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SPECIAL FEATURE – EDITORIAL

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Matrix projection models meet variation in the real world

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Summary

1. Projection matrices have become the dominant modelling approach in plant demography because they (i) are relatively easy to formulate, (ii) compile complex data in a structured and analytically tractable manner, (iii) provide numerous parameters with direct biological meaning, (iv) allow the investigator to address broad or specific, experimental and/or theoretical, ecological and evolutionary questions, and (v) produce uniform outputs, enabling direct comparisons between the results of different studies.

2. The last decade has witnessed major advancements in this field that have brought demographic models much closer to the real world, in particular in the analysis of effects of spatial and temporal environmental variation on populations. The present Special Feature contributes to that progress with novel methodologies and applications on Integral Projection Models, stochastic Life Table Response Experiment analyses, stochastic elasticities, transient dynamics and phylogenetic analyses.

3. *Synthesis.* Environmental stochasticity is an integral part of ecosystems, and plant populations exhibit a tremendous array of demographic strategies to deal with its effects. The analytical challenge of understanding how populations avoid, tolerate or depend on stochasticity is finally overcome with the new matrix approaches. The tools are now available to interpret the effects of changes in temporal and spatial variation on plant populations.

Key-words: demographic buffering, integral projection model, plant demography, population dynamics, projection matrix, stochastic elasticity, stochastic life table response experiment (SLTRE), transient dynamics

Introduction

Plant demography has grown exponentially since its emergence as an ecological discipline, some 50 years ago, from pioneering work in John L. Harper's School of Plant Biology, summarized in his land-mark volume *Population Biology of Plants* (Harper 1977). Since then, plant demography has matured and flourished, both experimentally and methodologically. Studies of plant populations have contributed answers to an array of fundamental and applied research questions on topics that range from individual species to plant communities.

Matrix models have become extremely abundant in the demographic literature because of their transparency, ease of computation and the wealth of matrix output parameters with direct ecological and evolutionary interpretations (Caswell 2001). For instance, the growth rate of the population (λ, a mathematical property of the projection matrix) has been recognized as the common currency of fitness in complex life cycles (Lande 1982; van Groenendael, de Kroon & Caswell 1988). In addition, matrix models allow for the identification and study of demographic responses that play a central role in evolutionary dynamics (e.g. van Tienderen 2000; Metcalf & Pavard 2007). Furthermore, it is widely acknowledged that community dynamics depend on the population dynamics of the constituent species (McGill *et al.* 2006) and studies explaining community dynamics from underlying population trajectories are beginning to emerge (Angert *et al.* 2009). The use of projection models in plant population studies is particularly relevant in management because conservation of rare plant species depends on the principles of plant demography, which

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are widely applied in population viability analyses (PVAs; e.g. Menges 2000; Morris & Doak 2002). Likewise, invasive species management (Shea & Kelly 1998; Neubert & Caswell 2000) and weed control in agriculture (Mertens, van den Bosch & Heesterbeek 2002) have profited from insights gained from matrix-based studies of plant demography.

The present *Journal of Ecology* Special Feature contains nine novel contributions that mark the enormous progress made in studies of plant population dynamics in recent years. The field is rapidly expanding towards analysis and interpretation of more realistic demographic scenarios that take into account environmental stochasticity, life-history complexity and phylogenetic relationships in comparative frameworks. These methodologies now make it possible to achieve goals that have been out of reach for a long time because appropriate tools were not available.

Application of novel modelling tools: a decennial delay

The earliest accounts of matrix projection models for plants include Usher's (1966) model for renewable tree harvesting, followed by comparative studies on herbs (Sarukhán & Gadgil 1974; Werner & Caswell 1977) and trees (Hartshorn 1975; Enright & Ogden 1979). These studies already pioneered the analysis of growth rate sensitivities, seasonal variation of environmental conditions and comparative methods, but their goals were restricted by the most basic assumptions (e.g. asymptotic projections of deterministic models) and lack of appropriate analytical protocols for the study of more realistic scenarios.

