile-biased and it attenuates.
Tortamp <- c(1,1,2,3,5,8,13,21)
Tortatt <- c(21,13,8,5,3,2,1,1)

#Project these vectors using the project function. We are standardising the
#matrix using 'standard.A=T' to remove effects of asymptotic dynamics. This
#means that the projection has a long-term growth rate of unity, i.e. it does
#not grow or decline in the long-term.  We also standardise the population
#vector to sum to 1 using 'standard.vec=T'. These standardisations make it
```

175

```
#easier (and fairer) to compare between models with different population
#sizes, and different long-term growth rates.
pr2.1 <- project(Tort, vector=Tortamp, time=50,
                 standard.A=T, standard.vec=T)
pr2.2 <- project(Tort, vector=Tortatt, time=50,
                 standard.A=T, standard.vec=T)


#Plot the amplification projection and label it
plot(pr2.1, ylim=c(0.5,10), log="y", cex.axis=0.8)
text(52, pr2.1[51], "amplification",
     adj=c(1,-0.5), cex=0.8)


#Calculate the transient dynamics of the amplification projection
reac <- reactivity(Tort, vector=Tortamp)
maxamp <- maxamp(Tort, vector=Tortamp, return.t=T)
upinertia <- inertia(Tort, vector=Tortamp)


#Add points on the projection for amplification and label them
points(c(1,maxamp$t,31), c(reac,maxamp$maxamp,upinertia),
       pch=3, col="red")
text(1, reac, expression(bar(P)[1]),
     adj=c(-0.3,0.5), col="red", cex=0.8)
text(maxamp$t, maxamp$maxamp, expression(bar(P)[max]),
     adj=c(0.1,-0.5), col="red", cex=0.8)
text(31, upinertia, expression(bar(P)[infinity]),
     adj=c(0.1,-0.5), col="red", cex=0.8)


#Add in the second projection using the 'lines' command and label it
lines(0:50, pr2.2)
text(52, pr2.2[51], "attenuation", adj=c(1,1), cex=0.8)


#Calculate the transient dynamics of the attenuation projection
firstep <- firststepatt(Tort, vector=Tortatt)
maxatt <- maxatt(Tort, vector=Tortatt, return.t=T)
lowinertia <- inertia(Tort, vector=Tortatt)


#Add points on the attenuation projection and label them
points(c(1,maxatt$t,31), c(firstep,maxatt$maxatt,lowinertia),
       pch=3, col="red")
text(1, firstep, expression(underline(P)[1]),
     adj=c(0,-0.6), col="red", cex=0.8)
text(maxatt$t, maxatt$maxatt, expression(underline(P)[min]),
     adj=c(0.1,1.5), col="red", cex=0.8)
text(31, lowinertia, expression(underline(P)[infinity]),
     adj=c(0.1,1.5), col="red", cex=0.8)


#Add in a dotted line at y=1
```

176

```
lines(c(0,50),c(1,1),lty=2)


#_____


#Fig. 2b: Transient bounds
#This figure is designed to be 3.5" by 3.5"
#(Check size of plot window using 'par(din)').
#
#Set margins:
par(mar=c(5,4,1,1))


#Transient bounds result from projections of the stage-biased dynamics of the
#model. When using the function 'project', the stage-biased model dynamics are
#projected automatically if no population vector is specified. We can do this
#for the desert tortoise, using a standardised matrix like before:
pr2 <- project(Tort, standard.A=TRUE, time=50)


#Now we need to plot these population dynamics. The S3 method for projections
#automatically plots all stage-biased projections:
plot(pr2, log="y", cex.axis=0.8, ylim=c(0.1,10))


#Add in a dotted line at y=1
lines(c(0,50), c(1,1), lty=2)


#Calculate the bounds on transient dynamics for the desert tortoise.  This is
#also done automatically if no population vector is specified.
reacb<-reactivity(Tort)
firstepb<-firststepatt(Tort)
maxampb<-maxamp(Tort,return.t=T)
maxattb<-maxatt(Tort,return.t=T)
upinertiab<-inertia(Tort, bound="upper")
lowinertiab<-inertia(Tort, bound="lower")


#Add points on the projection and label them
points(c(1,1,maxampb$t,maxattb$t,31,31),
       c(reacb,firstepb,maxampb$maxamp,maxattb$maxatt,upinertiab,lowinertiab),
       pch=3,col="red")
text(1, reacb, expression(bar(rho)[1]),
     adj=c(-0.5,0.5), col="red", cex=0.8)
text(1, firstepb, expression(underline(rho)[1]),
     adj=c(-0.5,1.5), col="red", cex=0.8)
text(maxampb$t, maxampb$maxamp, expression(bar(rho)[max]),
     adj=c(0.1,-0.5),col="red",cex=0.8)
text(maxattb$t, maxattb$maxatt, expression(underline(rho)[min]),
     adj=c(0.1,1.5), col="red", cex=0.8)
text(31, upinertiab, expression(bar(rho)[infinity]),
     adj=c(0.1,-0.5), col="red", cex=0.8)
```

```
text(31, lowinertiab, expression(underline(rho)[infinity]),
     adj=c(0.1,1.5), col="red", cex=0.8)


#Amplification bounds result from the projection of a population with 100%
#stage 8 individuals.  Attenuation bounds result from the projection of a
#population with 100% stage 1 individuals.




###############################################################################

#FIGURE 3: TRANSFER FUNCTIONS


#_____


#Fig. 3a: Transfer function of asymptotic growth
#
#This figure is designed to be 3.5" by 3.5"
#(Check size of plot window using 'par(din)').
#
#Set margins:
par(mar=c(5,4,1,1))


#Create a transfer function using 'tfa'. The perturbation structure is
#determined by two vectors d and e.  The matrix d%*%e gives the structure,
#where nonzero elements in this matrix are the elements of the PPM to be
#perturbed.  The relative size of entries in this matrix are the relative
#sizes of perturbation to those elements. In this case, we are perturbing
#element [8,7]. We are going to look at the effect of perturbing up to 0.25.
#The largest biologically reasonable perturbation is about 0.12.
tf1 <- tfa(Tort, d=c(0,0,0,0,0,0,0,1), e=c(0,0,0,0,0,0,1,0),
          prange=seq(0,0.25,0.01))


#Now we plot this using an S3 method for transfer functions (for information
#see '?plot.tfa').
plot(tf1, cex.axis=0.8)


#Now we're going to add in the sensitivity tangent.  This has an intercept of
#lambda-max, and a slope of the sensitivity of the same transfer function.
#Calculate lambda-max of the desert tortoise PPM:
lambda <- Re(eigen(Tort)$values[1])


#Calculate the sensitivity using the function 'tfsens':
sens1<-tfsens(Tort, d=c(0,0,0,0,0,0,0,1), e=c(0,0,0,0,0,0,1,0))


#Now add in the line, specifying the correct intercept and slope:
abline(lambda, sens1, lty=2, col="red")
```

```
#_____

#Fig. 3b: Transfer function of population inertia
#
#This figure is designed to be 3.5" by 3.5"
#(Check size of plot window using 'par(din)').
#
#Set margins:
par(mar=c(5,4,1,1))

#The process is very similar to above.  We need to specify a PPM, perturbation
#structure and perturbation range.  For inertia we either have to specify a
#population vector using the 'vector' argument, or the bound to be calculated
#using the 'bound' argument. Create a population vector:
Tortvec <- c(1,1,2,3,5,8,13,21)

#Now calculate the transfer function using inertia.tfa:
tf2 <- inertia.tfa(Tort, vector=Tortvec, d=c(0,0,0,0,0,0,0,1),
                   e=c(0,0,0,0,0,0,1,0), prange= seq(0,0.25,0.01))

#Plot the transfer function using the same S3 method as before:
plot(tf2,cex.axis=0.8,ylim=c(3.9,4.43))

#The sensitivity tangent for transfer function of inertia has an intercept of
#equal to the relevant inertia (either using the same population vector, or
#the correct bound), and a slope of the sensitivity of the same transfer
#function. Calculate inertia of the desert tortoise PPM using the population
#vector:
inertia <- inertia(Tort, vector=Tortvec)

#Calculate the sensitivity using the function 'inertia.tfsens':
sens2 <- inertia.tfsens(Tort, vector=Tortvec, d=c(0,0,0,0,0,0,0,1),
                        e=c(0,0,0,0,0,0,1,0), tolerance=1e-5)

#(Here the 'tolerance' has had to be lowered to avoid calculation error: try
#the function without that argument and it will have trouble running)

#Now add in the line, specifying the correct intercept and slope:
abline(inertia, sens2, lty=2, col="red")



##########################################################################

#FIGURE 4: TRANSFER FUNCTION MATRIX
#
```

```
#This figure is designed to be 7" by 7"
#(Check size of plot window using 'par(din)').
#
#This is a nice, easy plot because the function does it all for you. The
#functions 'tfmat' and 'inertia.tfmat' calculate a transfer function for every
#PPM element.  They are saved as arrays of values.  The functions are
#customisable: see '?tfmat' and '?inertia.tfmat'.
#
#Create the array for inertia, using a specific population vector:
Tortvec <- c(1,1,2,3,5,8,13,21)
tfmat<-inertia.tfamatrix(Tort, vector=Tortvec)


