

SPECIAL FEATURE

ADVANCES IN PLANT DEMOGRAPHY USING MATRIX MODELS

Using experiments, demography and population models to estimate interaction strength based on transient and asymptotic dynamics

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Summary

1. Despite a large literature documenting the effects of mutualists and/or antagonists on plant performance, we still have limited insight into the strength of these interactions, as this involves quantifying how one species influences the *population dynamics* of another.

2. Here, we use data from two example systems, *Cynoglossum officinale* and *Calathea ovandensis*, to illustrate how experiments, demographic data and stage-based population models can be combined to estimate interaction strength of insect herbivores on plants. Because many plant populations may not be at equilibrium, we conduct transient analyses and contrast these results to more traditional asymptotic results.

3. We calculate three metrics of interaction strength, $\Delta\lambda_{\text{asymptotic}}$, the change in asymptotic annual *per capita* plant population growth rate resulting from herbivore exclusion, $\Delta\lambda(t)$, the change in transient λ caused by herbivores at $t = M$ (where M = the time of their maximum effect during the transient phase) and $\Delta\lambda_{\text{transient}}$, a time-averaged effect of consumers on λ across the entire transient phase.

4. Fairly strong impacts of insect consumers on plant fecundity do not translate similarly to $\Delta\lambda_{\text{asymptotic}}$. Results show that $\Delta\lambda(t)$ can be larger (or smaller) than $\Delta\lambda_{\text{asymptotic}}$ but in our examples $\Delta\lambda_{\text{transient}}$ was similar in magnitude to $\Delta\lambda_{\text{asymptotic}}$.

5. The transient effects of consumers on λ were driven by changes in the elasticity of fecundity across the transient phase. These effects were dynamic even though consumer impacts on demography and vital rates were held constant. The importance of particular stages and transitions to annual population growth vary during the transient phase.

6. *Synthesis.* We describe three metrics of interaction strength, $\Delta\lambda_{\text{asymptotic}}$, $\Delta\lambda(t)$ and $\Delta\lambda_{\text{transient}}$. These metrics have several advantages over more commonly used trait or performance measures that quantify the outcome of interactions. We illustrate how the transient impacts of consumers on λ are dynamic, with the changing stage distribution of a population and transient elasticities driving these effects. More generally, this study shows that the impacts of animals on plant performance do not translate equivalently to plant population growth, thereby underscoring the importance of using population models to extend the inference of individual-level experiments.

Key-words: *Calathea ovandensis*, *Cynoglossum officinale*, interaction strength, matrix model, plant population growth, plant–herbivore interactions, transient dynamics

Introduction

Determining the extent to which species interactions influence plant abundance is central to understanding ecological

systems. At the population-level, understanding the outcome of species interactions helps shed light on whether biotic interactions fundamentally set limits on plant distribution and abundance. At the community level, it is of interest to understand how plant–plant, plant–microbe or plant–animal interactions influence plant diversity and dominance. Whole

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branches of ecological theory are built on understanding and predicting the conditions under which one species influences the population dynamics of an interacting partner, yet quantifying the strength of interactions has proved challenging (Power *et al.* 1996). Although there are many ways in which interaction strength can be inferred (reviewed by Wootton & Emmerson 2005), the venerable approach long used by field ecologists has been enclosure experiments. One or several species are experimentally denied access to one or more focal populations and then one determines how the abundance of the focal population changes as a result of this exclusion (Brown & Heske 1990; Paine 1992; Louda & Potvin 1995; Carson & Root 2000). Unfortunately, experiments of this type are not always practical. First, long-term enclosures can be difficult to construct and maintain, particularly if they are applied at the community level. Second, for long-lived species, any population response to such a manipulation can take many years to develop – far longer than may be practical to empirically quantify.

Because of these difficulties, rather than measuring interaction strength, many studies assess how one species influences the performance or traits of another. For example, of the hundreds of studies on plant–plant competition (Goldberg & Barton 1992), most involve removing competitors around focal individuals (either in pots in a glasshouse or in the field) and determining impacts on a single response variable (e.g. biomass) at a single life stage (Howard & Goldberg 2001). Similar experiments have been used to study other types of interactions (see reviews by Ashman *et al.* 2004; Kolb, Ehrlén & Eriksson 2007). Since these studies measure impacts of an interaction on plant performance rather than abundance, their methodology is often disconnected from the hypotheses that are being tested. For example, a question such as ‘what makes an exotic invasive?’ is a question about the factors that influence plant abundance, both where the plant is native and where it is introduced. Although insight can be gained by quantifying how various factors influence the growth, survival or fecundity of individuals, ultimately the question cannot be answered without understanding how variation in individual performance metrics translates to changes in population growth or abundance. Isolated changes in size, biomass, survival or fecundity do not inexorably lead to meaningful alterations in plant abundance in the next generation (Crawley 1989). Although this issue has been commented on in the past (McPeck & Peckarsky 1998; Goldberg *et al.* 1999; Maron & Crone 2006) here we provide some additional amplification.