The popularity of matrix projection tools rapidly increased in the 1980s and by the early 1990s matrix models had already been published on 66 plant species (Silvertown *et al.* 1993). Over time, the rate of publication of case studies has paralleled the development of new modelling tools, albeit with an inevitable delay. New tools typically become established in research methodology some 10 years after their introduction. For example, elasticities were introduced by Caswell (1984) and de Kroon *et al.* (1986), but became the prime method of perturbation analysis for comparative demography and conservation only in the 1990s, after ground-breaking applications on conservation (Crouse, Crowder & Caswell 1987) and the seminal comparative study of Silvertown *et al.* (1993). Life Table Response Experiment analysis (LTRE) is now the established technique for analysing differences in growth rates between populations, but it took a number of years from its original formulation (Caswell 1989) before exciting applications emerged (Levin *et al.* 1996).

This decennial period is also reflected in the fact that this Special Feature appears exactly 10 years after the publication of the Special Feature on 'Elasticity Analysis in Population Biology: Methods and Applications' (Heppell, Pfister & de Kroon 2000), which witnessed the genesis of integral projection models (IPMs; Easterling, Ellner & Dixon 2000) and stimulated the establishment of LTREs (Caswell 2000; de Kroon, van Groenendael & Ehrlén 2000), among other advances. Developments over the last decade have been characterized by an increasing attention to spatial and temporal variation in population trajectories. Although the principles of stochastic demography were formulated several decades ago (Cohen 1976; Tuljapurkar 1990), their applications only started to proliferate relatively recently, partly because of new techniques (e.g. stochastic elasticities; Tuljapurkar, Horvitz & Pascarella 2003) and partly because more long-term data sets are being published. Together with advanced LTRE techniques, the retrospective analysis of variation (Caswell 2000) and novel analytical tools in prospective stochastic simulations mark a new era of population projection models.

If the increase in page numbers between the first and second editions of *Matrix Population Models* (Caswell 1989, 2001) is indicative of the progress in matrix modelling techniques, the demographer's toolbox has increased annually by 7% over that period ($\lambda = 1.07$). This growth rate has not slowed since 2001, and this Special Feature contributes to it by presenting new techniques and applications in the context of demographic variation, as well as comparative demography and integral model construction. Where applicable, the authors of this Special Feature have published their R/MatLab codes in online appendices including guidelines for their implementation. We hope that this will help to shorten the decennial delay in their application by the larger research community.

Measuring effects of temporal and spatial variation

Life Table Response Experiment analyses have revolutionized the way in which we study demographic variation between years, sites, treatments and their interactions, but they treat temporal and spatial variation in the same manner. Temporal variation, however, appears to contribute to demographic variation in a distinctly different manner than spatial variation, but those processes are yet to be disentangled. This Special Feature provides methodology to do this, and contributes to our understanding of the effects of temporal and spatial variation on population responses.

Caswell (2010) begins the Special Feature with the mathematical foundation of the Stochastic LTRE (SLTRE). His approach allows us to decompose differences in stochastic population growth rate (λ_s) as a function of the distribution of environmental states and the stage-specific vital rate responses to each environmental state. This method is particularly useful when the stochastic sequence is influenced by distinct events (e.g. years after a perturbation, different abiotic conditions). Research programmes in which years are more appropriately treated as a random sample of environmental variation than as a linear sequence of events call for the implementation of the complementary SLTRE methodology of Davison *et al.* (2010). Their SLTRE is based on stochastic elasticities (Tuljapurkar, Horvitz & Pascarella 2003), and it decomposes variation in λ_s into contributions of differences in mean and variance of vital rates.