#...and plot it!
plot(tfmat)
```

APPENDIX 5.1

Detailed results from principal components analyses (Chapter 5)
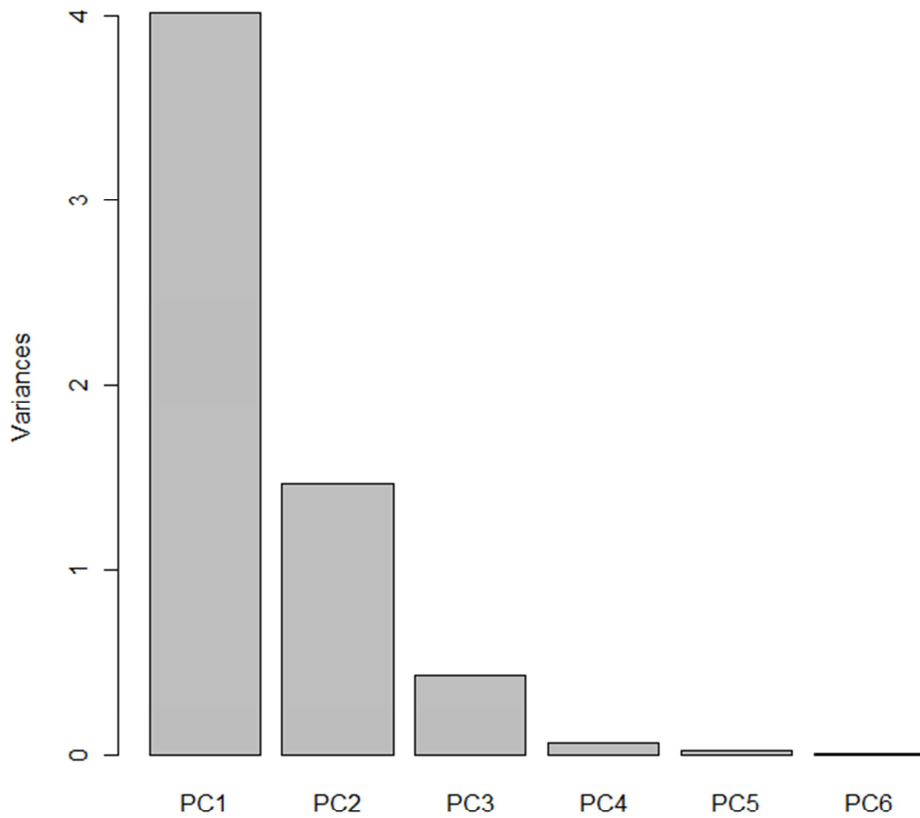
FIG. A5.1.1: Barplot of variance explained by the principal components

TABLE A5.1.1: Table of variances according to principal component, detailing percentage and cumulative percentages explained. PC1 and PC2 explain >90% of variance in all transient indices.

	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	2.003	1.212	0.6563	0.2526	0.15039	0.05195
Proportion of Variance	0.669	0.245	0.0718	0.0106	0.00377	0.00045
Cumulative Proportion	0.669	0.913	0.9851	0.9958	0.99955	1
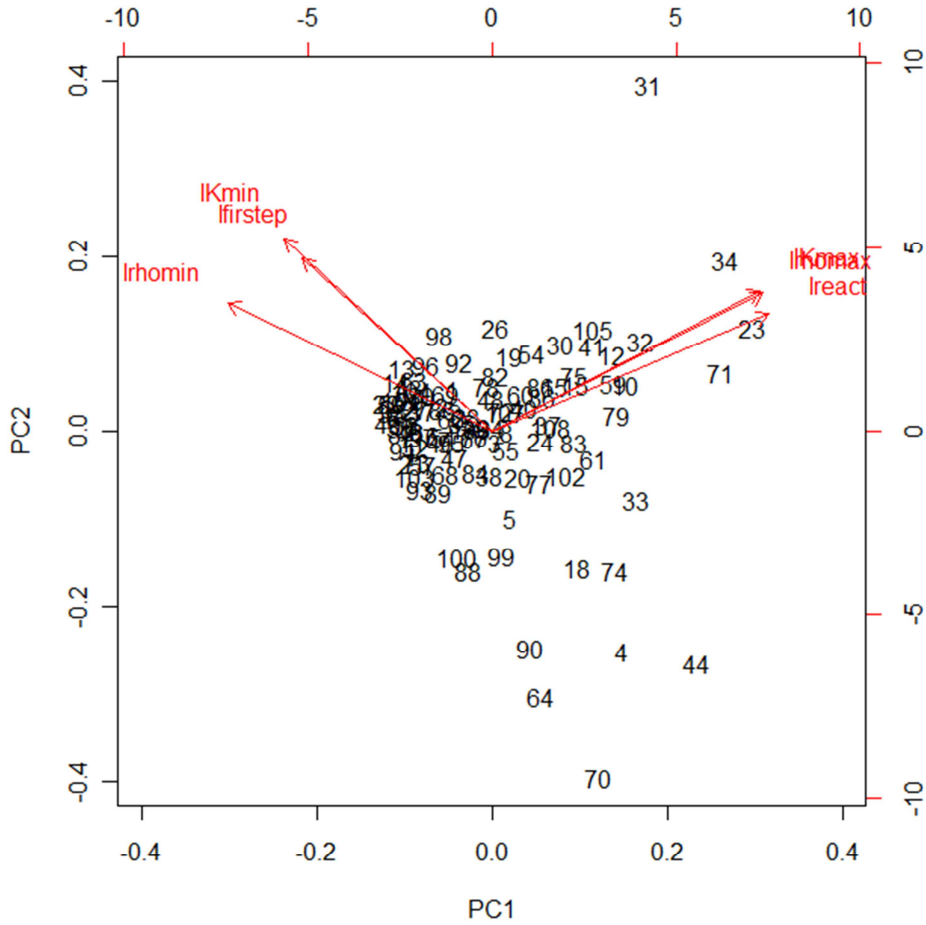
FIG. A5.1.2: Plot of PC1 against PC2, detailing loadings of the transient indices. "l" denotes log10, so e.g. lKmax=$\log_{10}$(Kmax). The amplified transients (Kmax = upper Kreiss bound, rhomax = maximum amplification and react = reactivity) show positive loadings on both PC1 and PC2. The attenuated transients (Kmin=lower Kress bound, rhomin=maximum attenuation, firstep=first-timestep attenuation) show negative loadings on PC1 but positive loadings on PC2.

TABLE A5.1.2: Table of loadings by transient index and principal component.

	PC1	PC2	PC3	PC4	PC5	PC6
$\log_{10}(K_{max})$	0.439149	0.380868	-0.05002	0.334535	-0.42675	0.604616
$\log_{10}(K_{min})$	-0.34274	0.521909	0.504305	-0.52118	-0.2861	0.048327
$\log_{10}(\rho_{max})$	0.444282	0.373189	-0.00173	0.124331	-0.21215	-0.77645
$\log_{10}(\rho_{min})$	-0.4339	0.348342	0.270527	0.716311	0.318156	-0.05368
$\log_{10}(reactivity)$	0.454045	0.317374	0.13277	-0.25652	0.763771	0.162289
$\log_{10}(first\text{-}timestep\ attenuation)$	-0.31284	0.470332	-0.80769	-0.14864	0.080359	0.00309

APPENDIX 6.1

Detailed information on construction of angiosperm phylogeny (Chapter 6)

The phylogeny used in MCMCglmm analyses is presented in Figure A6.1.1. The full phylogeny consists of 147 angiosperm species representing 57 different families. This phylogeny was trimmed to 143 species for general resilience analyses and 70 species for specific resilience analyses. Details on which species were used in each analysis can be found in Appendix 7, which also includes species' taxonomic information.

The topology of the phylogeny to family level was found using phylomatic (http://phylodiversity.net/phylomatic), and branch lengths of this tree were fitted using the `bladj` function included in phylocom (Webb, Ackerly & Kembel 2008). Remaining within-family polytomies were resolved using information from the literature. These polytomies, and the studies used to resolve them, are listed below.

POLYTOMIES AT FAMILY LEVEL:

Arecaceae (*Astrocaryum mexicanum, Borassus aethiopum, Chamaedorea radicalis, Coccothrinax readii, Euterpe edulis, Euterpe precatoria, Geonoma deversa, Geonoma orbignyana, Iriartea deltoidea, Neodypsis decaryi, Phytelephas seemannii, Podococcus barteri, Thrinax radiata*): Baker *et al.* (2009)

Asteraceae (Asteroidea, Carduoidea, Cichorioidea)

    Asteroidea (*Ambrosia dumosa, Eupatorium perfolatium, Eupatorium resinosum, Helianthus divaricatus*): Stevens (2001)

    Carduoidea (*Carduus nutans, Carlina vulgaris, Centaurea maculosa, Cirsium palustre*): Haffner & Hellwig (1999)

    Cichorioidea (*Hieracium floribundum, Picris hieracioides, Scorzonera humilis*): Whitton, Wallace & Jansen (1995)

Cacataceae (*Carnegiea gigantica, Neobuxbaumia mezcalaensis, Neobuxbaumia tetetzo, Neobuxbaumia macrocephala, Mammillaria crucígera, Mammillaria magnimamma, Pterocereus gaumeri*): Gibson & Horak (1978)

Caryophyllaceae (*Minuartia obtusiloba, Paryonychia pulvinata, Silene acaulis, Silene douglasii*): Fior *et al.* (2006)

Fabaceae (*Anthyllis vulneraria, Astragalus scaphoides, Cassia nemophila, Dicymbe altsonii, Lathyrus vernus, Machaerium cuspidatum, Pentaclethra macroloba, Periandra mediterranea, Prosopis glandulosa, Ulex gallii, Ulex minor*): Wojciechowski *et al.* (2004)

Liliaceae (*Calochortus, Clintonia borealis, Erythronium japonicum, Fritillaria meleagris*): Peruzzi *et al.*(2009)

    Calochortus: Patterson & Givnish (2003)

Poaceae (Chloridoidea, Panicoideae, Pooideae) Liang & Hilu (1996)

Chloridoidea (*Aristida bipartita*, *Danthonia sericea*, *Spartina alterniflora*, *Swallenia alexandrae*): Peterson *et al.* (2010).

Panicoideae (*Andropogon semiberbis*, *Bothriochloa insculpta*, *Digitaria eriantha*, *Heteropogon contortus, Themeda triandra, Setaria incrassata*): Giussani *et al.* (2001), Teerawatananon *et al.* (2011)

Pooideae (*Achnatherum calamigrostris*, *Agropyron repens*): Hsiao *et al.*(1995)

Primulaceae (*Ardisia escallonioides, Myrsine guianensis, Primula vulgaris, Primula veris*): Anderberg, Ståhl & Källersjö (1998), Mast *et al.* (2001)

Proteaceae (*Banksia ericifolia, Petrophile pulchella, Roupala montana*): Stevens (2001)

Rosaceae (*Agrimonia eupatoria, Geum rivale, Geum reptans, Potentilla anserina*): Stevens (2001)
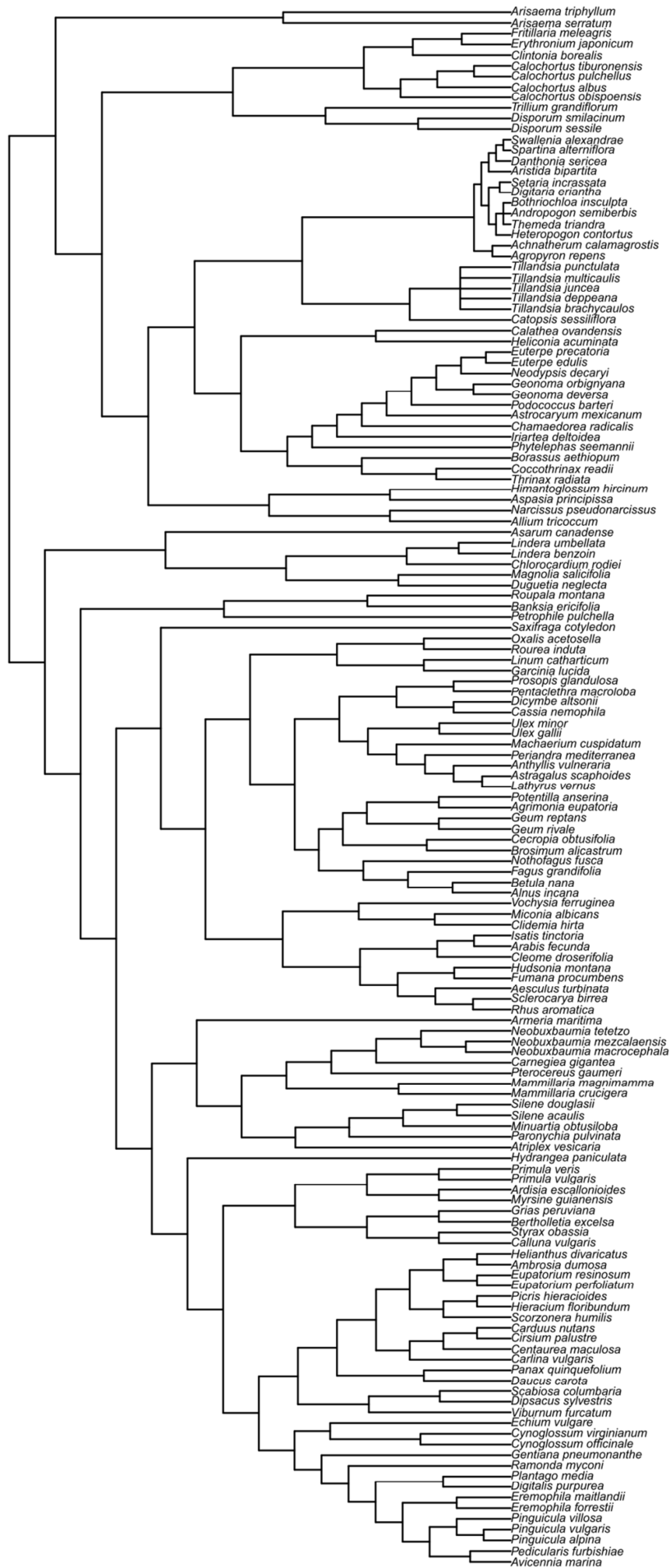
FIG. A6.1.1: Phylogeny used in MCMCglmm analyses, including branch lengths. Species' taxonomy can be found in Appendix 7.

185

APPENDIX 6.2

Detailed information on MCMCglmm analyses (Chapter 6)

We used the R package `MCMCglmm` to explore how shared ancestry and life history affects propensity for transient amplification. The software uses Markov Chain Monte Carlo algorithms to fit parameter estimates to data in a Bayesian framework. Bayesian glmm models are relatively robust to non-gaussian data, such as the proportion and binary data that we use in this study.

MODEL STRUCTURE

`MCMCglmm` allows multivariate responses, fixed effects, random effects and residuals. There are many different combinations of interactions to choose from when estimating fixed effect means and variances, and random effect (co)variances.

RANDOM EFFECTS

`MCMCglmm` allows incorporation of a phylogenetic relatedness variance-covariance matrix in the random effects structure. This means that the exact relationship between species can be modelled, including both topological relatedness and phylogenetic distance. We built a phylogeny representing the 147 species in our dataset (see Appendix 6.1). This phylogeny was converted to a Newick-coded format, read into `R` as a `phylo` object in the `ape` package, trimmed using the `drop.tip` function to exclude species for which there were no irreducible matrices, where appropriate trimmed further to exclude species for which there were no recorded demographic distribution, and modelled in `MCMCglmm` analyses using the `pedigree` argument.

FIXED EFFECTS

We modelled life form as a fixed effect, with 5 levels: monocarps (M), perennial herbs in open habitats (O), perennial herbs in forest habitats (F), shrubs (S) and trees (T), following Franco & Silvertown (2004).

RESPONSE VARIABLES

Data generated from Dirichlet draws (general resilience) consists of a mean probability of amplification per species for any possible demographic structure, either in the first timestep [reactivity; $p(P_1>1)$], or the long term [inertia; $p(P_\infty>1)$]. This proportion data was logit-transformed and analysed in a Gaussian glmm. An alternative would be to use raw 'counts' of amplification and attenuation and analyse the data in a binomial glmm with logit link, but as

each data point is calculated from the same number of Dirichlet draws, the two approaches are almost equivalent. Due to the high number of proportions close to 1, this had a bimodal distribution after transformation and we relied on the robustness of `MCMCglmm` to cope with this. We analysed both variables simultaneously as bivariate responses, fitting an interaction between trait and life form, and using the `us` function to fit full variance and covariance between the two traits in random and residual variance, which accounts for the correlation between the two responses.

Case-specific transient data (specific resilience) consists of the mean projected first-timestep (reactivity) and long-term (inertia) transient dynamics per species. This data was transformed into binary response variables, where a 0 was assigned if the population attenuates and a 1 was assigned if the population amplifies. We then fit a binary glmm model to this data, which effectively fits the probability of amplification of populations given their recorded demographic structure. This is subtly, but notably, different to the proportion models, which estimate the probability of amplification given any possible random demographic structure. In binary glmm models, the residual variance is not used in calculation of the log-likelihood, and the `MCMCglmm` course notes recommend that the best approach to take is to fix the residual variance at an arbitrary value and then rescale posterior distributions after the model is fit. As `MCMCglmm` does not yet allow multivariate models where variance is fixed but covariance is still fit by the model, we were not able to model this data in a bivariate model and so univariate models were used, with residual variance fixed at 1.

ITERATIONS/BURNIN/THINNING

Chains seemed to mix well in all cases when using 300000 iterations and a burnin interval of 30000. For both sets of models, we used a thinning interval of 100 to deal with autocorrelated chains. We checked autocorrelation of fixed parameters of all models to ensure it was kept low at the level of the thinning interval (at least <0.1 as suggested in the `MCMCglmm` course notes, but usually far lower). Autocorrelation remained high in chains estimating random effects and residuals, and increasing thinning intervals did not remedy this. This might be expected, given that variance estimates are bounded at 0, and we note that it should have little effect on parameter estimates (Link & Eaton 2012).

PRIORS

`MCMCglmm` models fixed-effect priors using a gaussian distribution, which takes 2 parameters: mean and variance. Random and residual priors are usually modelled using an inverse Wishart distribution, which is a multivariate relative of the inverse gamma distribution and takes a shape parameter ν (nu) and a scale parameter V. This distribution tends to a point mass on V as ν goes

to infinity, therefore V can be thought of as a prior variance and ν can be thought of as a 'degree-of-belief' parameter: the higher ν is, the more confidence is placed in the prior variance. We aimed to make all priors as uninformative as possible. It is possible to specify improper priors for random effects and residuals using V≈0 and/or ν ≤0: such priors are very uninformative, however none of our models would accept improper priors and so we used proper uninformative priors for all random and residual parameters.

LOGIT-TRANSFORMED DIRICHLET DATA (GENERAL RESILIENCE)

We used default uninformative priors for fixed effects (mean=0, variance=10^8) in general resilience data, and this gave gaussian marginal posteriors for fixed effects in all models. There are no default priors for random effects and residuals, but the `MCMCglmm` course notes suggest an uninformative proper of V=1 and ν =0.002, with V split evenly over the number of parameters being estimated. However, for our models these priors gave bad mixing for random effects and residuals as chains became stuck at 0. To deal with this, we decided to use parameter-expanded priors. This method introduces variables into the prior that are not identified in the log-likelihood (and therefore should not affect DIC, unlike changing V or ν). The prior is multiplied by the extra variables, which convert the posterior distribution to a non-central scaled F distribution. Parameter expansion prevented chains from sticking at 0, and latent variables estimated by parameter-expanded priors were similar to those from models that didn't use parameter expansion. Posteriors for random effects and residuals were positively-skewed, however this is expected to a lesser or greater extent, as variances are bounded at 0 and +∞.

BINARY-TRANSFORMED TRANSIENT DATA (SPECIFIC RESILIENCE)

Whilst the default fixed effects priors of `MCMCglmm` are uninformative on the logit scale, where within-group proportions are close to 1 in binary response models, they are often not uninformative on the probability scale (see figure A6.2.2). In our specific resilience data, within-group probabilities for life form were close to or equal to 1 as most species amplify in both the short- and long-term. Because of this, default fixed effects priors had chains with bad mixing (especially for monocarpic species, which all amplify) and so we used a prior that is uninformative on the probability scale as suggested in the `MCMCglmm` course notes (in our case mean = 0, variance = $\sigma^2_{units}+\pi^2/3 = 1+ \pi^2/3$). This gave much better mixing and gaussian posteriors for fixed effects. Again, we used an uninformative prior of V=1, ν=0.002 for random effects in binary models. However, we fixed variance for residuals at 1 (as recommended in the `MCMCglmm` course notes), as residual variance is not identified in the log-likelihood of binary response models. Again, chains for random effects frequently stuck at 0. The `MCMCglmm` course notes suggest parameter expansion in binary response models where this is the case, and so we also used parameter expansion here to give chains with better mixing, which didn't stick

at 0. We rescaled fixed and random chains to assume a residual variance of 0 for posterior checks, again following suggestions in the MCMCglmm course notes. Posterior distributions for random effects variances were quite positively skewed, as variances were close to 0.

BEST-FIT MODELS

For both data sets, we fit four models: 1. including both phylogeny and life form; 2. including phylogeny and excluding life form; 3. excluding phylogeny and including life form; 4. excluding both phylogeny and life form.

LOGIT-TRANSFORMED DIRICHLET DATA (GENERAL RESILIENCE)

The best-fit model was including phylogeny and excluding life form. Including life form was supported over excluding life form, but the fact that the phylogeny-only model was preferred overall suggests that most of the similarity between life forms is better explained by ancestral relatedness.

BINARY-TRANSFORMED TRANSIENT DATA (SPECIFIC RESILIENCE)

The null model was the best-fit model, excluding both phylogeny and life form. This indicates that the distribution of amplification and attenuation is very similar across life forms, and shows no relationship to phylogeny.

CODE

The following presents the code used for MCMCglmm analyses:

```
#LOGIT-TRANSFORMED MODELS (GENERAL RESILIENCE)
#model 1.1: 2-response, +phylogeny, +Ecotype
#set prior model 1.1
prior1.1<-list(R = list(V = diag(2)*0.5, nu=0.002),
               G = list(G1=list(V = diag(2)*0.5, nu=0.002, alpha.mu=c(0,0),
                                alpha.V=diag(2)*1000)))
#model 1.1
m1.1<-MCMCglmm(cbind(reac.prob.logit,inert.prob.logit) ~ trait:Ecotype - 1,
               random=~us(trait):animal, rcov=~us(trait):units,
               family=c("gaussian","gaussian"),
               prior=prior1.1, data=meandata, pedigree=meantree, nodes="TIPS",
               thin=100, nitt=150000, burnin=30000, verbose=F)

###2-response, +phylogeny, -Ecotype
#set prior model 1.2
prior1.2<-list(R = list(V = diag(2)*0.5, nu=0.002),
```

```
                       G = list(G1=list(V = diag(2)*0.5, nu=0.002, alpha.mu=c(0,0),
                                        alpha.V=diag(2)*10)))
#model 1.2
m1.2<-MCMCglmm(cbind(reac.prob.logit,inert.prob.logit) ~ trait - 1,
               random=~us(trait):animal, rcov=~us(trait):units,
               family=c("gaussian","gaussian"),
               prior=prior1.2, data=meandata, pedigree=meantree, nodes="TIPS",
               thin=100, nitt=150000, burnin=30000, verbose=F)


###2-response, -phylogeny, +Ecotype
#set prior model 1.2
prior1.3<-list(R = list(V = diag(2)*0.5, nu=0.002))
#model 1.3
m1.3<-MCMCglmm(cbind(reac.prob.logit,inert.prob.logit) ~ trait:Ecotype - 1,
               rcov=~us(trait):units, family=c("gaussian","gaussian"),
               prior=prior1.3, data=meandata,
               thin=100, nitt=150000, burnin=30000, verbose=F)


###2-response, -phylogeny, -Ecotype
#set prior model 1.2
prior1.4<-list(R = list(V = diag(2)*0.5, nu=0.002))
#model 1.4
m1.4<-MCMCglmm(cbind(reac.prob.logit,inert.prob.logit) ~ trait - 1,
               rcov=~us(trait):units, family=c("gaussian","gaussian"),
               prior=prior1.4, data=meandata,
               thin=100, nitt=150000, burnin=30000, verbose=F)


#BINARY MODELS (SPECIFIC RESILIENCE)
#set prior model 1.1
#Use a non-informative prior on the probability scale to prevent
autocorrelation.
#Use an uninformative prior for random effects, adding parameter expansion to
#prevent random effects chains sticking at 0.  alpha.V=100 gives good mixing,
#large effective sample and is robust.
#Fix residual variance at 1
prior1.1<-list(R = list(V = 1, fix=1),
               G = list(G1=list(V = 1, nu=0.002, alpha.mu=0, alpha.V=100)),
               B = list(mu=rep(0,5), V=diag(5)*(1+pi^2/3)))
#model 1.1: Reactivity, +phylogeny, +Ecotype
m1.1<-MCMCglmm(reac.mean.bin ~ Ecotype,
               random=~animal, family="categorical",
               prior=prior1.1, data=meanvecdata, pedigree=vectree,
               nodes="TIPS", thin=50, nitt=150000, burnin=30000, verbose=F)


#set prior model 1.2
prior1.2<-list(R = list(V = 1, fix=1),
               G = list(G1=list(V = 1, nu=0.002, alpha.mu=0, alpha.V=100)),
```

```
                        B = list(mu=0, V=(1+pi^2/3)))
#model1.2: 1 Reactivity, +phylogeny, -Ecotype
m1.2<-MCMCglmm(reac.mean.bin ~ 1,
               random=~animal, family="categorical",
               prior=prior1.2, data=meanvecdata, pedigree=vectree,
               nodes="TIPS", thin=50, nitt=150000, burnin=30000, verbose=F)


#set prior model 1.3
prior1.3<-list(R = list(V = 1, fix=1),
               B = list(mu=rep(0,5), V=diag(5)*(1+pi^2/3)))
#model 1.3: 1 Reactivity, -phylogeny, +Ecotype
m1.3<-MCMCglmm(reac.mean.bin ~ Ecotype,
               family="categorical",
               prior=prior1.3, data=meanvecdata,
               thin=50, nitt=150000, burnin=30000, verbose=F)