Determining logistically feasible methods for empirically quantifying the strength of interactions is essential if we are to have some common currency for comparing how interactions vary in their outcome across taxa or geographic gradients. Here, we discuss a powerful but underutilized method to quantify interaction strength. This approach involves a combination of: (i) small-scale targeted experiments to determine how an interacting species influences a particular demographic transition of a focal plant species, (ii) demographic monitoring of a focal plant population and (iii) stage-based population modelling. Until relatively recently, population models have

not been used as tools to extend results from targeted experiments to determine how particular interactions influence plant population size, structure or dynamics (Ehrlén & Eriksson 1995; Maron & Crone 2006; Horvitz, Ehrlén & Matlaga 2010; Williams, Auge & Maron 2010). In studies that have combined experimental results and demographic data for structured populations, typically what has been estimated is the impact of an interaction on the asymptotic population growth (λ). When populations are at or near their stable stage distribution (SSD), asymptotic models may well reflect what is occurring over shorter time spans. However, many plant populations may not be at the SSD and near-term effects could be quite different from asymptotic effects (Koons *et al.* 2005).

In this study, we explore how population models can be used to project the near-term effects of ecological interactions on plant abundance. We utilize demographic modelling to project what might be expected if one were to empirically determine how the population of one species responded to the exclusion of another after running the experiment for 5–10 years. This approach takes advantage of newly developed theory related to transient dynamics (Haridas & Tuljapurkar 2007). We illustrate our approach with data from two different plant–animal systems. The first case examines the impacts of insect herbivores on a monocarpic perennial herb in the plant’s native range in Europe. We then extend this analysis to explore the potential for those insects to be effective biocontrol agents where the plant is an invader in North America. The second case explores how ant guards and insect herbivores individually and jointly impact the abundance and dynamics of a tropical forest perennial herb in Mexico.

Materials and methods

We use experimental and demographic data from two disparate systems to determine the strength of interaction between insect herbivores and their host plants. Specifically, we quantify the extent to which insect herbivores that reduce plant fecundity alter both transient and asymptotic estimates of plant population growth and dynamics. We first describe methods and some of the key parameters of transient analysis of stage-structured population models since these methods are relatively new. We then describe population parameters that are useful for quantifying interaction strength, both during the transient phase and after populations reach their SSD. Finally, we introduce the example study species, methods of field data collection and the construction of population projection models.

TRANSIENT DYNAMICS: UNDERLYING PARAMETERS AND ELASTICITY

Transient dynamics refer to changes in population size and structure before populations have reached SSD. The fundamental point for our application is that the importance of particular stages and transitions to annual population growth may vary during the transient phase. Thus, any interaction that influences a particular stage may wax and wane in its influence on population growth through the transient phase. Since methods for performing a sensitivity analysis of non-asymptotic annual population growth rate are relatively new and developing rapidly (Fox & Gurevitch 2000; Koons *et al.* 2005; Caswell 2007; Haridas & Tuljapurkar 2007; Stott *et al.* 2010), we

clarify how we apply these methods and briefly recap some of the important parameters underlying transient dynamics, taking into account the distance an initial stage structure is from the SSD (as in Haridas & Tuljapurkar 2007). A distinct, but related, approach to transient analysis that does not take into account initial structure is presented by Stott *et al.* 2010.

For a population where vital rates differ among individuals of different stages, population dynamics can be modelled by a population projection matrix. Over the long term, the dominant eigenvalue (λ_0) (and its associated eigenvectors) of the matrix determines the changes in population number and structure; however, during the near term, all of the eigenvalues (and their associated eigenvectors) will have noticeable effects on how population number and structure change (Caswell 2001; chapter 4). As the matrix acts to redistribute individuals among the stages at each time step, the number of individuals in each stage and in the entire population may go up and down. Thus, for structured populations over the near term, even though the environment is constant, the stage structure will change over time and there may be cycles both in population number and structure. These cycles will damp out over the long run. The subdominant eigenvalue (λ_1), the second largest in absolute magnitude, plays a particularly important role. Therefore, one important parameter is the damping ratio $\rho = |\lambda_1|/|\lambda_0|$ (Haridas & Tuljapurkar 2007; note that Caswell 2001 reports the reciprocal). The closer ρ is to 1, the longer it will take for the cycles to damp out. In our examples, we examine how the presence or absence of insect herbivores affects ρ .

In addition to the dynamic properties of the matrix, the initial stage distribution and its distance from the SSD can noticeably influence near-term changes in population size and structure. α is a useful measure of the distance between a particular stage distribution and the SSD. As explained in Haridas & Tuljapurkar (2007), $\alpha(t)$ is given by the scalar product of the reproductive value (RV; appropriately scaled) with the stage distribution at time t . When the population is at the SSD, $\alpha = 1$ (the RV used in these calculations has been scaled to make this true); when there are excess (compared with the SSD) individuals in stages with high RV, $\alpha > 1$, and when there are excess (compared with the SSD) individuals in stages with low RV, $\alpha < 1$. If a plant–animal interaction perturbs the stage distribution, it will also, therefore, affect α . For example, adding seed predators may change the proportion of seeds or seedlings in the population vector at a particular time.