Horvitz, Ehrlén & Matlaga (2010) present a novel application of stochastic elasticities to explore reproductive benefits and demographic costs in variable environments. Their results show that the cost–benefit relationships and their ultimate effects on fitness depend on the frequency and sequence of years favouring specific vital rates. Finally, Jongejans *et al.* (2010) study the population dynamics of three short-lived perennials in multiple sites. They analyse the spatio-temporal variation of vital rates using spatially nested LTREs, and apply a novel fixed-LTRE index that decomposes variation in λ into net contributions from variation in each of the vital rates. They show that species with very similar life histories and elasticity patterns can differ markedly in their responses to spatial and temporal variation.

Responses to changing conditions: transient dynamics

The approaches described above apply matrix models in more realistic scenarios of natural variation than have been addressed in previous studies. In addition, because fluctuations in the environment continually push populations away from their asymptotic equilibria (stable stage distributions), the study of transient (short-term) dynamics has gained momentum in the last decade. Usher (1976) and Caswell & Werner (1978) opened the debate of long-term vs. short-term dynamics and, since then, various tools have been developed to characterize transient dynamics (e.g. Fox & Gurevitch 2000; Haridas & Tuljapurkar 2007; Townley *et al.* 2007).

This Special Feature applies these tools in three directions. Maron, Horvitz & Williams (2010) develop a novel application of transient dynamics analysis that allows for the scaling from effects of experimental manipulations on given vital rates to expected demographic trajectories. Based on theory developed by Haridas & Tuljapurkar (2007), they propose three measures that capture the interaction strengths of herbivores on transient plant population dynamics, using information about the initial stage distribution of plants in the population. For generalized interspecific comparisons of transient dynamics, independent of stage distribution, Stott *et al.* (2010) review the utility and limitations of a new set of transient indices (Townley *et al.* 2007) characterized by amplifying and attenuating transient dynamics. Contrary to previous knowledge (Fox & Gurevitch 2000), both studies independently find a direct relationship between transient and asymptotic population growth rates. The third contribution to transient dynamics (Salguero-Gómez & Casper 2010) reports that the ability of individuals to shrink – an overlooked demographic phenomenon in plants – increases demographic resilience *via* higher damping ratios.

These contributions, together with transient sensitivity analyses (Caswell 2007), represent a significant maturation of transient analysis methodologies. These tools are now ready for application to the many situations where non-equilibrium dynamics are prominent (e.g. experimental manipulations, natural disturbances).

Comparative demography and categorization

Although the first demographic works were already comparative (Sarukhán & Gadgil 1974; Werner & Caswell 1977), the true advent of comparative demography came decades later as a result of the standardization of protocols for species' projection matrices (Silvertown *et al.* 1993). The number of species available in this format is now overwhelming: over 465 plant species (Salguero-Gómez, unpublished data), 21 animal species in the order Carnivora (M. van de Kerk and E. Jongejans, pers.comm.), 100 birds (Sæther, Ringsby & Roskaft 1996), 88 freshwater fishes (Velez-Espino, Fox & McLaughlin 2006). Since the seminal work by M. Franco and J. Silvertown, we have witnessed the continuous publication of more comparative demographic investigations (e.g. Franco & Silvertown 2004; Bruna, Fiske & Trager 2009), and there is still scope for work of this nature, as illustrated in this Special Feature.

Burns *et al.* (2010) utilize published data for over 200 plant species to explore contemporary life-history questions about the costs and benefits of delay in reproduction. In exploring phylogenetic constraints imposed by common ancestry, Burns *et al.* (2010) and Stott *et al.* (2010) independently find that sensitivities carry a more consistent phylogenetic signal than elasticities. Burns *et al.* offer insight into this discovery, which may be related to the link between selective gradients and sensitivities (van Tienderen 2000). Salguero-Gómez & Casper (2010), using projection matrices for 80 herbaceous perennials, show that shrinkage allows populations to cope better with disturbances by increasing survival. Their comparative loop analysis (van Groenendael *et al.* 1994) reveals that plastic reductions in size increase life spans. This study and others (Caswell 2000; de Kroon, van Groenendael & Ehrlén 2000; Jongejans *et al.* 2010) have emphasized the need for a careful evaluation of perturbation analyses, as vital rates with small elasticities may be of significance in buffering demographic variation. Finally, Stott *et al.* (2010) calculate various transient dynamic indexes for over 100 plant species and conclude that annuals and trees have a greater potential for immediate responses to disturbance than herbaceous perennials and shrubs. They attribute this to the shaping of these life histories by selective pressures to maximize their colonization strategies in stochastic environments (e.g. drought, canopy gaps).