#set prior model 1.4
prior1.4<-list(R = list(V = 1, fix=1),
               B = list(mu=0, V=(1+pi^2/3)))
#model 1.4: 1 Reactivity, -phylogeny, -Ecotype
m1.4<-MCMCglmm(reac.mean.bin ~ 1,
               family="categorical",
               prior=prior1.4, data=meanvecdata,
               thin=50, nitt=150000, burnin=30000, verbose=F)
```

APPENDIX 6.3

Analytical solutions to Dirichlet sampling procedures for calculating general transient resilience (Chapter 6)

Figure 6.3 shows a geometric representation of the Dirichlet sampling procedures that we used to calculate general transient resilience. Below we present the algebraic solution for calculating probability of amplification in this 3-stage case.

These equations use either $\mathbf{c}$ (the vector of column sums of the standardised PPM $\hat{\mathbf{A}} = \mathbf{A}/\lambda_{max}$), or $\mathbf{v}$ (the reproductive value vector, equal to the dominant left eigenvector of the PPM $\hat{\mathbf{A}}$, rescaled so that $\mathbf{v}^T\mathbf{w} = 1$ where $\|\mathbf{w}\|_1 = 1$). $\mathbf{c}$ is used for calculating the probability of amplification in the first timestep (reactivity), whereas $\mathbf{v}$ is used for calculating the probability of amplification in the long term (inertia). In both cases, the algebraic solution is the same.

The first case exists when two $c_i<1$ and one $c_i>1$, or two $v_i<1$ and one $v_i>1$:

$$p(P_1 > 1) = \frac{(1 - c_{>1})^2}{(c_{<1,1} - c_{>1})(c_{<1,2} - c_{>1})} \quad , \quad p(P_\infty > 1) = \frac{(1 - v_{>1})^2}{(v_{<1,1} - c_{>1})(v_{<1,2} - c_{>1})}$$

The second case exists when one $c_i<1$ and two $c_i>1$ or one $v_i<1$ and two $v_i>1$:

$$p(P_1 > 1) = 1 - \frac{(1 - c_{<1})^2}{(c_{>1,1} - c_{<1})(c_{>1,2} - c_{<1})} \quad , \quad p(P_\infty > 1) = 1 - \frac{(1 - v_{<1})^2}{(v_{>1,1} - c_{<1})(v_{>1,2} - c_{<1})}$$

The first case is illustrated in Figure 6.3a, and the second is illustrated in Figure 6.3b (note that the dashed triangles plotted in Figure 6.3 have vertices that lie on the reciprocals of $\mathbf{c}$ and $\mathbf{v}$).

In the first case, a higher probability of amplification is achieved by increasing the numerator of the fraction and/or decreasing the denominator of the fraction. The former is achieved by increasing the $c_{>1}$ or $v_{>1}$, and the latter is achieved by keeping the $c_{<1}$ or $v_{<1}$ close to 1. In the second case, a higher probability of amplification is achieved by increasing the denominator of the fraction and/or decreasing the numerator of the fraction. Again, the former is achieved by increasing $c_{>1}$ or $v_{>1}$, and the latter is achieved by keeping the $c_{<1}$ or $v_{<1}$ close to 1. Given that the vertices of the dashed simplexes in Figure 6.3 lie on the reciprocals of $\mathbf{c}$ and $\mathbf{v}$, the $c_{>1}$ or $v_{>1}$ result in vertices <1 of the dashed simplexes in Figure 3, and the $c_{<1}$ or $v_{<1}$ result in vertices >1. Therefore, increasing $c_{>1}$ or $v_{>1}$ moves vertices <1 closer to 0 whilst increasing $c_{<1}$ or $v_{<1}$ therefore moves vertices >1 closer to 1.

These equations show that stage-structuring achieves transient dynamics. If all c_i or v_i equal 1, then there is no solution to the above equations: there is no amplification or attenuation. There are two ways to achieve stage-structuring in life cycles: asymmetry in survival and

asymmetry in reproduction. Concentrating reproduction effort to one area of the life cycle is an efficient way to increase $c_{>1}$ and $v_{>1}$, giving high probability of amplification both immediately and in the long term. Hence, delaying reproduction will favour amplification. Maintaining relatively high adult survival will also increase $c_{>1}$ and $v_{>1}$, whilst maintaining relatively high juvenile survival keeps $c_{<1}$ and $v_{<1}$ close to 1, in both cases favouring high probabilities of amplification. However, trade-offs will dictate that an organism cannot maintain high juvenile survival, adult survival and reproduction. Maintaining relatively high adult survival causes a disproportionate increase in $v_{>1}$ whilst giving a relatively smaller increase in $c_{>1}$, therefore populations that experience relatively irregular disturbance may wish to invest in adult survival over juvenile survival to ensure amplification is maintained in the long term. On the other hand, investing in high juvenile survival over adult survival will ensure $c_{<1}$ close to 1 giving high probability of immediate amplification, but will disproportionately decrease $v_{>1}$ giving lower probability of long-term amplification. This strategy may be favourable for organisms that experience frequent disturbance, where high probability of long-term amplification is less important.

In summary, stage-structuring achieves transient dynamics. An efficient way to achieve this and simultaneously favour high probabilities of amplification is through delayed reproduction. High survival across the life cycle favours amplification, but allocation of resources to either juvenile or adult survival may be differentially favoured according to what sort of disturbance regime they experience. Of course, life cycles are shaped by countless other factors, but it seems that features common in natural life cycles (stage-structuring, delayed reproduction, asymmetry in survival) favour amplification of population dynamics, inferring a high transient resilience to disturbance. Generalising the above equations to n dimensions is difficult. However, we may assume that the same results may hold: increasing any $c_{>1}$ and $v_{>1}$ will favour amplification, as will keeping any $c_{<1}$ and $v_{<1}$ close to 1. Hence, whatever the dimension of the life cycle, the same solutions to achieving high probability of amplification should exist.

APPENDIX 7

Metadata for database of PPM models(Chapter1, Chapter 5, Chapter 6)

This appendix presents metadata for the PPM models used in comparative analyses in chapters. The models themselves and their associated data are available as an excel file upon request. This metadata presents the species present in the database, their taxonomy, the reference(s) from which models were obtained, the number of matrices in the database, the number of different populations for which matrices are available, whether or not at least one irreducible matrix is available, and whether or not at least one model includes a known demographic vector.

PLANTS

Class	Order	Family	*Species*	Reference	Number matrices	Number populations	Irreducible	Vector
Gymnospermae	Pinales	Pinaceae	*Abies concolor*	van Mantgem & Stephenson (2005)	5	5	Y	N
Gymnospermae	Pinales	Pinaceae	*Abies magnifica*	van Mantgem & Stephenson (2005)	4	4	Y	N
Gymnospermae	Pinales	Cupressaceae	*Calocedrus decurrens*	van Mantgem & Stephenson (2005)	3	3	Y	N
Angiospermae	Poales	Poaceae	*Achnatherum calamagrostis*	Guardia *et al.* (2000)	1	1	Y	Y
Angiospermae	Sapindales	Sapindaceae	*Aesculus turbinata*	Kaneko *et al.* (1999)	2	1	Y	Y
Angiospermae	Rosales	Rosaceae	*Agrimonia eupatoria*	Kiviniemi (2002)	10	2	Y	Y
Angiospermae	Poales	Poaceae	*Agropyron repens*	Mortimer (1983)	1	1	Y	N
Angiospermae	Asparagales	Alliaceae	*Allium tricoccum*	Nault & Gagnon (1993)	5	1	Y	Y
Angiospermae	Corylales	Betulaceae	*Alnus incana*	Huenneke & Marks (1987)	7	2	Y	N
Angiospermae	Asterales	Asteraceae	*Ambrosia dumosa*	Miriti *et al.* (2001)	2	1	Y	Y
Angiospermae	Poales	Poaceae	*Andropogon semiberbis*	Silva *et al.* (1991)	2	2	Y	Y
Angiospermae	Fabales	Fabaceae	*Anthyllis vulneraria*	Sterk (1975)	3	2	Y	N
Angiospermae	Brassicales	Brassicaceae	*Arabis fecunda*	Lesica & Shelly (1995)	15	3	Y	N
Gymnospermae	Pinales	Araucariaceae	*Araucaria cunninghamii*	Enright & Watson (1991)	3	1	Y	Y
Gymnospermae	Pinales	Araucariaceae	*Araucaria hunsteinii*	Enright (1982)	3	3	Y	Y
Angiospermae	Ericales	Primulaceae	*Ardisia escallonioides*	Pascarella & Horvitz (1998)	7	4	Y	N
Angiospermae	Arales	Araceae	*Arisaema serratum*	Kinoshita (1987)	1	1	Y	Y
Angiospermae	Arales	Araceae	*Arisaema triphyllum*	Bierzychudek (1982)	7	2	Y	Y

Angiospermae	Poales	Poaceae	*Aristida bipartita*	O'Connor (1993)	11	1	Y	N
Angiospermae	Plumbaginales	Plumbaginaceae	*Armeria maritima*	Lefèbvre & Chandler-Mortimer (1984)	1	1	Y	N
Angiospermae	Aristolochiales	Aristolochiaceae	*Asarum canadense*	Damman & Cain (1998)	44	2	Y	N
Angiospermae	Asparagales	Orchidaceae	*Aspasia principissa*	Zotz & Schmidt (2006)	1	1	Y	Y
Angiospermae	Fabales	Fabaceae	*Astragalus scaphoides*	Lesica (1995)	11	2	Y	N
Angiospermae	Arecales	Arecaceae	*Astrocaryum mexicanum*	Piñero *et al.* (1984)	7	6	Y	Y
Angiospermae	Caryophyllales	Amaranthaceae	*Atriplex vesicaria*	Hunt (2001)	27	9	Y	Y
Angiospermae	Lamiales	Acanthaceae	*Avicennia marina*	Burns & Ogden (1985)	1	1	N	Y
Angiospermae	Proteales	Proteaceae	*Banksia ericifolia*	Bradstock & O'Connell (1988)	1	1	Y	N
Angiospermae	Lecythidales	Lecythidaceae	*Bertholletia excelsa*	Zuidema & Boot (2002)	1	1	Y	Y
Angiospermae	Corylales	Betulaceae	*Betula nana*	Ebert & Ebert (1989)	1	1	Y	N
Angiospermae	Arecales	Arecaceae	*Borassus aethiopum*	Barot *et al.* (2000)	1	1	Y	Y
Angiospermae	Poales	Poaceae	*Bothriochloa insculpta*	O'Connor (1993)	11	1	Y	N
Angiospermae	Rosales	Moraceae	*Brosimum alicastrum*	Peters (1990)	1	1	Y	N
Angiospermae	Zingiberales	Marantaceae	*Calathea ovandensis*	Horvitz & Schemske (1995)	17	4	Y	Y
Angiospermae	Ericales	Ericaceae	*Calluna vulgaris*	Barclay-Estrup & Gimingham (1975)	1	1	Y	N
Angiospermae	Liliales	Liliaceae	*Calochortus albus*	Fiedler (1987)	3	2	Y	N
Angiospermae	Liliales	Liliaceae	*Calochortus obispoensis*	Fiedler (1987)	3	2	Y	N
Angiospermae	Liliales	Liliaceae	*Calochortus pulchellus*	Fiedler (1987)	3	2	Y	N
Angiospermae	Liliales	Liliaceae	*Calochortus tiburonensis*	Fiedler (1987)	3	2	Y	N

Angiospermae	Asterales	Asteraceae	*Carduus nutans*	Shea & Kelly (1998)	2	2	Y	N
Angiospermae	Asterales	Asteraceae	*Carlina vulgaris*	Löfgren *et al.* (2000)	8	8	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Carnegiea gigantea*	Steenbergh & Lowe (1977)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Cassia nemophila*	Silander (1983)	1	1	Y	Y
Angiospermae	Poales	Bromeliaceae	*Catopsis sessiliflora*	Winkler *et al.* (2007)	1	1	Y	Y
Angiospermae	Rosales	Urticaceae	*Cecropia obtusifolia*	Alvarez-Buylla (1994)	5	1	Y	N
Angiospermae	Asterales	Asteraceae	*Centaurea maculosa*	Emery & Gross (2005)	7	1	Y	Y
Cycadopsida	Cycadales	Zamiaceae	*Ceratozamia mirandae*	Perez-Farrera *et al.* (2006)	2	2	Y	N
Angiospermae	Arecales	Arecaceae	*Chamaedorea radicalis*	Endress *et al.* (2004)	2	1	Y	Y
Angiospermae	Laurales	Lauraceae	*Chlorocardium rodiei*	Zagt (1997)	2	2	Y	N
Angiospermae	Asterales	Asteraceae	*Cirsium palustre*	Ramula *et al.* (2009)	1	1	Y	Y
Angiospermae	Brassicales	Brassicaceae	*Cleome droserifolia*	Hegazy (1990)	1	1	Y	N
Angiospermae	Myrtales	Melastomataceae	*Clidemia hirta*	De Walt (2006)	6	2	Y	Y
Angiospermae	Liliales	Liliaceae	*Clintonia borealis*	Pitelka *et al.* (1985)	1	1	Y	Y
Angiospermae	Arecales	Arecaceae	*Coccothrinax readii*	Olmsted & Alvarez-Buylla (1995)	1	1	Y	N
Angiospermae	Boraginales	Boraginaceae	*Cynoglossum officinale*	Boorman & Fuller (1984)	1	1	Y	N
Angiospermae	Boraginales	Boraginaceae	*Cynoglossum virginianum*	Cipollini *et al.* (1993)	1	1	Y	N
Angiospermae	Poales	Poaceae	*Danthonia sericea*	Moloney (1988)	11	2	Y	Y
Angiospermae	Apiales	Apiaceae	*Daucus carota*	Verkaar & Schenkeveld (1984)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Dicymbe altsonii*	Zagt (1997)	2	2	Y	N
Angiospermae	Lamiales	Plantaginaceae	*Digitalis purpurea*	van Baalen (1982)	1	1	Y	N
Angiospermae	Poales	Poaceae	*Digitaria eriantha*	O'Connor (1993)	10	10	Y	N
Angiospermae	Dipsacales	Caprifoliaceae	*Dipsacus sylvestris*	Werner & Caswell (1977)	1	1	Y	N

Angiospermae	Liliales	Colchicaceae	*Disporum sessile*	Kawano *et al.* (1987)	1	1	N	N
Angiospermae	Liliales	Colchicaceae	*Disporum smilacinum*	Kawano *et al.* (1987)	1	1	Y	N
Angiospermae	Annonales	Annonaceae	*Duguetia neglecta*	Zagt (1997)	2	2	Y	N
Angiospermae	Boraginales	Boraginaceae	*Echium vulgare*	Klemow & Raynal (1985)	1	1	Y	N
Angiospermae	Lamiales	Scrophulariaceae	*Eremophila forrestii*	Watson *et al.* (1997)	7	2	Y	N
Angiospermae	Lamiales	Scrophulariaceae	*Eremophila maitlandii*	Watson *et al.* (1997)	13	2	Y	N
Angiospermae	Liliales	Liliaceae	*Erythronium japonicum*	Kawano *et al.* (1987)	1	1	Y	N
Angiospermae	Asterales	Asteraceae	*Eupatorium perfoliatum*	Byers & Meagher (1997)	4	3	Y	Y
Angiospermae	Asterales	Asteraceae	*Eupatorium resinosum*	Byers & Meagher (1997)	4	2	Y	N
Angiospermae	Arecales	Arecaceae	*Euterpe edulis*	Silva Matos *et al.* (1999)	4	1	Y	Y
Angiospermae	Arecales	Arecaceae	*Euterpe precatoria*	Peña-Claros & Zuidema (2000)	1	1	Y	N
Angiospermae	Fagales	Fagaceae	*Fagus grandifolia*	Batista *et al.* (1998)	2	1	Y	Y
Angiospermae	Liliales	Liliaceae	*Fritillaria meleagris*	Zhang (1983)	3	2	Y	N
Angiospermae	Malvales	Cistaceae	*Fumana procumbens*	Bengtsson (1993)	7	1	Y	N
Angiospermae	Malpighiales	Clusiaceae	*Garcinia lucida*	Guedje *et al.* (2003)	1	1	Y	Y
Angiospermae	Gentianales	Gentianaceae	*Gentiana pneumonanthe*	Chapman *et al.* (1989)	1	1	Y	N
Angiospermae	Arecales	Arecaceae	*Geonoma deversa*	Zuidema (2000)	1	1	Y	N
Angiospermae	Arecales	Arecaceae	*Geonoma orbignyana*	Rodríguez-Buriticá *et al.* (2005)	1	1	Y	Y
Angiospermae	Rosales	Rosaceae	*Geum reptans*	Weppler *et al.* (2006)	4	2	Y	Y
Angiospermae	Rosales	Rosaceae	*Geum rivale*	Kiviniemi (2002)	6	2	Y	Y
Angiospermae	Lecythidales	Lecythidaceae	*Grias peruviana*	Peters (1991; 1992)	1	1	Y	N

Angiospermae	Asterales	Asteraceae	*Helianthus divaricatus*	Nantel & Gagnon (1999)	9	4	Y	N
Angiospermae	Zingiberales	Heliconiaceae	*Heliconia acuminata*	Bruna (2003)	6	1	Y	Y
Angiospermae	Poales	Poaceae	*Heteropogon contortus*	O'Connor (1993)	11	1	Y	N
Angiospermae	Asterales	Asteraceae	*Hieracium floribundum*	Thomas & Dale (1975)	1	1	Y	N
Angiospermae	Asparagales	Orchidaceae	*Himantoglossum hircinum*	Pfeifer *et al.* (2006)	1	1	Y	Y
Angiospermae	Malvales	Cistaceae	*Hudsonia montana*	Gross *et al.* (1998)	4	1	Y	N
Angiospermae	Cornales	Hydrangeaceae	*Hydrangea paniculata*	Hara *et al.* (2004)	1	1	Y	Y
Bryopsida	Hypnales	Hylocomiaceae	*Hylocomium splendens*	Okland (1995)	1	1	Y	Y
Angiospermae	Arecales	Arecaceae	*Iriartea deltoidea*	Pinard (1993)	6	5	Y	Y
Angiospermae	Brassicales	Brassicaceae	*Isatis tinctoria*	Farah *et al.* (1988)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Lathyrus vernus*	Ehrlén & van Groenendael (1998); Ehrlén (1995)	19	7	Y	Y
Angiospermae	Laurales	Lauraceae	*Lindera benzoin*	Cipollini *et al.* (1994)	3	2	N	N
Angiospermae	Laurales	Lauraceae	*Lindera umbellata*	Hara *et al.* (2004)	1	1	Y	Y
Angiospermae	Malphigiales	Linaceae	*Linum catharticum*	Verkaar & Schenkeveld (1984)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Machaerium cuspidatum*	Nabe-Nielsen (2004)	2	1	Y	Y
Angiospermae	Magnoliales	Magnoliaceae	*Magnolia salicifolia*	Hara *et al.* (2004)	1	1	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Mammillaria crucigera*	Contreras & Valverde (2002)	3	2	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Mammillaria magnimamma*	Valverde *et al.* (2004)	4	2	Y	Y
Angiospermae	Myrtales	Melastomataceae	*Miconia albicans*	Hoffmann (1999)	3	1	Y	N
Angiospermae	Caryophyllales	Caryophyllaceae	*Minuartia obtusiloba*	Forbis & Doak (2004)	1	1	Y	Y

Angiospermae	Ericales	Primulaceae	*Myrsine guianensis*	Hoffmann (1999)	3	1	Y	N
Angiospermae	Asparagales	Amaryllidaceae	*Narcissus pseudonarcissus*	Barkham (1980)	3	2	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Neobuxbaumia macrocephala*	Esparza-Olguin *et al.* (2002); Godínez-Alvarez & Valiente-Banuet (2004)	4	2	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Neobuxbaumia mezcalaensis*	Esparza-Olguín *et al.* (2005)	1	1	Y	Y
Angiospermae	Caryophyllales	Cactaceae	*Neobuxbaumia tetetzo*	Godínez-Alvarez & Valiente-Banuet (2004)	1	1	Y	Y
Angiospermae	Arecales	Arecaceae	*Neodypsis decaryi*	Ratsirarson *et al.* (1996)	4	3	Y	Y
Angiospermae	Fagales	Nothofagaceae	*Nothofagus fusca*	Enright & Ogden (1979)	1	1	Y	Y
Angiospermae	Oxalidales	Oxalidaceae	*Oxalis acetosella*	Berg (2002)	6	3	Y	Y
Angiospermae	Apiales	Araliaceae	*Panax quinquefolium*	Nantel *et al.* (1996)	5	4	Y	N
Angiospermae	Caryophyllales	Caryophyllaceae	*Paronychia pulvinata*	Forbis & Doak (2004)	1	1	Y	Y
Angiospermae	Lamiales	Orobanchaceae	*Pedicularis furbishiae*	Menges (1990)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Pentaclethra macroloba*	Hartshorn (1975)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Periandra mediterranea*	Hoffmann (1999)	3	1	Y	N
Angiospermae	Proteales	Proteaceae	*Petrophile pulchella*	Bradstock & O'Connell (1988)	1	1	Y	N
Angiospermae	Arecales	Arecaceae	*Phytelephas seemannii*	Bernal (1998)	1	1	Y	Y
Angiospermae	Asterales	Asteraceae	*Picris hieracioides*	Klemow & Raynal (1985)	1	1	Y	N
Angiospermae	Lamiales	Lentibulariaceae	*Pinguicula alpina*	Svensson *et al.* (1993)	1	1	Y	Y

Angiospermae	Lamiales	Lentibulariaceae	*Pinguicula villosa*	Svensson *et al.* (1993)	1	1	Y	Y
Angiospermae	Lamiales	Lentibulariaceae	*Pinguicula vulgaris*	Svensson *et al.* (1993)	1	1	N	Y
Gymnospermae	Pinales	Pinaceae	*Pinus jeffreyi*	van Mantgem & Stephenson (2005)	1	1	N	N
Gymnospermae	Pinales	Pinaceae	*Pinus lambertiana*	van Mantgem & Stephenson (2005)	3	3	Y	N
Gymnospermae	Pinales	Pinaceae	*Pinus palustris*	Platt *et al.* (1988)	1	1	Y	N
Gymnospermae	Pinales	Pinaceae	*Pinus ponderosa*	van Mantgem & Stephenson (2005)	1	1	Y	N
Angiospermae	Lamiales	Plantaginaceae	*Plantago media*	Eriksson & Eriksson (2000)	8	2	Y	Y
Angiospermae	Arecales	Arecaceae	*Podococcus barteri*	Bullock (1980)	1	1	Y	N
Angiospermae	Rosales	Rosaceae	*Potentilla anserina*	Eriksson (1986)	4	1	Y	N
Angiospermae	Ericales	Primulaceae	*Primula veris*	Ramula *et al.* (2009)	1	1	Y	Y
Angiospermae	Ericales	Primulaceae	*Primula vulgaris*	Valverde & Silvertown (1998)	14	8	Y	Y
Angiospermae	Fabales	Fabaceae	*Prosopis glandulosa*	Golubov *et al.* (1999)	1	1	Y	N