Transient elasticity measures how sensitive population growth rate at each time, $\lambda(t)$, is to a small proportional perturbation in a matrix element, as compared with asymptotic elasticity which measures how sensitive the long-term population growth rate is to similar perturbations. For our application, we were interested in how sensitive $\lambda(t)$ was to changes in plant fecundity caused by insect herbivores. Note that transient elasticity changes over time because many things change over time during the transient phase: the growth rate of the population, the structure of the population and the influence of the non-dominant eigenvalues on population size and structure. It is quite possible that insect herbivores could be very important to near-term dynamics, even if they are not important to long-term dynamics. Such differences would show up as a difference between transient and asymptotic elasticity to fecundity.

Haridas & Tuljapurkar (2007) show that transient elasticity can be decomposed into two additive components, $e_{transient}(t) = e_1(t) + e_2(t)$. A perturbed matrix generates a sequence of stage structures that differs from the sequence generated by an unperturbed matrix. $e_1(t)$ and $e_2(t)$ estimate how those small perturbations create two effects: (i) an effect generated by the perturbed matrix elements acting on the structure that would have been generated by the original

matrix and (ii) an effect generated by the unperturbed matrix elements acting on the structure that would have been generated by the perturbed matrix, or actually on the difference between the structures generated by each of the two matrices at a particular time. Transient elasticities can be positive or negative. For details on how to use the dynamic properties of the matrix and the distance of the initial population from the SSD to calculate these components, see Haridas & Tuljapurkar (2007) (C. Haridas kindly provided MATLAB code to us; our modified version of this code is available in Appendix S1 in Supporting Information).

Finally, we note that there is no clear-cut end to the transient phase and beginning of the asymptotic phase. As more attention is paid to transient dynamics, perhaps some conventions will be agreed upon. Different possible metrics could exist when α is smaller than some threshold value or the number of time periods it takes for the effects of the subdominant eigenvalue to be x -fold less than it is initially. Neither the threshold nor the x is a currently agreed upon value. In the absence of such conventions, in this study, after inspecting the behaviour of our populations, we arbitrarily set the first 10 time steps to be the transient phase.

ESTIMATES OF INTERACTION STRENGTH

In addition to performing the transient analyses described above, we calculated a time series of population size ($N(t)$), population growth rate ($\lambda(t) = N(t)/N(t-1)$) and most germane to our question, the difference in population growth rate with and without insect herbivores $\Delta\lambda(t) = \lambda(t)_{\text{natural}} - \lambda(t)_{\text{herbivore suppression}}$ for each of our two example systems. $\Delta\lambda_{\text{asymptotic}}$ is the difference in the annual *per capita* growth rate of a population when it reaches its SSD and is a relevant metric of interaction strength since it encapsulates how an interaction influences asymptotic λ . We also calculated the time-averaged annual population growth rate across the transient phase (assumed to be between $t = 0$ and 11), defined as $\lambda_{\text{transient}} = ((N_{11}/N_0)^{1/10})$. The difference in $\lambda_{\text{transient}}$ between plants exposed to or protected from interacting animals is $\Delta\lambda_{\text{transient}}$ and represents another estimate of interaction strength.

STUDY SPECIES AND HERBIVORY EXPERIMENTS

We used data from two different example study systems to explore how insect herbivory that influences fecundity affects both transient and asymptotic dynamics. The first system involves *Cynoglossum officinale* L. (Boraginaceae), or houndstongue, a self-compatible, facultatively monocarpic perennial (de Jong, Klinkhamer & Boorman 1990) that is native to Europe. It was introduced to North America in the mid-19th century and has now spread across the US and southern Canada. It is of interest to determine both the extent to which native herbivores influence the population size of *Cynoglossum* where it is native as well as the potential for these herbivores to act as biocontrol agents in the introduced range. Previously, Williams, Auge & Maron (2010) examined the effects of insect herbivores on plant performance using an herbivore exclusion experiment at two study sites in the native range and three in the introduced range. This research focused on the effects of the major consumer on *Cynoglossum*, a specialist root-boring weevil, *Mogulones cruciger*, which is present only in the native range and preferentially attacks large rosettes and flowering plants (Prins, Nell & Klinkhamer 1992). Native plants are also consumed by two leaf-feeding flea beetles, *Longitarsus* spp. (Schwarzlaender 2000; M. Schwarzlaender, personal communication). A systemic insecticide (imidacloprid) was applied every 3 weeks across 3 growing seasons (2004–2006) to individual plants, to assess the

effects of insects in both ranges on plant performance. In the native range, insect damage was mainly caused by the specialists *M. cruciger* and *Longitarsus* spp., with *M. cruciger* probably having a much larger negative impact. Details of this experiment are reported elsewhere (Williams, Auge & Maron 2010). In short, insect exclusion increased seed production but did not change other vital rates. In the introduced range, there were no specialist enemies and attack by generalist herbivores was relatively minor. Plants experimentally 'released' from herbivores in the introduced range did not do better than those exposed to them (Williams, Auge & Maron 2010).