It has been known for some time that stage classification and projection matrix dimension affect the estimation of demographic outputs (Enright, Franco & Silvertown 1995). Papers in the Special Feature provide novel solutions to this problem in three different ways: (i) treating matrix dimension as a covariate (Burns *et al.* 2010; Stott *et al.* 2010), (ii) normalizing matrix dimension prior to analysis (Salguero-Gómez & Casper 2010), and (iii) avoiding the grouping of continuous size distributions into discrete classes, by undertaking IPMs (Zuidema *et al.* 2010).

Integral projection models explore demographic dynamics from continuous functions of size changes, survival and reproduction (Easterling, Ellner & Dixon 2000) while retaining all advantages of classical projection matrices by approximating a continuous model structure via matrices of large dimensions. Zuidema *et al.* (2010) describe a new 'integration method' for IPMs which allows appropriate modelling of slow-growing, long-lived plants. They used tree ring data on six species to compare age and growth rate estimates when using different matrix dimensions. They conclude that matrix dimension also matters in IPMs of slow-growing species. These and other recent methodological developments, including IPM formulations for stochastic environments (Rees & Ellner 2009), will contribute to a further increase in the use of this modelling technique.

Current challenges for plant populations and for plant demographers

Stochasticity is the rule, not the exception, in the real world, and the study of its effects becomes even more relevant in the light of the expected increase in climatic variability and unpredictability (IPCC 2007). Environmentally driven fluctuations in population size may increase extinction probabilities (Morris & Doak 2002), aid invasions by alien species (Morris *et al.* 2008) and change the spatial configuration of populations (Bruna, Fiske & Trager 2009). One striking insight gained from the contributions presented here and elsewhere is that plants have an impressive array of features to counteract this variation. Longevity (Morris *et al.* 2008), shrinkage (Salguero-Gómez & Casper 2010) and persistent seed banks (Angert *et al.* 2009; Burns *et al.* 2010) are means of demographic storage, buffering demographic variation. Vital rates that make the largest contribution to mean population growth rates (often survival of individuals) are less variable than other vital rates such as reproduction (Burns *et al.* 2010). Transient indices reveal how and to what degree specific population characteristics may immediately buffer disturbance (Maron, Horvitz & Williams 2010; Stott *et al.* 2010). Negative covariances between vital rates can play an important role in buffering temporal and spatial variation (Horvitz, Ehrlén & Matlaga 2010; Jongejans *et al.* 2010). Small stochastic elasticities of variance in a vital rate are indicative of temporal buffering (Davison *et al.* 2010).

Novel analytical techniques are now at our disposal for measuring the effects of environmental variation, including stochastic elasticities (Horvitz, Ehrlén & Matlaga 2010), stochastic LTRE (Caswell 2010; Davison *et al.* 2010), and habitat-stage and environment-specific elasticities (Horvitz, Tuljapurkar & Pascarella 2005; Aberg *et al.* 2009). Matrix projection modelling is thus capable of more accurately monitoring and assessing the present and future effects of these buffering mechanisms for the survival and resilience of plant populations in the current changing world. Usher (1976) stated that the *behaviour* [of projection matrices] *in the real world is largely unattempted, and the effects of variation in the real world, both in terms of error of parameter estimation and stochastic variability due to season or year-to-year climatic fluctuations, is largely unknown*. We are now better equipped to address such aims, and the time is ripe to determine whether plant populations themselves can meet the challenges placed upon them by the myriad of ongoing environmental changes.

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