Angiospermae	Caryophyllales	Cactaceae	*Pterocereus gaumeri*	Mendéz *et al.* (2004)	4	2	Y	Y
Angiospermae	Lamiales	Gesneriaceae	*Ramonda myconi*	Picó & Riba (2002)	5	5	Y	Y
Angiospermae	Burserales	Anacardiaceae	*Rhus aromatica*	Nantel & Gagnon (1999)	9	4	Y	N
Angiospermae	Proteales	Proteaceae	*Roupala montana*	Hoffmann (1999)	3	1	Y	N
Angiospermae	Connarales	Connaraceae	*Rourea induta*	Hoffmann (1999)	3	1	Y	N
Angiospermae	Saxifragales	Saxifragaceae	*Saxifraga cotyledon*	Dinnétz & Nilsson (2002)	8	2	Y	Y
Angiospermae	Dipsacales	Caprifoliaceae	*Scabiosa columbaria*	Verkaar & Schenkeveld (1984)	1	1	Y	N
Angiospermae	Sapindales	Anacardiaceae	*Sclerocarya birrea*	Emanuel *et al.* (2005)	1	1	Y	Y
Angiospermae	Asterales	Asteraceae	*Scorzonera humilis*	Colling & Matthies (2006)	1	1	Y	Y
Gymnospermae	Pinales	Cupressaceae	*Sequoia sempervirens*	Bosch (1971); Namkoong & Roberds (1974)	3	2	Y	Y
Angiospermae	Poales	Poaceae	*Setaria incrassata*	O'Connor (1993)	20	2	Y	N

Angiospermae	Caryophyllales	Caryophyllaceae	*Silene acaulis*	Gross *et al.* (2006); Morris & Doak (2005)	25	5	Y	N
Angiospermae	Caryophyllales	Caryophyllaceae	*Silene douglasii*	Kephart & Paladino (1997)	2	2	Y	Y
Angiospermae	Poales	Poaceae	*Spartina alterniflora*	Hastings *et al.* (2006)	1	1	Y	Y
Angiospermae	Ericales	Styracaceae	*Styrax obassia*	Abe *et al.* (1998)	3	2	Y	Y
Angiospermae	Poales	Poaceae	*Swallenia alexandrae*	Pavlik & Barbour (1988)	1	1	Y	N
Angiospermae	Poales	Poaceae	*Themeda triandra*	O'Connor (1993)	21	2	Y	N
Angiospermae	Arecales	Arecaceae	*Thrinax radiata*	Olmsted & Alvarez-Buylla (1995)	5	4	Y	N
Angiospermae	Poales	Bromeliaceae	*Tillandsia brachycaulos*	Mondragón *et al.* (2004)	3	1	Y	Y
Angiospermae	Poales	Bromeliaceae	*Tillandsia deppeana*	Winkler *et al.* (2007)	1	1	Y	Y
Angiospermae	Poales	Bromeliaceae	*Tillandsia juncea*	Winkler *et al.* (2007)	1	1	Y	Y
Angiospermae	Poales	Bromeliaceae	*Tillandsia multicaulis*	Winkler *et al.* (2007)	1	1	Y	Y
Angiospermae	Poales	Bromeliaceae	*Tillandsia punctulata*	Winkler *et al.* (2007)	1	1	N	Y
Angiospermae	Liliales	Melanthiaceae	*Trillium grandiflorum*	Rooney & Gross (2003)	1	1	Y	Y
Angiospermae	Fabales	Fabaceae	*Ulex gallii*	Stokes *et al.* (2004)	1	1	Y	N
Angiospermae	Fabales	Fabaceae	*Ulex minor*	Stokes *et al.* (2004)	1	1	Y	N
Angiospermae	Dipsacales	Adoxaceae	*Viburnum furcatum*	Hara *et al.* (2004)	1	1	Y	Y
Angiospermae	Myrtales	Vochysiaceae	*Vochysia ferruginea*	Boucher & Mallona (1997)	1	1	Y	Y

ANIMALS

Class	Order	Family	*Species*	Reference	Number matrices	Number populations	Irreducible	Vector
Mammalia	Carnivora	Felidae	*Acinonyx jubatus*	Crooks *et al.* (1998)	1	1	Y	N
Osteichthyes	Acipenseriformes	Acipenseridae	*Acipenser medirostris*	Simpson & Kopp (2006)	1	1	Y	Y
Pterygota	Hemiptera	Aphididae	*Acyrthosiphon pisum*	Gross *et al.* (2002)	4	2	Y	Y
Aves	Strigiformes	Strigidae	*Aegolius funereus*	Hayward & McDonald, 2nd Owl Symposium.	1	1	Y	N
Anthozoa	Scleractinia	Agariciidae	*Agaricia agaricites*	Hughes & Tanner (2000)	4	1	Y	Y
Mammalia	Carnivora	Ursidae	*Ailuropoda melanoleuca*	Carter *et al.* (1999)	1	1	N	N
Mammalia	Artiodactyla	Cervidae	*Alces alces*	Gaillard & Yoccoz (2003)	1	1	Y	N
Anthozoa	Alcyonacea	Alcyoniidae	*Alcyonium sp*	McFadden (1991)	4	4	Y	N
Aves	Anseriformes	Anatidae	*Anser caerulescens*	Rockwell *et al.* (1997)	1	1	Y	N
Mammalia	Artiodactyla	Antilocapridae	*Antilocapra americana*	Berger & Conner (2008); Gaillard and Yoccoz (2003)	4	3	Y	N
Mammalia	Cetacea	Balaenopteridae	*Balaenoptera musculus*	Usher (1972)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Bos taurus*	Gaillard & Yoccoz (2003)	1	1	Y	N
Mammalia	Primates	Atelidae	*Brachyteles hypoxanthus*	Lawler (2010)	1	1	Y	N
Amphibia	Anura	Bufanoidea	*Bufo boreas*	Biek *et al.* (2002)	1	1	Y	N
Aves	Charadriiformes	Scolopacidae	*Calidris pusilla*	Hitchcock & Gratto-Trevor (1997)	1	1	Y	N
Malacostraca	Decapoda	Portunidae	*Callinectes sapidus*	Miller (2001)	4	1	Y	N
Mammalia	Carnivora	Phocidae	*Callorhinus ursinus*	Barlow & Boveng (1991)	1	1	N	N

Mammalia	Carnivora	Canidae	*Canis lupis*	Miller *et al.* (2002)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Capra ibex*	Gaillard & Yoccoz (2003)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Capra pyrenaica*	Escos *et al.* (1994)	2	2	Y	N
Mammalia	Artiodactyla	Cervidae	*Capreolus capreolus*	Gaillard & Yoccoz (2003)	1	1	Y	N
Chondrichthyes	Lamniformes	Odontaspididae	*Carcharias taurus*	Otway *et al.* (2004)	1	1	Y	N
Reptilia	Testudines	Cheloniidae	*Caretta caretta*	Crouse *et al.* (1987); Crowder *et al.* (1994)	2	1	Y	N
Mammalia	Primates	Cebidae	*Cebus capucinus*	Lawler (2010)	1	1	Y	N
Aves	Galliformes	Phasianidae	*Centrocercus urophasianus*	Johnson & Braun (1999)	1	1	Y	N
Mammalia	Primates	Cercopithecidae	*Cercopithecus mitis stuhlmanni*	Cords & Chowdhury (2010)	1	1	N	N
Mammalia	Artiodactyla	Cervidae	*Cervus elaphus*	Benton *et al.* (1995)	1	1	Y	N
Reptilia	Testudines	Cheloniidae	*Chelonia mydas*	Chaloupka (2002)	1	1	Y	N
Sauropsida	Testudines	Chelydridae	*Chelydra serpentina*	Congdon *et al.* (1994)	1	1	Y	N
Aves	Passeriformes	Tyrranidae	*Chiroxiphia linearis*	McDonald (1993)	2	1	Y	N
Actinopterygii	Scorpaeniformes	Cottidae	*Clinocottus globiceps*	Pfister (1996)	3	1	N	N
Mammalia	Artiodactyla	Bovidae	*Connochaetes taurinus*	Grange *et al.* (2004)	1	1	Y	N
Sauropsida	Falconiformes	Cathartidae	*Coragyps atratus*	Blackwell *et al.* (2007)	2	1	Y	N
Reptilia	Squamata	Elapidae	*Cryptophis nigrescens*	Webb *et al.* (2002)	1	1	Y	N
Mammalia	Rodentia	Sciuridae	*Cynomys gunnisoni*	Cully (1997)	2	2	N	N
Branchiopoda	Cladocera	Daphniidae	*Daphnia magna*	DJC unpublished	2	1	Y	N
Branchiopoda	Cladocera	Daphniidae	*Daphnia pulex*	Frank *et al.* (1957)	1	1	N	N
Chondrichthyes	Rajiformes	Dasyatidae	*Dasyatis violacea*	Mollet & Cailliet (2002)	1	1	Y	N

Aves	Procellariiformes	Diomedeidae	*Diomedea amsterdamensis*	Inchausti & Weimerskirch (2001)	1	1	Y	N
Mammalia	Rodentia	Geomyidae	*Dipodomys stephensi*	Price & Kelly (1994)	1	1	N	N
Sauropsida	Testudines	Emydidae	*Emydoidea blandingii*	Congdon *et al.* (1993)	1	1	Y	N
Actinopterygii	Clupeiformes	Engraulidae	*Engraulis mordax*	Lo *et al.* (1995)	1	1	Y	N
Mammalia	Carnivora	Mustelidae	*Enhydra lutris nereis*	Krkosek *et al.* (2007)	1	1	Y	N
Mammalia	Perissodactyla	Equidae	*Equus burchelli*	Grange *et al.* (2004)	1	1	Y	N
Mammalia	Perissodactyla	Equidae	*Equus caballus*	Garrott & Taylor (1990); Fernandez *et al.* (2006)	6	6	Y	N
Mammalia	Cetacea	Balaenidae	*Eubalaena glacialis*	Fujiwara & Caswell (2001)	1	1	Y	N
Mammalia	Carnivora	Otariidae	*Eumetopias jubatus*	York (1994)	1	1	Y	N
Aves	Falconiformes	Falconidae	*Falco naumanni*	Hiraldo *et al.* (1996)	1	1	Y	N
Aves	Falconiformes	Falconidae	*Falco peregrinus*	Wootton & Bell (1992)	1	1	Y	N
Actinopterygii	Cyprinodontiformes	Fundulidae	*Fundulus grandis*	Sable (2007)	1	1	Y	N
Anthozoa	Scleractinia	Faviidae	*Goniastrea aspera*	Orive (1995)	1	1	Y	Y
Anthozoa	Scleractinia	Faviidae	*Goniastrea favulus*	Orive (1995)	1	1	Y	Y
Reptilia	Testudines	Testudinidae	*Gopherus agassizii*	Doak *et al.* (1994)	1	1	Y	N
Mammalia	Primates	hominidae	*Gorilla beringei*	Lawler (2010)	1	1	Y	N
Mammalia	Carnivora	Phocidae	*Halichoerus grypus*	Harding *et al.* (2007)	1	1	Y	N
Gastropoda	Archegastropoda	Haliotidae	*Haliotis rufescens*	Rogers-Bennett & Leaf (2006)	1	1	Y	N
Gastropoda	Archegastropoda	Haliotidae	*Haliotis sorenseni*	Rogers-Bennett & Leaf (2006)	1	1	Y	N
Gastropoda	Pulmonata	Helicidae	*Helix aspera*	Laskowski & Hopkin (1996)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Hemitragus jemlahicus*	Caughley (1966)	1	1	Y	N
Mammalia	Artiodactyla	Cervidae	*Hippocamelus bisulcus*	Wittmer *et al.* (2010)	1	1	Y	N

Reptilia	Squamata	Elapidae	*Hoplocephalus bungaroides*	Webb *et al.* (2002)	1	1	Y	N
Aves	Passeriformes	Turdidae	*Hylocichla mustelina*	Noon & Sauer (1992)	1	1	Y	N
Reptilia	Testudines	Kinosternidae	*Kinosternon flavescens*	Heppell *et al.* (1996)	1	1	Y	N
Pterygota	Coleoptera	NA	*Lasioderma serricorne*	Lefkovitch (1965)	1	1	Y	N
Reptilia	Testudines	Cheloniidae	*Lepidochelys kempi*	Heppell *et al.* (1996)	1	1	Y	N
Anthozoa	Gorgonacea	Gorgoniidae	*Leptogorgia virgulata*	Gotelli (1991)	1	1	Y	N
Anthozoa	Scleractinia	Agariciidae	*Leptoseris cucullata*	Hughes & Tanner (2000)	4	1	Y	Y
Mammalia	Rodentia	Geomyidae	*Liomys adspersus*	Oli & Zinner (2001)	1	1	Y	N
Mammalia	Primates	Cercopithecidae	*Macaca fascicularis*	Crockett *et al.* (1996)	9	1	N	N
Mammalia	Primates	Cercopithecidae	*Macaca Thibetana*	Oli & Zinner (2001)	1	1	Y	N
Mammalia	Cetacea	Balaenopteridae	*Megaptera novaeangliae*	Barlow & Clapham (1997)	1	1	N	N
Mammalia	Carnivora	Mustelidae	*Meles meles*	Messick & Hornocker (1981)	1	1	N	Y
Mammalia	Rodentia	Muridae	*Microtus orcadensis*	Leslie *et al.* (1965)	1	1	N	N
Mammalia	Rodentia	Muridae	*Microtus pennsylvanicus*	Oli & Dobson (1999)	3	1	Y	N
Anthozoa	Scleractinia	Faviidae	*Montastrea annularis*	Hughes & Tanner (2000)	4	1	Y	Y
Mammalia	Carnivora	Mustelidae	*Mustela erminea*	Wittmer *et al.* (2007)	5	1	Y	N
Mammalia	Carnivora	Mustelidae	*Mustela nigripes*	Grenier *et al.* (2007)	1	1	N	N
Chondrichthyes	Carchariniformes	Carcharhinidae	*Negaprion brevirostris*	Hoenig & Gruber (1990)	1	1	Y	N
Aconoidasida	Piroplasmorida	Babesiidae	*Nuttallia obscurata*	Dudas *et al.* (2007)	2	2	Y	Y
Mammalia	Lagomorpha	Ochotonindae	*Ochotona princeps*	Smith (1974)	1	1	N	Y
Mammalia	Artiodactyla	Cervidae	*Odocoileus hermionus*	Gaillard & Yoccoz (2003)	1	1	Y	N

Mammalia	Artiodactyla	Cervidae	*Odocoileus virginianus*	Jensen (1996)	1	1	N	N
Actinopterygii	Scorpaeniformes	Cottidae	*Oligocottus maculosus*	Pfister (1996)	3	1	N	N
Actinopterygii	Salmoniformes	Salmonidae	*Onchorhynchus clarki*	Hilderbrand (2003)	1	1	Y	N
Actinopterygii	Salmoniformes	Salmonidae	*Onchorhynchus tshawytscha*	Kareiva *et al.* (2000); Wilson 2003	4	5	Y	N
Mammalia	Marsupialia	Macropodidae	*Onychogalea fraenata*	Fisher *et al.* (2000)	1	1	Y	Y
Mammalia	Cetacea	Delphinidae	*Orcinus orca*	Brault & Caswell (1993)	19	18	N	N
Mammalia	Artiodactyla	Bovidae	*Oreamnos americanus*	Gaillard & Yoccoz (2003)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Ovis aeries*	Gaillard & Yoccoz (2003)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Ovis canadensis*	Gaillard & Yoccoz (2003)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Ovis dall*	Gaillard & Yoccoz (2003)	1	1	Y	N
Malacostraca	Decapoda	Paguroidea	*Pagurus longicarpus*	Damiani (2005)	1	1	Y	N
Malacostraca	Decapoda	Palaemonoida	*Palaemonetes pugio*	Sable (2007)	1	1	Y	N
Mammalia	Primates	hominidae	*Pan troglodytes schweinfurthii*	Lawler (2010)	1	1	Y	N
Mammalia	Carnivora	Felidae	*Panthera leo*	Oli & Zinner (2001)	1	1	Y	N
Mammalia	Primates	Cercopithecidae	*Papio cynocephalus*	Oli & Zinner (2001)	1	1	Y	N
Anthozoa	Gorgonacea	Plexuridae	*Paramuricea clavata*	Linares *et al.* (2007)	6	2	Y	Y
Aves	Passeriformes	Passeridae	*Passer domesticus*	Maclean *et al.* (2008)	1	1	Y	N
Mammalia	Artiodactyla	Suidae	*Phacochoerus aethiopicus*	Oli & Zinner (2001)	1	1	Y	N
Mammalia	Marsupialia	Phascolarctidae	*Phascolarctos cinereus*	Baxter *et al.* (2006)	1	1	Y	N
Sauropsida	Galliformes	Phasianidae	*Phasianus colchicus torquatus*	Clark *et al.* (2008)	3	2	Y	N

Aves	Procellariiformes	Diomedeidae	*Phoebastria nigripes*	Lewison & Crowder (2003)	1	1	Y	N
Aves	Piciformes	Picidae	*Picoides borealis*	MacGuire *et al.* (1995)	4	1	Y	N
Anthozoa	Scleractinia	Faviidae	*Platygyra sinensis*	Orive (1995)	1	1	Y	Y
Osteichthyes	Cyprinodontiformes	Poeciliidae	*Poecilia reticulata*	Branikowski *et al.* (2002)	5	1	Y	N
Mammalia	Primates	Indridae	*Propithecus Verreuxi*	Lawler *et al.* (2009)	1	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Pseudois nayaur*	Oli & Zinner (2001)	1	1	Y	N
Aves	Procellariiformes	Procellariidae	*Pterodroma phaeopygia sandwichensis*	Simons (1984)	1	1	Y	N
Aves	Procellariiformes	Procellariidae	*Puffinus opisthomelas*	Keitt *et al.* (2002)	1	1	Y	N
Amphibia	Anura	Ranidae	*Rana aurora*	Biek *et al.* (2002)	1	1	Y	N
Amphibia	Anura	Ranidae	*Rana catesbeiana*	Purnima *et al.* (2005)	1	1	N	N
Amphibia	Anura	Ranidae	*Rana sylvatica*	US EPA (2003)	2	2	N	N
Amphibia	Anura	Ranidae	*Rana temporaria*	Biek *et al.* (2002)	1	1	Y	N
Mammalia	Artiodactyla	Cervidae	*Rangifer tarandus*	Oli & Zinner (2001)	1	1	Y	N
Aves	Falconiformes	Accipitridae	*Rostrhamus sociabilis*	Beissinger (1995)	3	1	Y	N
Actinopterygii	Salmoniformes	Salmonoidae	*Salvelinus fontinalis*	Letcher *et al.* (2007)	1	1	Y	N
Actinopterygii	Clupeiformes	Clupeoidae	*Sardinops sagax*	Lo *et al.* (1995)	1	1	Y	N
Mammalia	Rodentia	Sciuridae	*Sciurus carolinensis*	Barkalow *et al.* (1970)	1	1	Y	Y
Mammalia	Rodentia	Sciuridae	*Spermophilus armatus*	Slade & Balph (1974)	8	3	Y	N
Mammalia	Rodentia	Sciuridae	*Spermophilus columbianus*	Dobson & Oli (2001)	6	6	Y	N
Mammalia	Rodentia	Sciuridae	*Spermophilus lateralis*	Bronson (1979)	4	4	Y	N
Demospongiae	Dictyoceratida	Spongiidae	*Spongia graminea*	Cropper & Di Resta (1999)	3	1	Y	Y

Sauropsida	Charadriiformes	Laridae	*Sterna antillarum*	Akçakaya *et al.* (2003)	6	1	Y	N
Polychaeta	Spionida	Spionidae	*Streblospio benedicti*	Levin *et al.* (1987)	2	1	Y	N
Aves	Strigiformes	Strigidae	*Strix occidentalis*	Lande (1988)	1	1	Y	N
Mammalia	Artiodactyla	Suidae	*Sus scrofa*	Bieber & Ruf (2005)	3	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Syncerus caffer*	Grange *et al.* (2004)	1	1	Y	N
Mammalia	Rodentia	sciuridae	*Tamiasciurus hudsonicus*	McAdam *et al.* (2007)	1	1	N	N
Mammalia	Marsupialia	Didelphidae	*Thylamys elegans*	Lima *et al.* (2001)	5	1	Y	N
Mammalia	Artiodactyla	Bovidae	*Tragelaphus strepsiceros*	Gaillard & Yoccoz (2003)	1	1	Y	N
Pterygota	Coleoptera	NA	*Tribolium sp*	Costantino (1987)	2	1	Y	N
Mammalia	Sirenia	Trichechidae	*Trichechus manatus latirostris*	Runge *et al.* (2004)	4	4	Y	N
Aves	Passeriformes	Troglodytedae	*Troglodytes troglodytes*	Maclean *et al.* (2008)	1	1	Y	N
Mammalia	Cetacea	Delphinidae	*Tursiops truncatus*	Stolen & Barlow (2003)	3	1	Y	N
Aves	Galliformes	Phasianidae	*Tympanuchus cupido pinnatus*	Wisdom & Mills (1997)	3	1	N	N
Gastropoda	Archegastropoda	Trochidae	*Umbonium costatum*	Noda & Nakao (1996)	9	1	Y	N
Aves	Charadriiformes	Alcidae	*Uria lomvia*	Wiese *et al.* (2004)	1	1	Y	N
Mammalia	Carnivora	Canidae	*Urocyon littoralis*	Roemer *et al.* (2001)	4	3	Y	N
Mammalia	Carnivora	Ursidae	*Ursus americanus*	Oli & Zinner (2001)	1	1	Y	N
Mammalia	Carnivora	Ursidae	*Ursus arctos*	Wielgus (2002)	1	1	Y	N
Mammalia	Carnivora	Ursidae	*Ursus maritimus*	Hunter (2010)	6	1	Y	N
Reptilia	Squamata	Viperidae	*Vipera aspis*	Altwegg *et al.* (2005)	3	2	Y	N

Aves	Passeriformes	Vireonidae	*Vireo latimeri*	Woodworth (1999)	8	1	Y	N
Aves	Passeriformes	Vireonidae	*Vireo olivaceus*	Noon & Sauer (1992)	1	1	Y	N
Mammalia	Carnivora	Canidae	*Vulpes vulpes*	Nelson *et al.* (2010)	1	1	Y	N
Reptilia	Squamata	Xenosauridae	*Xenosaurus grandis*	Zuniga-Vega *et al.* (2007)	5	1	Y	Y
Bivalvia	Nuculoida	Yoldiidae	*Yoldia notabilis*	Nakaoka (1997)	3	2	Y	N
Mammalia	Carnivora	Otariidae	*Zalophus californianus*	Wielgus *et al.* (2008)	1	1	Y	N

_____

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, λ_{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, **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.

REFERENCES

REFERENCES IN MAIN TEXT

Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. Oikos, 65, 225–232.

Abe, S., Nakashizuka, T. & Tanaka, H. (1998) Effects of canopy gaps on the demography of the subcanopy tree Styrax obassia. Journal of Vegetation Science, 9, 787–796.

Åberg, P., Svensson, C.J., Caswell, H. & Pavia, H. (2009) Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. Ecological Modelling, 220, 605–610.

Angiosperm Phylogeny Group (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. Botanical Journal of the Linnean Society, 141, 399–436.

Armsworth, P.R. (2002) Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology,83, 1092–1104.

Ballantine, J.E. & Forde, B.T. (1970) The effect of light intensity and temperature on plant growth and chloroplast ultrastructure in soybean. American Journal of Botany, 57, 1150-1159.

Bapat, R.B. (1998) A max version of the Perron–Frobenius theorem. Linear algebra and Its Applications, 275/276, 3–18.

Batista, W.B., Platt, W.J. & Macchiavelli, R.E. (1998) Demography of a shade-tolerant tree (Fagus grandifolia) in a hurricane-disturbed forest. Ecology, 79, 38–53.

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

Bell, G. 1980. The costs of reproduction and their consequences. American Naturalist, 116, 45–76.

Benton T.G. & Grant A. (1996). How to keep fit in the real world: Elasticity analyses and selection pressures on life histories ln a variable environment. American Naturalist, 147, 115-139.

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

Bierzychudek, P. (1982) The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs, 52,335–351.

Bjørnstad, O.N. & Grenfell, B.T. (2001) Noisy clockwork: time series analysis of population fluctuation in animals. Science, 293, 638–643.

Bode, M., Bode, L. & Armsworth, P.R. (2006) Larval dispersal reveals regional sources and sinks in the great barrier reef. Marine Ecology Progress Series, 308, 17–25.

Brands, S.J. (comp.) (1989-2005) Systema Naturae 2000. Amsterdam, The Netherlands. Available at: http://sn2000.taxonomy.nl/. Accessed 31 December 2009.

Brault, S. & Caswell, H. (1993) Pod-specific demography of killer whales (Orcinus orca). Ecology, 74, 1444–1454.

Buckley, Y.M., Ramula, S.R., Blomberg, S.P., Burns, J.H., Crone, E.E., Ehrlen, J., Knight, T.M., Pichancourt, J.B., Quested, H. & Wardle, G.M. (2010) Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. Ecology Letters, 13, 1182-1197.

Burns, J.H., Blomberg, S.P., Crone, E.E., Ehrlén, J., Knight, T. M., Pinchancourt, J.-B., Ramula, S., Wardle, G.M. & Buckley, Y.M. (2010)Empirical tests of life-history evolution theory using phylogenetic analysis of plant demography. Journal of Ecology, 98, 334–344.

Carrillo, J., Danielson-François, A., Siemann, E. & Meffert, L. (2012) Male-biased sex ratio increases female egg laying and fitness in the houseful, Musca domestica. Journal of Ethology, doi: 10.1007/s10164-011-0317-6