The second example system is *Calathea ovandensis* Matuda (Marantaceae), a perennial understorey herb of seasonal tropical forests in southern Mexico and Guatemala. The interaction between this plant and its consumers and mutualists was previously studied by Horvitz & Schemske (1984) and the plant's demography at a secondary forest at Laguna Encantada, Los Tuxtlas, Veracruz, Mexico, was also extensively analysed (Horvitz & Schemske 1995). Among the studies that were conducted was an experimental investigation of the effects on plant reproduction of an ant-tended herbivore and of extrafloral nectary-visiting ants. At least 16 species of ants are regularly found tending extrafloral nectaries located on plant inflorescences and are thought to be mutualists who defend plants from herbivores. Nevertheless, larvae of the Riodinid butterfly *Eurybia elvina* as well as many other insects (including small flies and wasps) feed on developing buds, flowers and fruits. *Eurybia elvina* is specialized for living among ants. These insects have a pair of eversible glands on the dorsal surface of the eighth abdominal segment that secretes a fluid rich in sugars and amino acids, which is harvested by ants. To determine the relative effects of *E. elvina* (hereafter *Eurybia* for simplicity) and the ant guards in this system, Horvitz and Schemske performed a large field experiment, randomly assigning about 600 new inflorescences to one of four treatment categories, defined by the fully crossed treatments with and without ants, with and without the herbivore *Eurybia*. The experiment ran for c. 11 weeks in 1982; experimental treatments were maintained throughout the lifetime of inflorescences, using Tanglefoot (a sticky material that can trap insects that attempt to cross it; The Tanglefoot Company) to exclude ants and manually moving caterpillars to maintain *Eurybia* treatments. Flower and seed production were recorded. Details are reported in Horvitz & Schemske (1984).

DEMOGRAPHIC STUDIES AND INCORPORATING EXPERIMENTAL RESULTS INTO MATRICES

Cynoglossum

Williams, Auge & Maron (2010) combined the results from the insect exclusion experiment with integral projection models (IPMs) to calcu-

late the asymptotic population growth rate (λ) under scenarios with and without herbivores present. The effects of insects on asymptotic λ at all sites and years are reported elsewhere (Williams, Auge & Maron 2010). Here, to examine the effects of insects on transient dynamics, we chose one example site and year from the native and one example site and year from the introduced ranges (native range = Site 3, 2004–05, introduced range = Site 4, 2004–05; Williams 2009). We used the observed stage distribution in the monitoring transects at the beginning of the study (2004) as the initial population structure. The number of seeds in the seed bank in the native range (at site 3) was estimated based on the average number of seeds produced in all years and the proportion of seeds from the previous year that did not germinate (seeds do not survive for more than one year in the soil). It was possible to estimate this number directly for the introduced range (site 4) from data on 2003 seed production. To simplify the presentation of transient elasticities, we reduced the size of the approximating matrix of the IPM to 8×8 . The approximating matrix is composed of 5 size classes of vegetative plants, seeds in the seed bank, seeds from the current year's seed production and seedlings (Table 1). Higher dimensional matrices generated similar patterns in transient and asymptotic dynamics (J.L. Williams, unpublished data) although we note that this may not be the case for other species (Stott *et al.* 2010).

To explore the population-level consequence of herbivory in the native range we created a matrix representing plants without herbivores (all matrix elements were identical between these two scenarios, except fecundity). To investigate the potential effects of adding the specialist insect, *M. cruciger*, as a biocontrol agent to the introduced range, we again created two matrices, one with demographic rates from the introduced range without insects and one with fecundity reduced by a similar amount as the difference between plant fecundity with and without insects in the native range. (Appendix S2 shows the matrices for the native and introduced population without insects). For each matrix, we projected the population for 11 years, using current stage distributions from each site (2004 for both sites) as the initial population structure, but scaling it to sum to 1 (for ease of presentation and so results from *Cynoglossum* and *Calathea* could more easily be compared).

Calathea

Horvitz & Schemske (1995) previously reported the demography of *C. ovandensis* and its patterns of variability over time and space. We used eight stages to characterize the population: seeds (both newly produced and those in the seed bank) and seven other size classes (three non-reproductive and four reproductive) (Table 1). Seed production increases with plant size because the number of reproductive shoots increases. An annual demographic census was conducted at the time seeds could be counted in mature fruits on plants. Plants that

Table 1. Definition of stages used for each species

Stage	<i>Cynoglossum officinale</i>	<i>Calathea ovandensis</i>
1	Seeds in seedbank	Seeds (on plant and in seedbank)
2	Seeds on adult plants (current year's seed production)	Seedlings
3	Seedlings	Juveniles
4	Tiny vegetative plants*	Pre-reproductive plants*
5	Small vegetative plants*	Small reproductive plants*
6	Medium vegetative plants*	Medium reproductive plants*
7	Large vegetative plants*	Large reproductive plants*
8	Very large vegetative plants*	Very large reproductive plants*

*Stages that may become reproductive by next year and thus contribute to seeds at time = $t + 1$.

are non-reproductive in year t can become reproductive by $t + 1$ and thus contribute to seeds at $t + 1$. The number of seeds produced by a plant is a product of the number of inflorescences the plant produces with the number of seeds per inflorescence. The former is a function of plant size and the latter a function of biotic interactions. Using the observed numbers of inflorescences per plant of different stages, we calculate seed production *per capita* of each stage class. For this study, we pooled data among four study sites to construct an annual population projection matrix for the 1982–83 transition year. Here, we refer to this matrix as the one with ‘naturally occurring’ insects; the mean number of seeds produced per inflorescence for the calculations that went into producing this matrix was 14.2.

Against this demographic backdrop, we investigated the population-level impacts of the biotic interactions by changing the seed production per inflorescence and recalculating all the fecundities and related matrix entries. We created two altered matrices, one with high reproduction (the remove-*Eurybia*, with-ants treatment) and the other with low reproduction (the add-*Eurybia*, exclude-ants treatment). In the ‘good animals’ scenario, we increased seed production per inflorescence and in the ‘bad animals’ scenario we decreased seed production per inflorescence, both according to the results of Horvitz and Schemske’s experiment (Table 2). Thus, we had a matrix parameterized from demographic data and two matrices with altered fecundity, but the same in all other vital rates (see Appendix S2 for the ‘naturally occurring insects’ matrix values). For each matrix, we projected the population for 15 years, using a stage distribution consisting of all seeds to simulate a colonization event from each site as the initial population structure, but scaling it to sum to 1.

Results

EFFECTS OF HERBIVORES ON PLANT FECUNDITY AND ASYMPTOTIC POPULATION GROWTH, $\Delta\lambda_{\text{ASYMPTOTIC}}$

For both *Cynoglossum* and *Calathea* previous experiments showed that insect herbivores had reasonably strong effects on individual plant fecundity. The exclusion of herbivores increased *Cynoglossum* seed production by an average of 35% in its native range, and *Eurybia* exclusion (in the presence of ants) increased *Calathea* seed production by an average of 45%. For *Cynoglossum*, these effects translated into an increase in asymptotic growth rate from 0.97 to 1.04; for *Calathea* insect exclusion increased λ from 1.15 to 1.20 (Table 2). These differences in λ are represented as $\Delta\lambda_{\text{asymptotic}}$, the horizontal line in Fig. 1c,f,i.

SSD AND RV FOR *CYNOGLOSSUM* AND *CALATHEA*

Figure 2 illustrates the SSD and RV for each species. The baseline populations are taken to be the one without insects for *Cynoglossum* in both ranges (so that native and introduced range demography can be compared) and the one with natural insects for *Calathea*. Although there is an overall similarity in stage structure between the introduced and native *Cynoglossum* populations, the introduced population is composed of relatively greater proportions of individuals as seeds in the seed

Table 2. Demographic effects of insects on seed production and on population dynamics. Seed production is per large plant year⁻¹ for *Cynoglossum* and per inflorescence year⁻¹ for *Calathea*. For *Cynoglossum*, the experimental population in the native range (Aseleben) is without insects, the simulated population in the introduced range (Lavalley) is created by adding biocontrol agents as per experimental effects in the native range. For *Calathea* the population (all sites pooled) from the demographic study has natural levels of insects, the simulated populations have ‘additions and subtractions’ of the herbivore and the ant guard as per experimental effects on seed production. $\Delta\lambda_{\text{asymptotic}}$ is the difference in asymptotic λ with and without interacting species. The percent change in seed production as per experimental treatments and the corresponding simulated change in transient $\lambda(t)$ (at t of max effect) are shown in parentheses. The transient λ chosen for the table was for the time with the maximum effect of herbivores ($t = 1$ for *Cynoglossum* in both ranges and $t = 4$ for *Calathea*, see Fig. 1). Also given is a time-averaged summary measure of population growth during the transient period which we defined as the first ten time steps, $\lambda_{\text{transient}} = (N_{11}/N_0)^{1/10}$ and $\Delta\lambda_{\text{transient}}$, the difference in $\lambda_{\text{transient}}$ with and without interacting species. Both $\Delta\lambda_{\text{asymptotic}}$ and $\Delta\lambda_{\text{transient}}$ are measures of interaction strength

	<i>Cynoglossum officinale</i>				<i>Calathea ovandensis</i>		
	Native range		Introduced range		Natural insects	- <i>Eurybia</i> +ants	+ <i>Eurybia</i> -ants
	-Insects	+Insects	-Insects	+Biocontrol			
Parameters of plant performance							
Seeds produced	893.3 (+35%)	661.7	1081.3	756.9 (-30%)	14.2	20.8 (+46%)	6.2 (-56%)
Asymptotic λ	1.04	0.97	0.71	0.68	1.15	1.20	1.06
$\Delta\lambda_{\text{asymptotic}}$	+0.07		-0.03		+0.05		-0.09
$\lambda(t)$	1.88 (+0.32)	1.56	2.80	2.04 (-0.76)	1.19	1.38 (+0.19)	0.88 (-0.31)
$\lambda_{\text{transient}}$	1.06	0.98	0.80	0.75	0.98	1.03	0.89
$\Delta\lambda_{\text{transient}}$	+0.08		-0.05		+0.05		-0.09
Parameters underlying transient dynamics							
Angle λ_I (deg)	-82.4	-81.1	-59.4	-57.0	-33.8	-40.2	-24.9
μ (years)	4.4	4.4	6.1	6.3	10.6	9.0	14.5
$\rho = \lambda_1 / \lambda_0 $	0.77	0.77	0.63	0.62	0.53	0.51	0.53
τ (years) = -log(2)/log(ρ)	2.70	2.70	1.52	1.44	1.10	1.04	1.11
$\alpha(0)$	1.05	0.93	3.85	3.11	0.20	0.21	0.16