Carslake, D., Townley, S. & Hodgdon, D.J. (2008) Nonlinearity in eigenvalue-perturbation curves of simulated population projection matrices. Theoretical Population Biology, 73, 498–505.

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

Carslake, D., Townley, S. & Hodgson, D.J. (2009b) Patterns and rules for sensitivity and elasticity in population projection matrices. Ecology, 90, 3258–3267.

Caswell, H. (2001) Matrix Population Models: Construction, Analysis and Interpretation. Sinauer, Sunderland, MA.

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

Caswell, H. (1989) Population Matrix Models: Construction, Analysis and Interpretation, 1st edn. Sinauer, Sunderland, Massachusetts, USA.

Caughley G. (1966). Mortality patterns in mammals. Ecology, 47, 906-&.

Charnov, E.L. & Schaffer, W.M. (1973) Life history consequences of natural selection: Cole's result revisited. American Naturalist, 107, 791-793.

Chesson, P. (1991) A need for niches? Trends in Ecology and Evolution, 6, 26–28.

Chesson, P.L. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. The American Naturalist, 117, 923–943.

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. Proceedings of the Royal Society of London B: Biological Sciences, 271, 425–434.

Cohen, J.E. (1979) The cumulative distance from an observed to a stable age structure. SIAM Journal of Applied Mathematics, 36, 169–175.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology, 29, 103–137.

Connell, J. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist, 122, 661-696.

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. Advances in Ecological Research, 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.

Crone, E.E. (2001) Is survivorship a better fitness surrogate than fecundity? Evolution, 55, 2611–2614.

Crooks, K.R., Sanjayan, M.A. & Doak, D.F. (1998) New insights on cheetah conservation through demographic modelling. Conservation Biology, 12, 889–895.

Cropper Jr, W.P. & DiResta, D. (1999) Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after hurricane Andrew. Ecological Modelling, 118, 1–15.

Crowder, L.B., Crouse, D.T., Heppell, S.S. & Martin, T.H. (1994) Predicting the impact of turtles excluder devices on loggerhead sea turtle populations. Ecological Applications, 4, 437–445.

Cuddington, K. (2001) The 'balance of nature' metaphor and equilibrium in population ecology. Biological Philosophy, 16, 463–479.

Day, J.R. & Possingham, H.P. (1995) A stochastic metapopulation model with variability in patch size and position. Theoretical Population Biology, 48, 333–360.

de Matos, M.B. & Silva Matos, D.M. (1998) Mathematical constraints on transition matrix elasticity analysis. Journal of Ecology, 86, 706–708.

De Walt, S.J. (2006) Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. Biological Invasions, 8, 1145–1158.

Dennis, B. & Costantino, R.F. (1988) Analysis of steady-state populations with the gamma abundance model: application to Tribolium. Ecology, 69, 1200–1213.

Dennis, B., Desharnais, R.A., Cushing, J.M., Henson, S.M. & Costantino, R.F. (2001) Estimating chaos and complex dynamics in an insect population. Ecological Monographs, 71, 277–303.

Dennis, B., Desharnais, R.A., Cushing, J.M. & Costantino, R.F. (1997) Transitions in population dynamics: equilibria to periodic cycles to aperiodic cycles. Journal of Animal Ecology, 66, 704–729.

Dietzenbacher, E. (1991) Chapter 12: a limiting property for the powers of a reducible, nonnegative matrix. Perturbations and eigenvectors: essays. PhD Thesis, University of Groningen, Groningen.

Doak, D., Kareiva, P. & Klepetka, B. (1994) Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications, 4, 446–460.

Drake, J.M. (2005) Risk analysis for invasive species and emerging infectious diseases: concepts and applications. American Midland Naturalist, 153, 4–19.

Dudas, S.E., Dower, J.F. & Anholt, B.R. (2007) Invasion dynamics of the varnish clam (Nuttallia obscurata): a matrix demographic modelling approach. Ecology, 88, 2084–2093.

Easterling, M.R., Ellner, S.P. & Dixon, P.M. (2000) Size-specific sensitivity: applying a new structured population model. Ecology, 81,694–708.

Egley, G.H. (1990) High-temperature effects on germination and survival of weed seeds in soil. Weed Science, 38, 429-435.

Ehrlén, J. & Lehtilä, K. (2002) How perennial are perennial plants? Oikos, 98, 308–322.

Ehrlén, J. & Van Groenendael, J.M. (1998) The trade-off between dispersability and longevity: an important aspect of plant species diversity. Applied Vegetation Science, 1, 29–36.

Elhashash, A. & Szyld, D. (2008) On general matrices having the Perron–Frobenius property. Electronic Journal of Linear Algebra, 17,389–413.

Ellner, S.P. & Rees, M. (2006) Integral projection models for species with complex demography. American Naturalist, 167, 410–428.

Ellner, S.P. & Rees, M. (2007) Stochastic stable population growth in integral projection models: theory and application. Journal of Mathematical Biology, 54, 227–256.

Enright, N.J., Franco, M. & Silvertown, J. (1995) Comparing plant life histories using elasticity analysis: the importance of life span and the number of life-cycle stages. Oecologia, 104, 79–84.

Esparza-Olguín, L., Valverde, T. & Vilchis-Anaya, E. (2002) Demographic analysis of a rare columnar cactus (Neobuxbaumia macrocephala) in the Tehuacan Valley, Mexico. Biological Conservation, 103, 349–359.

Ezard, T.H.G., Bullock, J.M., Dalgleish, H.J., Millon, A., Pelletier, F., Ozgul, A. & Koons, D.N. (2010) Matrix models for a changeable world: the importance of transient dynamics in population management. Journal of Applied Ecology, 47, 515-523.

Ezard, T.H.G., Pearson, P.N., Aze, T. & Purvis, A. (2012) The meaning of birth and death (in macroevolutionary birth-death models). Biology Letters, 8, 139-142.

Felsenstein, J. (1985) Phylogenies and the comparative method. The American Naturalist, 125, 1–15.

Fenner, M. (2000) Seeds: The Ecology of Regeneration in Plant Communities. CABI Publishing, Wallingford, UK.

Fieberg, J. & Ellner, S.P. (2001) Stochastic matrix models for conservation and management: a comparative review of methods. Ecology Letters, 4, 244–266.

Fiedler, P.L. (1987) Life history and population dynamics of rare and common mariposa lilies (Calochortus Pursh: Liliaceae). Journal of Ecology, 75, 977–995.

Förster, J., Famili, I., Fu, P., Palsson, B. & Nielsen, J. (2003) Genome-scale reconstruction of the Saccharomyces cerevisiae metabolic network. Genome Research, 13, 244-253.

Fowler, M.S. & Ruxton, G.D. (2002) Population dynamic consequences of Allee effects. Journal of Theoretical Biology, 215, 39–46.

Fox, G.A. & Gurevitch, J. (2000) Population numbers count: tools for near-term demographic analysis. American Naturalist, 156, 242–256.

Franco, M. & Silvertown, J. (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology, 85, 531–538.

Freckleton, R.P. (2009) The seven deadly sins of comparative analysis. Journal of Evolutionary Biology, 22, 1367-1376.

Freckleton, R.P. (2000) Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. Functional Ecology, 14, 129–134.

Frobenius, G. (1912) Uber Matrizen aus Nicht-Negativen Elementen. Sitzungsberichte der Berliner Akademie der Wissenschaften,1912, 456–477.

Fujiwara, M. & Caswell, H. (2001) Demography of the endangered North Atlantic right whale. Nature, 414, 537–541.

Gaillard J.M., Allaine D., Pontier D., Yoccoz N.G. & Promislow D.E.L. (1994). Senescence in natural-populations of mammals - a reanalysis. Evolution, 48, 509-516.

Galindo, H.M., Olson, D.B. & Palumbi, S.R. (2006) Seascape genetics: a coupled oceanographic-genetic model predicts population strucutre of Caribbean corals. Current Biology, 16, 1622-1626.

Gillespie, J.H. (1974) Natural selection for within-generation variance in offspring number. Genetics, 76, 601-606.

Gleeson, S.K. & Tilman, D. (1990) Allocation and the transient dynamics of succession on poor soils. Ecology, 71, 1144–1155.

Grant, T.G. & Benton, A. (2000) Elasticity analysis of density-dependent populations in stochastic environments. Ecology, 81,680–693.

Grenfell B.T., Price O.F., Albon S.D. & Clutton-Brock T.H. (1992). Overcompensation and population-cycles in an ungulate. Nature, 355, 823-826.

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. Conservation Biology, 12, 1291–1301.

Gunderson, L.H. (2000) Ecological resilience - in theory and application. Annual Review of Ecology and Systematics, 31, 425-439.

Hadfield, J.D. (2010) MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. Journal of Statistical Software, 33, 1-22.

Haldane, A.G. & May, R.M. (2011) Systemic risk in banking ecosystems. Nature, 469, 351-355.

Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. (1993) Population oscillations of boreal rodents: regulation my mustelid predators leads to chaos. Nature, 364, 232-235.

Harding, E.K., Crone, E.E., Elderd, B.D., Hoekstra, J.M., McKerrow, A.J., Perrine, J.D., Regetz, J., Rissler, L.J., Stanley, A.G., Walters, E.L. & NCEAS Habitat Conservation Plan Working Group (2001) The scientific foundations of habitat conservation plans: a quantitative assessment. Conservation Biology, 15, 488–500.

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

Hastings, A. (2001) Transient dynamics and persistence of ecological systems. Ecology Letters, 4, 215–220.

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

Hastings, A., Hall, R.J. & Taylor, C.M. (2006) A simple approach to optimal control of invasive species. Theoretical Population Biology,70, 431–435.

Hastings, A., Hom, C.L., Ellner, S., Turchin, P. & Godfray, H.C.J. (1993) Chaos in ecology: is mother nature a strange attractor? Annual Review of Ecology and Systematics, 24, 1–33.

Heppell, S.S., Caswell, H. & Crowder, L.B. (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology, 81, 654–665.

Hodgson, D., Townley, S. & McCarthy, D. (2006) Robustness: predicting the effects of life history perturbations on stage-structured population dynamics. Theoretical Population Biology, 70, 214–224.

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.

Hoffmann, W.A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology,80, 1354–1369.

Holmes, E.E., Lewis, M.A., Banks, J.E. & Veit, R.R. (1994) Partial differential equations in ecology: spatial interactions and population dynamics. Ecology, 75, 17-29.

Hughes, T.P. & Tanner, J.E. (2000) Recruitment failure, life histories and long-term decline of Caribbean corals. Ecology, 81, 2250–2263.

Hunt, J. & Hodgson, D. (2010) What is fitness, and how do we measure it? In Westneat, D.F. & Fox, C. Evolutionary Behavioural Ecology. Oxford University Press, Oxford, U.K.

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

Inchausti, P. & Weimerskirch, H. (2001) Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. Biological Conservation, 100, 337–386.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., Van Veen, F.J.F., Warren, P.H., & Woodward, G. (2009) Ecological networks: beyond food webs. Journal of Animal Ecology, 78, 253-269.

Jensen, A.L. (1993) Simple density-dependent matrix model for population projection. Ecological Modelling, 77, 43–48.

Jensen, A.L. (1996) Density-dependent matrix yield equation for optimal harvest of age-structured wildlife populations. Ecological Modelling, 88, 125–132.

Jongejans, H., Jorritsma-Wienk, L.D., Becker, U., Dostál, P., Mildén, M.E. & De Kroon, H. (2010) Region versus site variation in the population dynamics of three short-lived perennials. Journal of Ecology, 98, 279–289.

Kareiva, P., Marvier, M. & McClure, M. (2000) Recovery and management options for spring/summer Chinook salmon in the Columbia River basin. Science, 290, 977–979.

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.

Kolotilina, L.Yu. (2004) Bounds and inequalities for the Perron root of a nonnegative matrix. Journal of Mathematical Sciences, 121,2481–2507.

Koons D.N., Metcalf C.J.E. & Tuljapurkar S. (2008) Evolution of delayed reproduction in uncertain environments: A life-history perspective. American Naturalist, 172, 797-805.

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., Holmes, R.R. & Grand, J.B. (2007) Population inertia and its sensitivity to changes in vital rates and population structure. Ecology, 88, 2857–2867.

Koons, D.N., Rockwell, R.F. & Grand, J.B. (2007) Population momentum: implications for wildlife management. Journal of Wildlife Management, 70, 19–26.

Lamar, W.R. & McGraw, J.B. (2005) Evaluating the use of remotely sensed data in matrix population modelling for eastern hemlock. Forest Ecology and Management, 212, 50–64.

Lande, R., Engen, S. & Saether, B.-E. (2003) Stochastic population dynamics in ecology and evolution. Oxford University Press, Oxford, UK.

Lawson, C.R., Bennie, J.J., Thomas, C.D., Hodgson, J.A. & Wilson, R.J. (2012) Local and landscape management of an expanding range margin under climate change. Journal of Applied Ecology, 49, 552-561.

Lefkovitch, 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.

Lewontin R.C. & Levins R. (1989). On the characterisation of density and resource availability. American Naturalist, 134, 513-524.

Li, C.-K. & Schneider, H. (2002) Applications of Perron–Frobenius theory to population dynamics. Journal of Mathematical Biology,44, 450–462.

Linares, C., Doak, D.F., Coma, R., Díaz, D. & Zabala, M. (2007) Life history and viability of a long-lived marine invertebrate: the octocoral Paramauricea clavata. Ecology, 88, 918–928.

Linkie, M., Dinata, Y., Nugroho, A. & Haidir, I.A. (2007) Estimating occupancy of a data deficient mammalian species living in tropical rainforests: sun bears in the Kerinci Seblat region, Sumatra. Biological Conservation, 137, 20–27.

Lion, S. & Boots, M. (2010) Are parasites prudent in space? Ecology Letters, 13, 1245-1255.

Lofgren P., Eriksson O. & Lehtila K. (2000). Population dynamics and the effect of disturbance in the monocarpic herb Carlina vulgaris (Asteraceae). Annales Botanici Fennici, 37, 183-192.

Lotka, A.J. (1932) The growth of mixed populations: two species competing for a common food supply. Journal of the Washington Academy of Sciences, 22, 461–469.

Lubben, J., Boeckner, D., Rebarber, R., Townley, S. & Tenhumberg, B. (2009) Parameterizing the growth-decline boundary for uncertain population projection models. Theoretical Population Biology, 75, 85–97.

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. Journal of Ecology, 98, 290–301.

Matlab version 7.11 (2011) The Mathworks, Nantick, Massachusetts, USA.

May R.M. (1975). Biological populations obeying difference equations: stable points, stable cycles and chaos. Journal of Theoretical Biology, 49, 511-524.

McGinnis, J.T., Golley, F.B., Clements, R.G., Child, G.I. & Duever, M.J. (1969) Elemental and hydrologic budgets of the Panamanian tropical moist forest. Bioscience, 19, 697–700.

McLean (2003) Ecology and Management of Overabundant Koala (Phascolarctos cinereus) Populations. PhD Thesis, University of Melbourne, Melbourne, Australia.

McMahon, S.M. & Metcalf, C.J.E. (2008) Transient sensitivities of non-indigenous shrub species indicated complicated invasion dynamics. Biological Invasions, 10, 833–846.

Menges, E.S. (1990) Population viability for an endangered plant. Conservation Biology, 4, 52–62.

Miller, D., Morgan, B.J.T., Ridout, M.S., Carey, P.D. & Rothery, P. (2011) Methods for exact perturbation analysis. Methods in Ecology and Evolution, 2, 283–288.

Mincheva, M. & Roussel, M.R. (2007) Graph-theoretic methods for the analysis of chemical and biochemical networks. I. Multistability and oscillations in ordinary differential equation models. Journal of Mathematical Biology, 55, 61-86.

Mitchell-Olds, T. (1996a) Genetic constraints on life-history evolution: quantitative-trait loci influencing growth and flowering in Arabidopsis thaliana. Evolution, 50, 140–145.

Mitchell-Olds, T. (1996b) Pleiotropy causes long-lerm genetic constraints on life-history evolution in Brassica rapa. Evolution, 50,1849–1858.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. (2005) A brief history of seed size. Science, 307,576–580.

Mollet, H.F. & Cailliet, G.M. (2002) Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Marine and Freshwater Research, 53, 503–516.

Moloney, K.A. (1986) A generalized algorithm for choosing category size. Oecologia, 69, 176–180.

Morris, W.F. & Doak, D.F. (2005) How general are the determinants of the stochastic population growth rate across nearby sites? Ecological Monographs, 75, 119–137.

Mumby, P.J., Vitolo, R. & Stephenson, D.B. (2011) Temporal clustering of tropical cyclones and its ecosystem impacts. Proceedings of the National Academy of Sciences of the United States of America, 108, 17626–17630.

Münzbergová, Z. & Ehrlén, J. (2005) How best to collect demographic data for population viability analysis models. Journal of Applied Ecology, 42, 1115–1120.

Nakaoka, M. (1997) Demography of the marine bivalve Yoldia notabilis in fluctuating environments: an analysis using a stochastic matrix model. Oikos, 79, 59–68.

Nantel, P., Gagnon, D. & Nault, A. (1996) Population viabiliity analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology, 10, 608-621.

Nault, A. & Gagnon, D. (1993) Ramet demography of Allium tricoccum, a spring ephemeral, perennial forest herb. Journal of Ecology,81, 101–119.

Neubert, M.G. & Caswell, H. (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology, 78, 653–665.

Noon, B.R. & Sauer, J.R. (1992) Population models for passerine birds: structure, parameterization and analysis. Wildlife 2001: Populations (eds D.R. McCullough & R.H. Barrett), pp. 441–464, Elsevier Science, Barking, UK.

O'Connor, T.G. (1993) The influence of rainfall and grazing on the demography of some African savanna grasses: a matrix modelling approach. Journal of Applied Ecology, 30, 119–132.