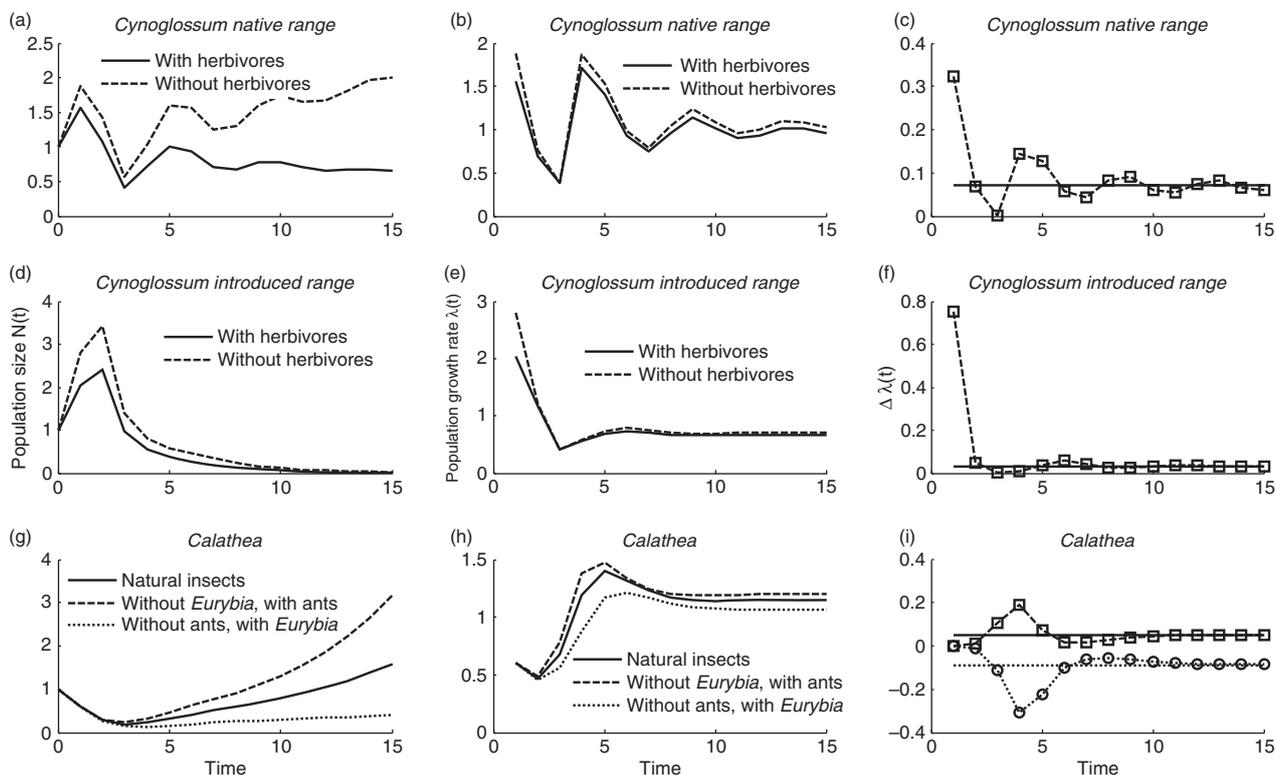


Fig. 1. Transient dynamics of population size $N(t)$ (a, d, g), population growth rate $\lambda(t)$ (b, e, h), and effect of insects on population growth rate $\Delta\lambda(t)$ (c, f, i) of *Cynoglossum* in its native (a–c) and introduced range (d–f) and of *Calathea* (g–i). Simulations of population size in panels a, d and g were begun with initial starting vectors scaled to sum to 1. Dashed horizontal lines in panels c, f and i show difference in asymptotic λ between populations with and without experimental levels of insects. Dashed horizontal line in panel i shows difference in asymptotic λ between populations with ant guards and herbivores and without ant guards but with *Eurybia*.

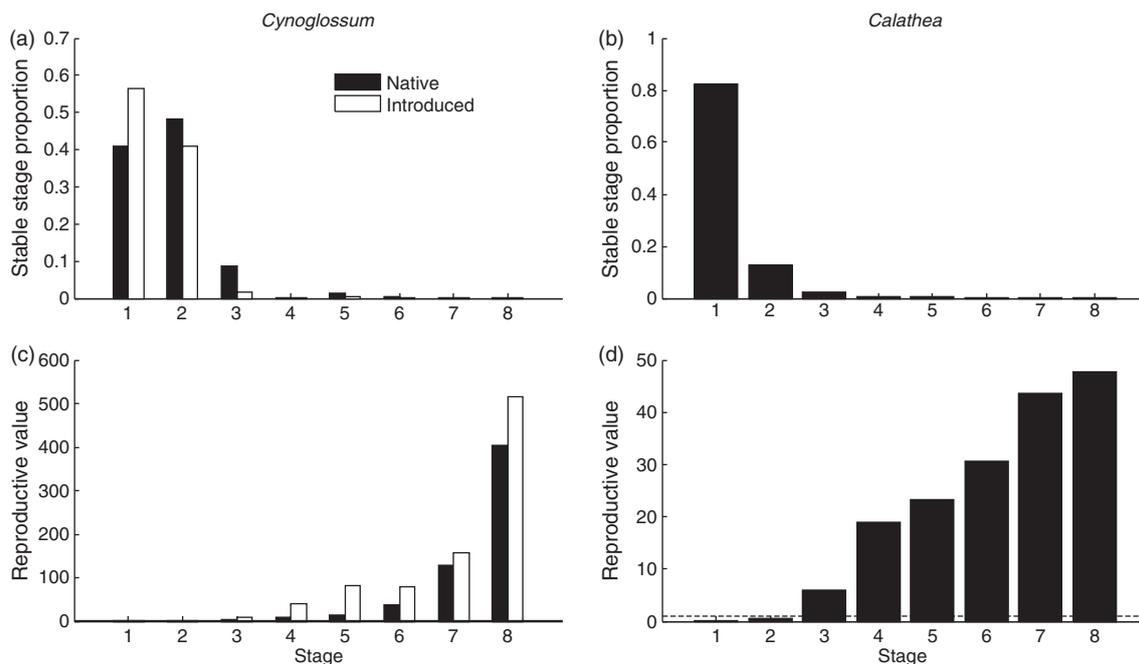


Fig. 2. Stable stage distribution (a, b) and reproductive value (c, d) of *Cynoglossum* for the matrices without insects and of *Calathea* for the matrix with naturally occurring insect levels. Stages are described briefly in Table 1.

bank compared with the native population and the RV is higher for smaller stages in the introduced range than in the native range. *Cynoglossum* and *Calathea* also have similarities

in their SSD, despite the fact that one is semelparous and the other iteroparous. Both species have an important seed bank, and include only a few stages with low reproductive values,

while most stages have a very high RV (defined as < 1 or > 1 , respectively).

EFFECTS OF CONSUMERS ON TRANSIENT DYNAMICS

The transient effects of insects on plants can be quite dynamic, changing in magnitude through time. Moreover, the ‘snapshot’ transient interaction strength estimate ($\Delta\lambda(t)$, Fig. 1c,f,i) can be different from what is obtained from asymptotic results (Table 2), depending on the time period at which it is evaluated. To illustrate, we focus on the times of maximum herbivore effect, $t = 1$ for *Cynoglossum* and $t = 4$ for *Calathea*. For *Cynoglossum* in its native range, herbivore exclusion resulted in an increase in annual *per capita* growth rate at $t = 1$ by an increment by 0.32, an effect nearly 5-fold larger than the asymptotic (Table 2). In its introduced range, a simulation of adding the specialist herbivore translated into a decrease in annual *per capita* growth rate at $t = 1$ of 0.75, a 25-fold larger effect than the asymptotic (Fig. 1f). The transient effects of herbivore exclusion (in the presence of ant-guards) for *Calathea* at $t = 4$ was 3- to 4-fold larger than asymptotic effects (Table 2, Fig. 1i).

For *Cynoglossum*, manipulating herbivores resulted in an effect on time-averaged (over 10 time steps) annual population growth rate of $\Delta\lambda_{\text{transient}} = +0.08$ and -0.05 in the native and introduced ranges, respectively, and for *Calathea* the manipulations of herbivores and ant guards resulted in an effect on $\Delta\lambda_{\text{transient}}$ of $+0.05$ and -0.09 for the without-*Eurybia*-

with-ants and the without-ants-with-*Eurybia* treatments, respectively. In these particular examples, $\Delta\lambda_{\text{transient}}$ and $\Delta\lambda_{\text{asymptotic}}$ were not very different (Table 2), but in other systems they might be. An issue to address in the future is to determine how best to define the ‘end’ of the transient period in the context of different amplitudes and frequencies of oscillations. Clearly, the result of time-averaging will depend upon how many of the included periods are close versus far from the asymptotic value as well as the amplitude of the oscillation.

Insect exclusion did not fundamentally alter the cyclicity or damping patterns during the transient dynamics, even though it did alter population growth rate. The effects of animals on both *Cynoglossum* and *Calathea* increase and decrease over time. This is driven by the fact that the elasticity of fertility also changes through time. To understand this result, first note that for both species, insect manipulations had relatively small effects on the parameters underlying the transient dynamics (Table 2, Appendix S3, Figs S1 and S2). Because of this, one can choose to analyse the transient elasticity of either matrix (with or without insects) as a reference and consider the other case(s) as ‘perturbation’. We choose the ‘without insects’ matrix for *Cynoglossum* in both the native and the introduced ranges and the ‘natural insects’ matrix for *Calathea* as the reference matrices.