Ogata, K. (2010) Modern Control Engineering, 5th edn. Prentice Hall, Upper Saddle River, NJ, USA.

Otto, S. & Day, T. (2007) A Biologist's Guide to Mathematical Modelling in Ecology and Evolution. Princeton University Press, Princeton, New Jersey, USA.

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. Biological Conservation, 119, 341–350.

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.

Pavlik, B.M. & Barbour, M.G. (1988) Demographic monitoring of endemic sand dune plants, Eureka valley, California. Biological Conservation, 46, 217–242.

Perron, O. (1907a) Jacobisher Kettenbruchalgorithmus. Mathematishe Annalen, 64, 1–76.

Perron, O. (1907b) Ueber Matrizen. Mathematishe Annalen, 64, 248–263.

Phylomatic: a database for applied phylogenies. Available at: http://www.phylodiversity.net/phylomatic/. Accessed 31 December 2009

Pinard, M. (1993) Impacts of stem harvesting on populations of Iriartea deltoidea in an extractive reserve in Acre, Brazil. Biotropica, 25, 2–14.

Price, M.V. & Kelly, P.A. (1994) An age-structured demographic model for the endangered Stephens' kangaroo rat. Conservation Biology, 8, 810–821.

R Development Core Team (2008) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org. Accessed 31 December 2009.

R Development Core Team (2009) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. URL http://www.R-project.org (accessed 31 December 2009).

R Development Core Team (2011) R: A Language and Environment for Statistical Computing, reference index version 2.13.1. R Foundation for Statistical Computing, Vienna, Austria. http://cran.r-project.org [accessed 1 January 2012].

Ramula, S. & Lehtilä, K. (2005) Matrix dimensionality in demographic analyses of plants: when to use smaller matrices? Oikos, 111, 563–573.

Ramula, S., Rees, M. & Buckley, Y.M. (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. Journal of Applied Ecology, 46, 1048–1053.

Ratsirarson, J., Silander Jr, J.A. & Richard, A.F. (1996) Conservation and management of a threatened Madagascar Palm species, Neodypsis decaryi, Jumelle. Conservation Biology, 10, 40–52.

Reed, L.J. & Pearl, R. (1927) On the summation of logistic curves. Journal of the Royal Statistical Society, 90, 729-746.

Roff, D.A. (2002) Life History Evolution. Sinauer Associates, Sunderland, MA.

Rohani, P., Keeling, M.T. & Grenfell, B.T. (2002) The interplay between determinism and stochasticity in childhood diseases. American Naturalist, 159, 469–481.

Runge, M.C., Langtimm, C.A. & Kendall, W.L. (2004) A stage-based model of Manatee population dynamics. Marine Mammal Science, 20, 361–385.

Sable, S.E. & Rose, K.A. (2010) Predicting yellow perch population responses using a density-dependent age-structured matrix projection model: how many annual data points are needed? Transactions of the American Fisheries Society, 139, 1857-1871.

Sæther, B.-E. & Bakke, O. (2000) Avian life history variation and contrubution of demographic rates to the population growth rate. Ecology, 81, 642–653.

Salguero-Gómez, R. & Casper, B.B. (2010) Keeping plant shrinkage in the demographic loop. Journal of Ecology, 98, 312–323.

Salguero-Gómez, R. & Plotkin, J.B. (2010) Matrix dimensions bias demographic inferences: implications for comparative plant demography. The American Naturalist, 176, 710–722.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, J.B. & Charnov, E.L. (2004) Effects of body size and temperature on population growth. American Naturalist, 163, 429-441.

Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: Carduus nutans in New Zealand. Ecological Applications, 8, 824–832.

Silvertown, J. & Dodd, M. (1996) Comparing plants and connecting traits. Philosophical transactions of the Royal Society B: Biological Sciences, 351, 1233–1239.

Silvertown, J., Franco, M. & Menges, E. (1996) Interpretation of elasticities as an aid to the management of plant populations for conservation. Conservation Biology, 10, 591–597.

Silvertown, J., Franco, M., Pisanty, I. & Menzoza, A. (1993) Comparative plant demography - relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology, 81, 465–476.

Smee, M.R., Smyth, W., Tunmore, M., ffrench-Constant, R., & Hodgson, D.J. (2011) Butterflies on the brink: habitat requirements for declining populations of the marsh fritillary (Euphydryas aurinia) in SW England. Journal of Insect Conservation, 15, 153-163.

Smith, D.T., Hosken, D.J., ffrench-Constant, R.H. & Wedell, N. (2009) Variation in sex peptide expression in D. melanogaster. Genetics Research, 91, 237-242.

Smith, G.C. & Trout, R.C. (1994) Using Leslie matrices to determine wild rabbit population growth and the potential for control. Journal of Applied Ecology, 31, 223–230.

Souza, A.F. & Martins, F.R. (2006) Demography of the clonal palm Geonoma brevispatha in a neotropical swamp forest. Austral Ecology, 31, 869–881.

Stephens P.A., Sutherland W.J. & Freckleton R.P. (1999). What is the Allee effect? Oikos, 87, 185-190.

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.

Stott, I., Franco, M., Carslake, D., Townley, S. & Hodgson, D.J. (2010a) Boom or bust? A comparative analysis of transient population dynamics in plants. Journal of Ecology, 98, 302–311.

Stott, I., Townley, S., Carslake, D. & Hodgson, D.J. (2010b) On reducibility and ergodicity of population projection matrix models. Methods in Ecology and Evolution, 1, 242–252.

Stott, I., Hodgson, D.J. & Townley, S. (2012a) popdemo: an R package for population demography using projection matrix analysis. Methods in Ecology and Evolution, 3, doi: 10.1111/j.2041-210X.2012.00222.x.

Stott, I., Hodgson, D.J. & Townley, S. (2012b) Beyond sensitivity: nonlinear perturbation analysis of transient dynamics. Methods in Ecology and Evolution, 3, doi: 10.1111/j.2041-210X.2012.00199.x.

Stott, I., Townley, S. & Hodgson, D.J. (2011) A framework for studying transient dynamics of population projection matrix models. Ecology Letters, 14, 959–970.

Stubben, C.J. & Milligan, B.G. (2007) Estimating and analyzing demographic models using the popbio package in R. Journal of Statistical Software, 22, 11.

Tavener, S., Mikucki, M., Field, S.G. & Antolin, M.F. (2011) Transient sensitivity analysis for nonlinear population models. Methods in Ecology and Evolution, 2, 560–575.

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.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O. & Williams, S.E. (2004) Extinction risk from climate change. Nature, 427, 145-148.

Tilman, D., May, R.M., Lehman, C. L. & Nowak, M.A. (1994) Habitat destruction and the extinction debt. Nature, 371, 65-66.

Tompkins, D.M., White, A.R. & Boots, M. (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. Ecology Letters, 6, 189-196.

Townley, S. & Hodgson, D. (2008) Erratum et addendum: transient amplification and attenuation in stage-structured population dynamics. Journal of Applied Ecology, 45, 1836–1839.

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.

Tudge, C. (2000) The Variety of Life: A Survey and Celebration of all the Creatures That Have Ever Lived. Oxford University Press, Oxford, UK.

Tuljapurkar S. (1990). Population Dynamics in Variable Environments. Springer-Verlag, New York.

Tuljapurkar, S., Horvitz, C.C. & Pascarella, J.B. (2003) The many growth rates and elasticities of populations in random environments. The American Naturalist, 162, 489–502.

Tuljapurkar, S.D. (1982) Population dynamics in variable environments. III. Evolutionary dynamics of r selection. Theoretical Population Biology, 21, 141–165.

Tuljapurkar, S.D. (1990) Population dynamics in variable environments. Lecture Notes in Biomathematics, 85. Springer-Verlag, New York.

Turchin, P. & Taylor, A.D. (1992) Complex dynamics in ecological time series. Ecology, 73, 289-305.

Turchin, P. (1993) Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. Oikos, 68, 167–172.

Turnbull L.A., Rees M. & Crawley M.J. (1999). Seed mass and the competition/colonization trade-off: a sowing experiment. Journal of Ecology, 87, 899-912.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant population seed-limited? A review of seed sowing experiments. Oikos, 88, 225–238.

Valverde, T., Quijas, S., Lópex-Villavicencio, M., Castillo, S. (2004) Population dynamics of Mammillaria magnimamma Haworth. (Cactaceae) in a lava-field in central Mexico. Plant Ecology, 170, 167-184.

van Mantgem, P.J. & Stephenson, N.L. (2005) The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. Journal of Ecology, 93, 737–747.

van Winkle, W., Rose, K.A. & Chambers, R.C. (1993) Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society, 122, 397–403.

Vandermeer, J. (1978) Choosing category size in a stage projection matrix. Oecologia, 32, 79–84.

Verhulst, P.F. (1838) Notice sur la loi que la population suit dans son accroiseement. 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)

Wallington, T.J., Hobbs, R.J. & Moore, S.A. (2005) Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. Ecology and Society, 10, 15.

Webb, C.O., Ackerly, D.D & Kembell, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics, 24, 2098-2100.

Wilbur, H.M. & Rudolf, V.H.W. (2006) Life history evolution in uncertain environments: bet-hedging in time. American Naturalist, 168, 398-411.

Wilson, P.H. (2003) Using population projection matrices to evaluate recovery strategies for Snake River spring and summer Chinook salmon. Conservation Biology, 17, 782–794.

Yearsley, J.M. (2004) Transient population dynamics and short-term sensitivity analysis of matrix population models. Ecological Modelling, 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.

REFERENCES IN APPENDICES

Baker, W.J., Savolainen, V., Asmussen-Lange, C.B., Chase, M.W., Dransfield, J., Forest, F., Harley, M.M., Uhl, N.W., & Wilkinson, M. (2009) Complete generic-level phylogenetic analysis of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. Systematic Biology, 58, 240-256.

Abe, S., Nakashizuka, T. & Tanaka, H. (1998) Effects of canopy gaps on the demography of the subcanopy tree Styrax obassia. Journal of Vegetation Science, 9, 787–796.

Akçakaya, H. R., Atwood, J. L., Breininger, D., Collins, C. T. & Duncan B. (2003) Metapopulation Dynamics of the California Least Tern. The Journal of Wildlife Management, 67, 829-842

Altwegg, R., Dummermuth, S., Anholt, B. R. & Flatt, T. (2005) Winter weather affects asp viper Vipera aspis population dynamics through susceptible juveniles. Oikos, 110, 55-66.

Alvarez-Buylla, E. R. (1994) Density dependence and patch dynamics in tropical rain forests: matrix models and applications to a tree species. American Naturalist, 143, 155–191.

Anderberg, A.A., Ståhl, B. & Källersjö, M. (1998) Phylogenetic relationships in the Primulales inferred from rbcL sequence data. Plant Systematics and Evolution, 211, 93-102.

Barclay-Estrup, E. & Gimingham, C. H. (1975) Seed-shedding in heather (Calluna vulgaris (L.) Hull). Transactions of the Botanical Society of Edinburgh, 42, 275–278 AND Mallik, A. U., Hobbs, R. J. & Legg, C. J. (1984) Seed Dynamics in Calluna-Arctostaphylos Heath in Northeastern Scotland. Journal of Ecology, 72, 855–871 AND Scandrett, E. & Gimingham, C. H. (1989) A model of Calluna population dynamics; the effects of varying seed and vegetative regeneration. Vegetatio, 84, 143–152.

Barkalow, Jr. F. S., Hamilton, R. B. & Soots, Jr. R. F. (1970) The Vital Statistics of an Unexploited Gray Squirrel Population. The Journal of Wildlife Management, 34, 489-500.

Barkham, J. P. (1980) population dynamics of the wild daffodil (Narcissus pseudonarcissus) I. Clonal growth, see reproduction, mortality and the effects of density. Journal of Ecology, 68, 607–633.

Barlow, J. & Boveng, P. (1991) Modeling age-specific mortality for marine mammal populations. Marine Mammal Science, 7, 50-65.

Barlow, J. & Clapham, P. J. (1997) A new birth-interval approach to estimating demographic parameters of humpback whales. Ecology, 78, 535-546.

Barot, S., Gignoux, J., Vuattoux, R. & Legendre, S. (2000) Demography of a savanna palm tree in Ivory Coast (Lamto): population persistence and life-history. Journal of Tropical Ecology, 16, 637-655.

Batista, W. B., Platt, W. J. & Macchiavelli, R. E. (1998) Demography of a shade-tolerant tree (Fagus grandifolia) in a hurricane-disturbed forest. Ecology, 79, 38-53.

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.

Beissinger, S. R. (1995) Modeling extinction in periodic environments: Everglades water levels and snail kite population viability. Ecological Applications, 5, 618-631.

Bengtsson (1993) Fumana procumbens on Öland - population dynamics of a disjunct species and the northern limit of its range. Journal of Ecology, 81, 745–758.

Benton, T. G., Grant, A. & Clutton-Brock, T. H. (1995) Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. Evolutionary Ecology, 9, 559-574.

Berg, H. (2002) Population dynamics in Oxalis acetosella: the significance of sexual reproduction in a clonal, cleistogamous forest herb. Ecography, 25, 233-243.

Berger, K. M. & Conner, M. M. (2008) Recognizing wolves and mesopredator suppression of coyotes: impacts on pronghorn population dynamics. Ecological Applications, 18, 599-612.

Bernal (1998) Demography of the vegetable ivory palm Phytelephas seemannii in Columbia, and the impact of seed harvesting. Journal of Applied Ecology, 35, 64–74.

Bieber, C. & Ruf, T. (2005) Population dynamics in wild boar Sus scrofa: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. Journal of Applied Ecology, 42, 1203-1213.

Biek, R., Funk, C., Maxell, B. A. & Mills, L. S. (2002) What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology, 16, 728-734.

Bierzychudek, P. (1982) The demography of jack-in-the-pulpit, a forest perennial that changes sex. Ecological Monographs, 52, 335–351.

Blackwell, B. F., Avery, M. L., Watts, B. D. & Lowney, M. S. (2007) Demographics of Black Vultures in North Carolina. The Journal of Wildlife Management, 71, 1976-1979

Boorman, L. A. & Fuller, R. M. (1984) The comparative ecology of two sand dune biennials: Lactuca virosa L. and Cynoglossum officinale L. New Phytologist, 96, 609–629.

Bosch, C. A. (1971) Redwoods: A population model. Science, 172, 345-349.

Boucher, D. H. & Mallona, M. A. (1997) Recovery of the rainforest tree Vochysia ferruginea over 5 years following hurricane Joan in Nicaragua: a preliminary population projection matrix. Forest Ecology and Management, 91, 195–204.

Bradstock, R. A. & O'Connell, M . A. (1988) Demography of woody plants in relation to fire: Banksia ericifolia L.f. and Petrophile pulchella (Schrad) R.Br. Australian Journal of Ecology, 13, 505–518.

Brault, S. & Caswell, H. (1993) Pod-specific demography of Killer Whales (Orcinus orca). Ecology, 74, 1444-1454.

Bronikowski, A. M., Clark, M. E., Rodd, F. H. & Reznick, D. N. (2002) Population-Dynamic Consequences of Predator-Induced Life History Variation in the Guppy (Poecilia reticulata). Ecology, 83, 2194-2204

Bronson, M. T. (1979) Altitudinal variation in the life history of the Golden Mantled Ground Squirrel (Spermophilus lateralis). Ecology, 60, 272-279.

Bruna, E. M. (2003) Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb. Ecology, 84, 932-947.

Bullock, S. H. (1980) Demography of an undergrowth palm in littoral Cameroon. Biotropica, 12, 247–255.

Burns, B. R. & Ogden, J. (1985) The demography of the temperate mangrove [Avicennia marina (Forsk.) Vierh.] at its southern limit in New Zealand. Australian Journal of Ecology, 10, 125-133.

Byers D. L. & Meagher T. R. (1997) A comparison of demographic characteristics in a rare and a common species of Eupatorium. Ecological Applications 7 519–530.

Carter, J., Ackleh, A. S., Leonard, B. P. & Wang, H. (1999) Giant panda (Ailuropoda melanoleuca) population dynamics and bamboo (subfamily Bambusoideae) life history: a structured population approach to examining carrying capacity when the prey are semelparous. Ecological Modelling, 123, 207-223.

Caswell, H. (2001) Matrix Population Models: Construction, Analysis and Interpretation. Sinauer, Sunderland, MA.

Caughley, G. (1966) Mortality Patterns in Mammals. Ecology, 47, 906-918.

Chaloupka, M. (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. Ecological Modelling, 148, 79-109.

Chapman, S. B., Rose, R. J. & Clarke, R. T. (1989) The behaviour of population of the marsh gentian (Gentiana pneumonanthe): a modelling approach. Journal of Applied Ecology, 26, 1059–1072.

Cipollini, M. L., Wallace-Senft, D. A. & Whigham, D. A. (1994) A model of patch dynamics, seed dispersal and sex ratio in the dioecious shrub Lindera benzoin (Lauraceae). Journal of Ecology, 82, 621–633.

Cipollini, M. L., Whigham, D. F. & O'Neill, J. (1993) Population growth, structure and seed dispersal in the understory herb Cynoglossum virginianum: a population and patch dynamics model. Plant Species Biology, 8, 117–129.

Clark, W. R., Bogenschutz, T. R. & Tessin, D. H. (2008) Sensitivity Analyses of a Population Projection Model of Ring-Necked Pheasants. The Journal of Wildlife Management, 72, 1605-1613.

Cohen, J.E. (1979) The cumulative distance from an observed to a stable age structure. SIAM Journal of Applied Mathematics, 36, 169–175.

Colling, G. & Matthies, D. (2006) Effects of habitat deterioration on population dynamics and extinction risk of an endangered, long-lived perennial herb (Scorzona humilis). Journal of Ecology, 94, 959-972.

Congdon, J. D., Dunham, A. E. & Van Loben Sels, R. C. (1993) Delayed Sexual Maturity and Demographics of Blanding's Turtles (Emydoidea blandingii). Conservation Biology, 7, 826-833.

Congdon, J. D., Dunham, A. E. & Van Loben Sels, R. C. (1994) Demographics of Common Snapping Turtles (Chelydra Serpentina): Implications for Conservation and Management of Long-Lived Organisms. American Zoologist, 34, 397-408.

Contreras, C. & Valverde, T. (2002) Evaluation of the conservation status of a rare cactus (Mammillaria crucigera) through the analysis of its population dynamics. Journal of Arid Environments, 51, 89-102

Cords, M. & Chowdhury, S. (2010) Life History of Cercopithecus mitis stuhlmanni. International Journal of Primatology, 31, 433-455.

Costantino (1987) [cited in Caswell (2001) Matrix Population Models: Construction, Analysis and Interpretation (2nd ed.), Sinauer Associates, Sunderland, Massachusetts.]

Crockett, C. M., Kyes, R. C. & Sajuthi, D. (1996) Modeling managed monkey populations: sustainable harvest of longtailed macaques on a natural habitat island. Journal of Primatology, 40, 343-360.

Crooks, K. R., Sanjauan, M. A. & Doak, D. F. (1998) New insights on Cheetah conservation through demographic modelling. Conservation Biology, 12, 889-895.

Cropper, W. P. Jr. & DiResta, D. (1999) Simulation of a Biscayne Bay, Florida commercial sponge population: effects of harvesting after hurricane Andrew. Ecological Modelling, 118, 1-15.

Crouse, D. T., Crowder, L. B. & Caswell, H. (1987) A stage-based population model for Loggerhead sea turtles and implications for conservation. Ecology, 68, 1412-1423.

Crowder, L. B., Crouse, D. T., Heppell, S. S. & Martin, T. H. (1994) Predicting the impact of turtles excluder devices on Loggerhead sea turtle populations. Ecological Applications, 4, 437-445.

Cully, J. F. Jr. (1997) Growth and life-history changes in Gunnison's prairie dogs after a plague epizootic. Journal of Mammalogy, 78, 146-157.

Daimani, C. C. (2005) Integrating direct effects and trait-mediated indirect effects using a projection matrix model. Ecology, 86, 2068-2074.

Damman, H. & Cain, M. L. (1998) Population growth and viability analyses of the clonal woodland herb, Asarum canadense. Journal of Ecology, 86, 13–26.

De Walt, S. (2006) Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. Biological Invasions, 8, 1145-1158.

Dinnétz, P. & Nilsson, T. (2002) Population viability analysis of Saxifraga cotyledon, a
    perennial plant with semelparous rosettes. Plant Ecology, 159, 61-71.

Doak, D., Kareiva, P. & Klepetka, B. (1994) Modeling population viability for the desert
    tortoise in the Western Mojave desert. Ecological Applications, 4, 446-460.

Dobson, F. S. & Oli, M .K. (2001) The demographic basis of poplation regulation in Columbian
    ground squirrels. The American Naturalist, 158, 236-247.

Dudas, S. E., Dower, J. F., & Anholt, B. R. (2007) Invasion dynamics of the Varnish Clam
    (Nuttallia obscurata): a matrix demographic modeling approach. Ecology, 88, 2084-2093.

Ebert, T. A. & Ebert, C. A. (1989) A method for studying vegetation dynamics when there are
    no obvious individuals: virtual-population analysis applied to the tundra shrub Betula
    nana L. Vegetatio, 85, 33–44.

Ehrlén, J. & van Groenendael, J. (1998) Direct perturbation analysis for better conservation.
    Conservation Biology, 12, 470-474.

Ehrlén, J. (1995) Demography of the perennial herb Lathyrus vernus: II. Herbivory and
    Population Dynamics. Journal of Ecology, 83, 297-208.

Emanuel, P. L., Schackleton, C. M. * Baxter, J. S. (2005) Modelling the sustainable harvest of
    Sclerocarya birrea subsp. Caffra fruits in the South African lowveld. Forest Ecology and
    Management, 214, 91-103.

Emery, S. M. & Gross, K. L. (2005) Effects of timing of prescribed fire on the demography of
    an invasive plant, spotted knapweed, Centaurea maculosa. Journal of Applied Ecology,
    42, 60-69.

Endress, B. A., Gorchov, D. L. & Noble, R. B. (2004) Non-timber forest product extraction:
    effects of harvest and browsing on an understory palm. Ecological Applications, 14,
    1139-1153.

Enright, N. & Ogden, J. (1979) Applications of transition matrix models in forest dynamics:
    Araucaria in Papua New Guinea and Nothofagus in New Zealand. Australian Journal of
    Ecology, 4, 3–23.

Enright, N. J. & Watson, A. D. (1991) A matrix population model analysis for the tropical tree,
    Araucaria cunninghamii . Australian Journal of Ecology, 16, 507–520.

Enright, N. J. (1982) The Ecology of Araucaria species in New Guinea. III. Population
    dynamics of sample stands. Australian Journal of Ecology, 7, 227–237.

Eriksson, Å, & Eriksson, O. (2000) Population dynamics of the perennial Plantago media in
    semi-natural grasslands. Journal of Vegetation Science, 11, 245-252.

Eriksson, O. (1986) Survivorship, reproduction and dynamics of ramets of Potentilla anserina
    on a Baltic seashore meadow. Vegetatio, 67, 17–25 AND Eriksson, O. (1988) Ramet
    behaviour and population growth in the clonal herb Potentilla anserina. Journal of
    Ecology, 76, 522–536.

Escos, J., Alados, C. L. & Emlen, J. M. (1994) Application of the stage-projection model with density-dependent fecundity to the population dynamics of Spanish ibex. Canadian Journal of Zoology, 72, 731-737.

Esparza-Olguín, L., Valverde, T. & Mandujano, M. C. (2005) Comparative demographic analysis of three Neobuxbaumia species (Cactaceae) with differing degree of rarity. Population Ecology, 47, 229-245.

Esparza-Olguín, L., Valverde, T. & Vilchis-Anaya, E. (2002) Demographic analysis of a rare columnar cactus (Neobuxbaumia macrocephala) in the Tehuacan valley, Mexico. Biological Conservation, 103, 349-359

Farah, K. O., Tanaka, A. F. & West, N. E. (1988) Autoecology and population biology of Dyers Woad (Isatis tinctoria). Weed Science, 36, 186–193.

Fernandez, P., Guadelli, J. & Fosse, P. (2006) Applying dynamics and comparing life tables for Pleistocene Equidae in anthropic (Bau de l'Aubesier, Combe-Grenal) and carnivore (Fouvent) contexts with modern feral horse populations (Akagera, Pryor Mountain). Journal of Archaeological Science, 33, 176-184.

Fiedler, P. L. (1987) Life history and population dynamics of rare and common mariposa lilies (Calochortus Pursh: Liliaceae). Journal of Ecology, 75, 977–995.

Fior, S., Karis, P.O., Casazza, G., Minuto, L. & Sala, F. (2006) Molecular phylogeny of the Caryophyllaceae (Caryophyllales) inferred from chloroplast matK and nuclear rDNA ITS sequences. American Journal of Botany, 93, 399-411.

Fisher, D. O., Hoyle, S. D. & Bloomberg, S. P. (2000) Population dynamics and survival of an endangered wallaby: a comparison of four methods. Ecological Applications, 10, 901-910.

Forbis, T. A. & Doak, D. F. (2004) Seedling establishment and life history trade-offs in alpine plants. American Journal of Botany, 91, 1147-1153.

Franco, M. & Silvertown, J. (2004) A comparative demography of plants based upon elasticities of vital rates. Ecology, 85, 531–538.

Frank, P. W., Boll, C. D. & Kelly, R. W. (1957) Vital statistics of laboratory cultures of Daphnia pulex DeGeer as related to density. Physiological Zoology, 30, 287-305.

Fujiwara, M. & Caswell, H. (2001) Demography of the endangered North Atlantic Right Whale. Nature, 414, 537-541.

Gaillard J.M, and Yoccoz M.G, (2003) Temporal variation in survival of mammals: A case of environmental canalization. Ecology 84(12) 3294-3306

Garrott, R. A. & Taylor, L. (1990) Dynamics of a feral horse population in Montana. Journal of Wildlife Management, 54, 603-612.

Gibson, A.C. & Horak, K.E. (1978) Systematic anatomy and phylogeny of Mexican columnar cacti. Annals of the Missouri Botanical Garden, 65, 999-1057.

233

Godínez-Alvarez, H. & Valiente-Banuet, A. (2004) Demography of the columnar cactus Neobuxbaumia macrocephala: a comparative approach using population projection matrices. Plant Ecology, 174, 109-118.

Golubov, J., Mandujano, M. D. C., Franco, M., Montaña, C., Eguiarte, L. E. & Lopez-Portillo, J. (1999) Demography of the invasive woody perennial Prosopis glandulosa (honey mesquite). Journal of Ecology, 87, 955–962.

Gotelli, N. J. (1991) Demographic models for Leptogorgia virgulata, a shallow-water gorgonian. Ecology, 72, 457-467.

Grange, S., Duncan, P., Gaillard, J.-M., Sinclair, A. R. E., Gogan, P. J. P., Packer, C., Hofer, H., & East, M. (2004) What limits the Serengeti zebra population? Oecologia, 140, 523-532.

Grenier, M. B., McDonald, D. B. & Buskirk, S. W. (2007) Rapid population growth of a critically endangered carnivore. Science, 317, 779-779.

Gross, K, Lockwood, J. R. III, Frost, C. C. & Morris, W. F. (1998) Modelling controlled burning and trampling reduction for conservation of Hudsonia montana. Conservation Biology, 12, 1291–1301.

Gross, K., Bruce, A. C & Hutchinson, W. D. (2002) Bayesian estimation of a demographic matrix model from stage-frequency data. Ecology, 83, 3285-3298.

Gross, K., Morris, W. F., Wolosin, M. S. & Doak, D. F. (2006) Modelling vital rates improves estimation of population projection matrices. Population Ecology, 48, 79-89.

Guardia, R., Raventos, J. & Caswell, H. (2000) Spatial growth and population dynamics of a perennial tussock grass (Achnatherum calamagrostis) in a badland area. Journal of Ecology, 88, 950-963.

Guedje, N. M., Lejoly, J., Nkongmeneck, B.-A. & Jonkers, W. B. J. (2003) Population dynamics of Garcinia lucida (Clusiaceae) in Cameroon Atlantic forests. Forest Ecology and Management, 177, 231-241.

Haffner, E. & Hellwig, F.H. (1999) Phylogeny of the tribe Cardueae (Compositae) with emphasis on the subtribe Carduinae: an analysis based on ITS sequence data. Willdenowia, 29, 27-39.

Hara, M., Kanno, H., Hirauki, Y. & Takehara, A. (2004) Population dynamics of four understorey shrub species in beech forest. Journal of Vegetation Science, 15, 475-484.

Harding. K, Harkonen.T, Helander.B, Karlsson.O (2007) Status of Baltic grey seals: Population assessment and extinction risk. NAMMCO 6 33-56

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

Hartshorn (1975) [cited in Golley, F. B. & Medina, E. (1975), Tropical Ecological Systems: Trends in Terrestrial and Aquatic Research. Springer-Verlag, New York, USA].

Hastings, A., Hall, R. J. & Taylor, C. M. (2006) A simple approach to optimal control of invasive species. Theoretical Population Biology, 70, 431-435

Hayward, G. D. & McDonald, D. B. (1997) Matrix population models as a tool in development of habitat models. 2nd Owl Symposium.

Hegazy, A. K. (1990) Population ecology and implications for the conservation of Cleome droserifolia: a threatened xerophyte. Journal of Arid Environments, 19, 269–282.

Heppell, S. S., Crowder, L. B. & Crouse, D. T. (1996) Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications, 6, 556-565.

Hilderbrand, R. H. (2003) The roles of carrying capacity, immigration and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation, 110, 257-266.

Hiraldo, F., Negro, J. T., Donazar, J. A. & Gaona, P. (1996) A demographic model for a population of the endangered Lesser Kestrel in Southern Spain. Journal of Applied Ecology, 33, 1085-1093.

Hitchcock, C. L. & Gratto-Trevor, C. (1997) Diagnosing a Shorebird Local Population Decline with a Stage-Structured Population Model. Ecology, 78, 522-534.

Hoenig, J. M. & Gruber, S. H. (1990) Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. National Oceanic and Atmospheric Administration technical report 90.

Hoffmann, W. A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology, 80, 1354–1369.

Horvitz, C. C. & Schemske, D. W. (1995) Spatiotemporal variation in demographic transitions of a tropical understory herb: projection matrix analysis. Ecological Monographs, 65, 155–192.

Hsiao, C., Chatterton, N.J., Asay, K.H. & Jensen, K.B. (1995) Molecular phylogeny of the Pooideae (Poaceae) beased on nuclear rDNA (ITS) sequences. Theoretical and Applied Genetics, 90, 389-398.

Huenneke, L. F. & Marks, P. L. (1987) Stem dynamics of the shrub Alnus incana ssp. Rugosa: transition matrix models. Ecology, 68, 1234–1242.

Hughes, T. P. & Tanner, J. E. (2000) Recruitment failure, life histories and long-term decline of Caribbean corals. Ecology, 81, 2250-2263.

Hunt, L. P. (2004) Heterogeneous grazing causes local extinction of edible perennial shrubs: a matrix analysis. Journal of Applied Ecology, 38, 238-252.

Hunter, C.M., Caswell, H., Runge, M.C., Regehr, E.V., Amstrup, S., & Stirling, I. (2010) Climate change threatens polar bear populations: a stochastic demographic analysis. Ecology, 91, 2883–2897.

Inchausti, P. & Weimerskirch, H. (2001) Risks of decline and extinction of the endangered Amsterdam albatross and the projected impact of long-line fisheries. Biological Conservation, 100, 377-386.

Jensen, A. L. (1996) Density-dependent matrix yield equation for optimal harvest of age-structured wildlife populations. Ecological Modelling, 88, 125-132.

Johnson, K. H. & Braun, C. E. (1999) Viability and conservation of an exploited sage grouse population. Conservation Biology, 13, 77-84.

Kaneko, Y., Takada, T. & Kawano, S. (1999) Population biology of Aesculus turbinata Blume: A demographic analysis using transition matrices on a natural population along a riparian environmental gradient. Plant Species Biology, 14, 47–68.

Kareiva, P., Marvier, M. & McClure, M. (2000) Recovery and management for spring/summer Chinook Salmon in the Columbia River Basin. Science, 290, 977-979.

Kawano et al. (1987) [cited in Urbanska, K. M. (1987) Differentiation patterns in higher plants. Academic Press, New York etc.]

Keitt, B. S., Wilcox, C., Tershy, B. R., Croll, D. A. & Donlan, C. J. (2002) The effect of feral cats on the population viability of black-vented shearwaters (Puffinus opisthomelas) on Natividad island, Mexico. Animal COnservation, 5, 217-223.

Kephart, S. R. & Paladino, C. (1997) Demographic change and microhabitat variability in a grassland endemic, Silene douglasii var. oraria (Caryophyllaceae). American Journal of Botany, 84, 179–189.

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.

Kinoshita, E. (1987) Sex change and population dynamics in Arisaema (Araceae) I. Arisaema serratum (Thunb.) Schott. Plant Species Biology, 2, 15-28.

Kiviniemi, K. (2002) Population dynamics of Agrimonia eupatoria and Geum rivale, two perennial grassland species. Plant Ecology, 159, 153-169.

Klemow, K. M. & Raynal, D. J. (1985) Demography of two facultative biennial plant species in an unproductive habitat. Journal of Ecology, 73, 147–167.

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.

Krkosek, M., Lauzon-Guay, J.-S. & Lewis, M. A. (2007) Relating dispersal and range expansion of California sea otters. Theoretical Population Biology, 71, 401-407.

Lande, R. (1988) Demographic models of the Northern Spotted Owl, Strix occidentalis caurina. Oecologia, 75, 601-607.

Laskowski, R. & Hopkin, S. P. (1996) Effect of Zn, Cu, Pb and Cd on fitness in Snails (Helix aspersa). Ecotoxicology and Environmental Safety, 34, 59-69.

Lawler, Caswell, Ratsirarson, Dewar, Schwartz (2009) Demography of Verreaux's sifaka in a stochastic rainfall environment, Oecologia,161; 491-506

Lawler, R.R, (2010) Demographic concepts and research pertaining to the study of wild primate populations. Yearbook of Physical Anthropology

Lefèbvre & Chandler-Mortimer (1984) Demographic characteristics of the perennial herb Armeria maritima on Zilc lead mine wastes. Journal of Applied Ecology, 21, 255–264.

Lefkovitch, L. P. (1965) The study of population growth in organisms grouped by stages. Biometrics, 21, 1-18.

Lesica, P. & Shelly, J. S. (1995) Effects of reproductive mode on demography and life history in Arabis fecunda (Brassicaceae). American Journal of Botany, 82, 752–762.

Lesica, P. (1995) Demography of Astragalus scaphoides and effects of herbivory on population growth. Great Basin Naturalist, 55, 142–150.

Leslie, P. H., Tener, J. S., Vizoso, M. & Chitty, H. (1965) The longevity and fertility of the Orkney Vole, Microtus orcadensis, as observed in the laboratory. Proceedings of the Zoological Society of London, 125, 115-125.

Letcher, B. H., Nislow, K. H., Coombs, J. A., O'Donnell, J. A. & Dubreuil, T. L. (2007) Population response to habitat fragmentation in a stream-dwelling brook trout population. PLoS One, e1139.

Levin, L. A., Caswell, H., DePatra, K. D. & Creed, E. L. (1987) Demographic consequences of larval development mode: planktrophy vs. lecithotrophy in Streblospio benedicti. Ecology, 68, 1877-1886.

Lewison, R. L. & Crowder, L. B. (2003) Estimating fishery bycatch and effects on a vulnerable seabird population. Ecological Applications, 13, 743-753.

Liang, H. & Hilu, K.W. (1996) Application of the matK gene sequences to grass systematics. Canadian Journal of Botany, 74, 125-134.

Lima, M., Stenseth, N. C., Yoccoz, N. G. & Jaksic, F. M. (2001) Demography and the population dynamics of the mouse opossum (Thylamys elegans) in semi-arid Chile: seasonality, feedback structure and climate. Proceedings of the Royal Society of London B: Biological Sciences, 268, 2053-2064.

Linares, C., Doak, D. F., Coma, R., Diaz, D. & Zabala, M. (2007) Life history and viability of a long-lived invertebrate: the octocoral Paramuricea clavata. Ecology, 88, 918-928.

Link, W.A. & Eaton, M.J. (2012) On thinning of chains in MCMC. Methods in Ecology and Evolution, 3, 112-115.

Lo, N. C. H., Smith, P. E. & Butler, J. L. (1995) Population growth of northern anchovy and pacific sardine using stage-specific matrix models. Marine Ecology Progress Series, 127, 15-26.

Löfgren, P. Eriksson, O. & Lehtilä, K. (2000) Population dynamics and the effect of disturbance in the monocarpic herb Carlina vulgaris (Asteraceae). Ann. Bot. Fennici, 37, 183-192.

MacGuire, L. A., Wilhere, G. F., Dong, Q. (1995) Population viability analysis for Red-Cockaded Woodpeckers in the Georgia Piedmont. Journal of Wildlife Management, 59, 533-542.

Maclean, M. M., Carslake, D. J., Evans, M. R., Townley, S. & Hodgson, D. J. (2008) The usefulness of sensitivity analysis for predicting the effects of cat predation on the population dynamics of their avian prey. Ibis, 150, 100-113.

Mast, A.R., Kelso, S., Richards, J., Lang, D.J., Feller, D.M.S. & Conti, E. (2001) Phylogenetic relationships in Primula L. and related genera (Primulaceae) based on noncoding chloroplast data. International Journal of Plant Sciences, 162, 1381-1400.

McAdam, A. G., Sykes, A. K. & Humphries, M. M. (2007) Life histories of female red squirrels and their contributions to population growth and lifetime fitness. EcoScience, 14, 362-369.

McDonald, D. B. (1993) Demographic consequences of sexual selection in the long-tailed manakin. Behavioural Ecology, 4, 297-309.

McFadden, C. S. (1991) A Comparative Demographic Analysis of Clonal Reproduction in a Temperate Soft Coral. Ecology, 72, 1849-1866.

Mendéz, M., Durán, R., Olmsted, I. & Oyama, K. (2004) Population dynamics of Pterocereus gaumeri, a rare and endemic columnar cactus of Mexico. Biotropica, 36, 492-504.

Menges, E. S. (1990) Population viability for an endangered plant. Conservation Biology, 4, 52-62.

Messick, J. P. & Hornocker, M. G. (1981) Ecology of the Badger in Southwestern Idaho. Wildlife Monographs, 76, 3-53.

Miller, D. H., Jensen, A. L. & Hammill, J. H. (2002) Density dependent matrix model for gray wolf population projection. Ecological Modelling, 151, 271-278.

Miller, T. J. (2001) Matrix-based modeling of blue crab population dynamics with applications to the Chesapeake Bay. Estuaries, 24, 535-544.

Miriti, M., Wright, J. & Howe, H. F. (2001) The effects of neighbours on the demography of a dominant desert shrub (Ambrosia dumosa). Ecological Monographs, 71, 491-509.

Mollet, H. F. & Caillet, G. M. (2002) Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Marine and Freshwater Research, 53, 503-516.

Moloney, K. A. (1988) Fine-scale spatial and temporal variation in the demography of a perennial bunchgrass. Ecology, 69, 1588–1598.

Mondragón, D., Durán, R., Ramírez, I. & Valverde, T. (2004) Temporal variation in the demography of the clonal epiphyte Tillandsia brachycaulos (Bromeliaceae) in the Yucatán peninsula, Mexico. Journal of Tropical Ecology, 20, 189-200.

Morris, W. F. & Doak, D. F. (2005) How general are the determinants of the stochastic population growth rate across nearby sites? Ecological Monographs, 75, 119-137.

Mortimer (1983) [cited in Fletcher, W. W. (1983) Recent advances in weed research, CABI publishing, Wallingford, UK.

Nabe-Nielsen, J. (2004) Demography of Machaerium cuspidatum, a shade-tolerant noetropical liana. Journal of Tropical Ecology, 20, 505-516.

Nakaoka, M. (1997) Demography of the marine bivalve Yoldia notabilis in fluctuating environments: an analysis using a stochastic matrix model. Oikos, 79, 59-68.

Namkoong, G. & Roberds, J. H. (1974) Extinction probabilities and the changing age structure of redwood forests. American Naturalist, 108, 355–368.

Nantel, P. & Gagnon, D. (1999) Variability in the dynamics of northern peripheral versus southern populations of two clonal plant species, Helianthus divaricatus and Rhus aromatica. Journal of Ecology, 87, 748–760.

Nantel, P., Gagnon, D. & Nault, A. (1996) Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology, 10, 608–621.

Nault, A. & Gagnon, D. (1993) Ramet demography of Allium tricoccum, a spring ephemeral, perennial forest herb. Journal of Ecology, 81, 101-119

Nelson, E.S.D., Harris, S., Soulsbury, C.D., Richards, S.A. & Stephens, P. (2010). Uncertainty in Population Growth Rates: Determining Confidence Intervals from Point Estimates of Parameters. PloS One, 5, 1-7.

Neubert, M.G. & Caswell, H. (1997) Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology, 78, 653–665.

Noda, T. & Nakao, S. (1996) Dynamics of an entire population of the subtidal snail Umbonium costatum: the importance of annual recruitment fluctuation. Journal of Animal Ecology, 65, 196-204.

Noon, B. R. & Sauer, J. R. (1992) Population models for passerine birds: structure, parameterization and analysis. In Wildlife 2001: Populations, Elsevier Applied Science, London & New York.

O'Connor, T. G. (1993) The influence of rainfall and grazing on the demography of some african savanna grasses: a matrix modelling approach. Journal of Applied Ecology, 30, 119-132

Okland, R. H. (1995) Population biology of the clonal moss Hylocomium splendens in Norwegian boreal spruce forests. Journal of Ecology, 83, 697-712.

Oli, M. K. & Dobson, F. S. (1999) Population cycles in small mammals: the role of age at sexual maturity. Oikos, 86, 557-565.

Oli, M. K. & Zinner, B. (2001) Partial life cycle analysis: a model for pre-breeding census data. Oikos, 93, 376-387.

Olmsted, I. & Alvarez-Buylla, E. R. (1995) Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. Ecological Applications, 5, 484-500.

Orive, M. E. (1995) Senescence in Organisms with Clonal Reproduction and Complex Life Histories. The American Naturalist, 145, 90-108.

Otway, N. M., Bradshaw, C. 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. Biological Conservation, 119, 341-350.

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.

Patterson, T.B. & Givnish, T.J. (2003) Geographic cohesion, chromosomal evolution, parallel adaptive radiations, and consequent floral adaptations in Calochortus (Calochortaceae): evidence from a cpDNA phylogeny. New Phytologist, 161, 253-264.

Pavlik, B. M. & Barbour, M. G. (1988) Demographic monitoring of endemic sand dune plants, Eureka Valley, California. Biological Conservation, 46, 217–242.

Peña-Claros, M. & Zuidema, P. A. (2000) Limitaciones demográficas para el aprovechamiento sostenible de Euterpe prectoria para producción se palmito: resultados de dos estudios en Bolivia. Ecología en Bolivia, 34, 7–25.

Pérez-Farrera, M., Vovides, A. O., Octavio-Aduilar, P., González-Astorga, J., de la Cruz-Rodríguez, J., Hernández-Jonapá, R. & Villalobos-Méndez, S. M. (2006) Demography of the cycad Ceratozamia mirandae (Zamiaceae) under disturbed and undisturbed conditions in a biosphere reserve of Mexico. Plant Ecology, 187, 97-108.

Peruzzi, L., Leitch, I.J. & Caparelli, K.F. (2009) Chromosome diversity and evolution in Liliaceae. Annals of Botany, 103, 459-475.

Peters (1990) [cited in Gomez-Pompa, A., Whitmore, T. C. & Hadley, M. (1991) Rain forest regeneration and management. Man and Biosphere Program (UNESCO), Paris, France.]

Peters (1991) [cited in Caswell, H. (2001) Matrix Population Models: Construction, Analysis and Interpretation: 2nd. Ed., Sinauer, Sunderland, Massachusetts, USA.]

Peterson, P.M., Romaschenko, K. & Johnson, G. (2010) A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Molecular Phylogenetics and Evolution, 55, 580-598.

Pfeifer, M., Wiegand, K., Heinrich, W. & Jetschke, G. (2006) Long-term demographic fluctuations in an orchid species driven by weather: implications for conservation planning. Journal of Applied Ecology, 43, 313-324.

Pfister, C. A. (1996) The role and importance of recruitment variability to a guild of tide pool fishes. Ecology, 77, 1928-1941.

Picó, F. X. & Riba, M. (2002) Regional-scale demography of Ramonda myconi: remnant population dynamics in a preglacial relict species. Plant Ecology, 161, 1-13.

Pinard, M. (1993) Impacts of stem harvesting on populations of Iriartea deltoidea (Palmae) in an extractive reserve in Acre, Brazil. Biotropica, 25, 2-14

Piñero, D., Martinez-Ramos, M. & Sarukhan, J. (1984) A population model of astrocaryum mexicanum and a sensitivity analysis of its finite rate of increase. Journal of Ecology, 72, 977–991.

Pitelka, L. F., Hansen, S. B. & Ashmun, J. W. (1985) Population biology of Clintonia borealis: I. Ramet and patch dynamics. Journal of Ecology, 73, 169–183.

Platt *et al.*(1988) The Population Dynamics of a Long-Lived Conifer (Pinus palustris). American Naturalist, 131, 491–525.

Price, M. V. & Kelly, P. A. (1994) An age-structured demographic model for the endangered Stephens' Kangaroo Rat. Conservation Biology, 8, 810-821.

Purnima, G., Altwegg, R. & Anholt, B. R. (2005) Matrix Model Investigation of Invasive Species Control: Bullfrogs on Vancouver Island. Ecological Applications, 6, 2161-2170.

Ramula, S., Rees, M. & Buckley, Y. M. (2009) Integral projection models perform better of small demographic data sets than matrix population models: a case study of two perennial herbs. Journal of Applied Ecology, 46, 1048-1053.

Ratsirarson, J., Silander, J. A. Jr. & Richard, A. F. (1996) Conservation and management of a threatened Madagascar palm species, Neodypsis decaryi, Jumelle. Conservation Biology, 10, 40-52

Rockwell *et al.* (1997) [cited in Caswell, H. (2001) Matrix Population Models: Construction, analysis and interpretation, 2nd ed., Sinauer, Sunderland, Massachusetts, USA].

Rodríguez-Buriticá, S., Orjuela, M. A. & Galeano, G. (2005) Demography and life history of Geonoma orbignyana: an understory palm used as foliage in Colombia. Forest Ecology and Management, 211, 329-340.

Roemer, G. W., Coonan, T. J., Garcelon, D. K., Bascompte, J. & Laughrin, L. (2001) Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. Animal Conservation, 4, 307-318.

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.

Rooney, T. P. & Gross, K. (2003) A demographic study of deer browsing impacts on Trillium grandiflorum. Plant Ecology, 168, 267-277.

Runge, M. C., Langtimm, C. A. & Kendall, W. L. (2004) A stage-based model of Manatee population dynamics. Marine Mammal Science, 20, 361-385.

Sable, S. E. (2007) A Comparison of individual-based and matrix projection models applied to fish population and community dynamics. Dissertation: Louisiana State University, Louisiana, USA.

Shea, K. & Kelly, D. (1998) Estimating biocontrol agent imapct with matrix models: Carduus nutans in New Zealand. Ecological Applications, 8, 824-832.

Silander, J. A. Jr. (1983) Demographic variation in the Australian desert cassia under grazing pressure. Oecologia, 60, 227–233.

Silva Matos, D. M., Freckleton, R. P. & Watkinson, A. R. (1999) The role of density dependence in the population dynamics of a tropical palm. Ecology, 80, 2635–2650.

Silva, J. F., Raventos, J., Caswell, C. & Trevisan, M. C. (1991) Population responses to fire in a tropical savanna grass, Andropogon semiberbis: a matrix model approach. Journal of Ecology, 79, 345-356

Simons, T. R. (1984) A population model of the endangered Hawaiian dark-rumped petrel. Journal of Wildlife Management, 48, 1065-1076.

Simpson, M. L. & Kopp, G. J. (2007) Use of life history information in a population model for Sacramento green sturgeon. Environmental biology of fishes, 79, 315-337.

Slade, N. A. & Balph, D. F. (1974) Population Ecology of Uinta Ground Squirrels. Ecology, 55, 989-1003.

Smith, A. T. (1974) The Distribution and Dispersal of Pikas: Consequences of Insular Population Structure. Ecology, 55, 1112-1119.

Steenbergh, W. F. & Lowe, C. H. (1977) Ecology of the saguaro, II: Reproduction, germination, establishment, growth and survival of the young plant. Scientific Monograph Series No. 8, National Park Service. AND Steenbergh, W. F. & Lowe, C. H. (1983) Ecology of the saguaro, III: Growth and demography. Scientific Monograph Series No. 17, National Park Service.

Sterk, A. A. (1975) Demographic studies of Anthyllis vulneraria L. in the Netherlands. Acta Botanica Neerlandica, 24, 315–337 AND Sterk, A. A., von Duykeren, A., Hogervorst, J. & Verbeek, E. D. M. (1982) Demographic studies of Anthyllis vulneraria L. in the Netherlands, II. Population density fluctuations, seed populations, seedling mortality and influence of the biocenosis on demographic features. Acta Botanica Neerlandica, 31, 11–40.

Stevens, P.F. (2001 onwards). Angiosperm Phylogeny Website. Version 9, June 2008 [and more or less continuously updated since]. http://www.mobot.org/MOBOT/research/Apweb

Stokes, K. E., Bullock , J. M. & Wakinson, A. R. (2004) Population dynamics across a parapatric range boundary: Ulex gallii and Ulex minor. Journal of Ecology, 92, 142-155.

Stolen, M. K. & Barlow, J. (2003) A model life table for bottlenose dolphins (Tursiops truncatus) from the Indian river lagoon system, Florida, U.S.A. Marine Mammal Science, 19, 630-649.

Svensson, B. M., Carlsson, B. A., Karlsson, P. S. & Nordell, K. O. (1993) The comparative long-term demography of three species of Pinguicula. Journal of Ecology, 81, 635–645.

Teerawatananon, A., Jacobs, S.W.L. & Hodkinson, T.R. (2001) Phylogenetics of Panicoideae (Poaceae) based on chloroplast and nuclear DNA sequences. Telopea, 13, 115-142.

Thomas, A. G. & Dale, H. M. (1975) The role of seed production in the dynamics of established population of Hieracium floribundum and a comparison with that of vegetative reproduction. Canadian Journal of Botany, 53, 3022–3031.

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.

United States Environmental Protection Agency (2003) A stochastic model incorporating PCB effects for wood frogs (Rana sylvatica) breeding in vernal pools associated with the Housatonic river. US Environmental Protection Agency, region 1, Massachusetts.

Usher (1972) [cited in Doubleday (1975) Harvesting in matrix population models. Biometrics, 31, 189-200.]

Valverde, T. & Silvertown, J. (1988) Variation in the demography of a woodland understorey herb (Primula vulgaris) along the forest regeneration cycle: projection matrix analysis. Journal of Ecology, 86, 545-562.

Valverde, T., Quijas, S., López-Villavicencio, M. & Castillo, S. (2004) Population dynamics of Mammillamma magnimamma Haworth. (Cactaceae) in a lava-field in central Mexico. Plant Ecology, 170, 167-184.

van Baalen, J. (1982) Germination ecology and seed population dynamics of Digitalis purpurea. Oecologia, 53, 61–67 AND van Baalen, J. & Prins, E. G. M. (1983) Growth and reproduction of Digitalis purpurea in different stages of succession. Oecologia 58, 84–91.

van Mantgem, P. J. & Stephenson, N. L. (2005) The accuracy of matrix population model projections for coniferous trees in the Sierra Nevada, California. Journal of Ecology, 93, 737-747.

Verkaar, H. J. & Schenkeveld, A. J. (1984) On the ecology of short-lived forbs in chalk grasslands: life-history characteristics. New Phytologist, 98, 659–672.

Watson, I. W., Westoby, M. & Holm, A. McR. (1997) Continuous and episodic components of demographic change in arid zone shrubs: models of two Eremophila species from Western Australia compared with published data on other species. Journal of Ecology, 85, 833–846.

Webb, C.O., Ackerly, D.D & Kembell, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics, 24, 2098-2100.

Webb, J. K., Brook, B. W. & Shine, R. (2002) What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecological Research, 17, 59-67.

Weppler, T., Stoll., P. & Stöcklin, J. (2006) The relative importance of sexual and clonal reproduction for population growth in the long-lived alpine plant Geum reptans. Journal of Ecology, 94, 869-879.

Werner, P. A. & Caswell, H. (1977) Population growth rates and age versus stage-distribution models for teasel (Dipsacus sylvestris Huds.) Ecology, 58, 1103-1111. [cited and corrected in Caswell, H. (2001) Matrix population models: Construction, analysis and interpretation, Sinauer, Sunderland, Massachusetts].

Whitton, J., Wallace, R.S. & Jansen, R.K. (1995) Phylogenetic relationships and patterns of character change in the tribe Lactuceae (Asteraceae) based on chloroplast DNA restriction site variation. Canadian Journal of Botany, 73, 1058-1073.

Wielgus, R. B. (2002) Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biological Conservation, 106, 381-388.

Wielgus.J, Gonzalez-Suarez. M, Aurioles-Gamboa.D, Gerber.L (2008) A noninvasive demographic assessment of sea lions based on stage-specific abundances. Ecological Applications 18(5) 1287-1296

Wiese, F. K., Robertson, G. J. & Gaston, A. J. (2004) Impacts of chronic marine oil pollution and the murre hunt in Newfoundland on thick-billed murre Uria lomvia populations in the eastern Canadian Arctic. Biological Conservation, 116, 205-216.

Wilson, P. H. (2003) Using population projection matrices to evaluate recovery strategies for snake river spring and summer Chinook Salmon. Conservation Biology, 17, 782-794.

Winkler, M., Hülber K. & Hietz, P. (2007) Population dynamics of epiphytic bromeliads: life strategies and the role of host branches. Basic and Applied Ecology, 8, 183-196.

Wisdom, M. J. & Mills, L. S. (1997) Sensitivity to guide population recovery: prairie-chickens as an example. Journal of Wildlife Management, 61, 302.

Wittmer.H, Corti.P, Saucedo.C, Galaz.J (2010) Learning to count: adapting population monitoring for endangered huemul deer to meet conservation objectives. Flora and Fauna International, Oryx 44(4) 516-522

Wittmer.H, Powell.R, King.C (2007) Understanding contributions of cohort effects to growth rates of fluctuating populations. Journal of Animal Ecology 76, 946-956

Wojciechowski, M.F., Lavin, M. & Sanderson, M.J. (2004) A phylogeny of the legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. Journal of Botany, 91, 1846-1862.

Woodworth, B. L. (1999) Modeling population dynamics of a songbird exposed to parasitism and predation and evaluation management options. Conservation Biology, 13, 67-76.

Wootton, J. T. & Bell, D. A. (1992) A metapopulation model of the Peregrine Falcon in California: viability and management strategies. Ecological Applications, 2, 307-321.

York, A. E. (1994) The population dynamics of Northern Sea Lions, 1975-1985. Marine Mammal Science, 10, 38-51.

Zagt, R. J. (1997) Tree demography in the tropical rain forest of Guyana. Tropenbos - Guyana Series 3. Tropenbos-Guyana Programme.

Zhang, L. (1983) Vegetation ecology and population biology of Fritillaria meleagris L. at the Kungsängen nature reserve, eastern Sweden. Acta Phytogeographica Suecica, 73, 1–96.

Zotz, G. & Schmidt, G. (2006) Population decline in the epophytic orchid Aspasia procipissa. Biological Conservation, 119, 82-90.

Zuidema (2000) Demography of exploited tree species in the Bolivian Amazon. PhD Thesis: Utrecht University, Utrecht.

Zuidema, P. A. & Boot, R. G. A. (2002) Demography of the Brazil nut tree (Bertholletia excelsa) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. Journal of Tropical Ecology, 18, 1–31.

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.