The effects of insects on α were similarly relatively small for both *Cynoglossum* and *Calathea* (Fig. 3a,b), so we focus on the stage dynamics generated by the reference matrices. In all three of our examples, the initial population was not

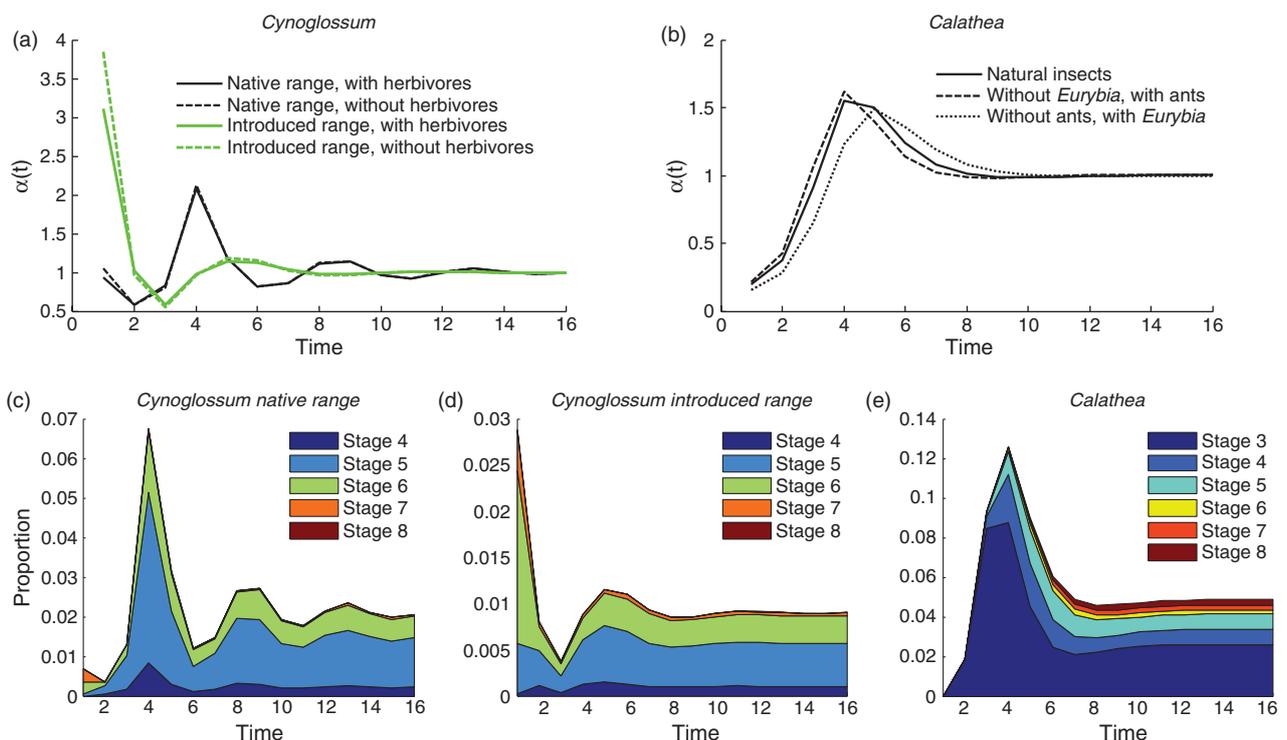


Fig. 3. Stage structure dynamics of *Cynoglossum* (a, c and d) and of *Calathea* (b and e). Panels a and b depict $\alpha(t)$, a measure which weights the proportion of each stage at time t by its representation in the asymptotic reproductive value before summing. Panels c, d, and e depict the stage structure at each time at t . Only those stages contributing to next year’s seeds are shown.

at the SSD. For *Cynoglossum* in the native range, the initial population had relatively more individuals in stages 6, 7 and in seeds and seedlings, with very few in stages 4 or 5 compared with its SSD (Fig. 3c); at $t = 4$, when α was large, it had a large excess of stage-5 individuals. In the introduced range, the initial population had fewer seeds and seedlings and many more individuals in stage 6 than in its SSD (Fig. 3d); at $t = 1$, with its large α , it had a large excess of stage-6 individuals. The initial population for *Calathea* was 100% seeds, although by $t = 4$, with its large α , all the stages were represented, even though there was an excess of stage 3 and relatively too few of stages 6, 7, 8 and seeds and seedlings. It is perhaps surprising that overall the $\alpha(t)$ for *Calathea*, which was initiated with a hypothetical population structure to simulate a colonization event, showed less dramatic variability than $\alpha(t)$ for *Cynoglossum* which were initiated with population structures observed in the field.

TRANSIENT ELASTICITIES

For *Cynoglossum* in both the native range and introduced ranges, most of the stages, except 6 and 7, have very low fertility elasticities. In the native range, the total fertility elasticity of stages 6 and 7 both show oscillations that damp out rather slowly and are out of phase with each other (Fig. 4c). In the introduced range, the fertility elasticities of stages 6 and 7 are in phase with each other, both showing a very low frequency oscillation that peaks early on and damps out quickly (Fig. 4f). Because the fertility elasticities of stages 6 and 7 coincide there is a very large effect of herbivores early on (Fig. 1f), as compared with the effect of herbivores in the native range which is more oscillatory and has a lower maximum (Fig. 1c). The fertility elasticity at the time of the maximum effect of animals on transient λ , $t = 1$, for contribution to seeds by stage 7 individuals is relatively high, an order of magnitude higher than the elasticity

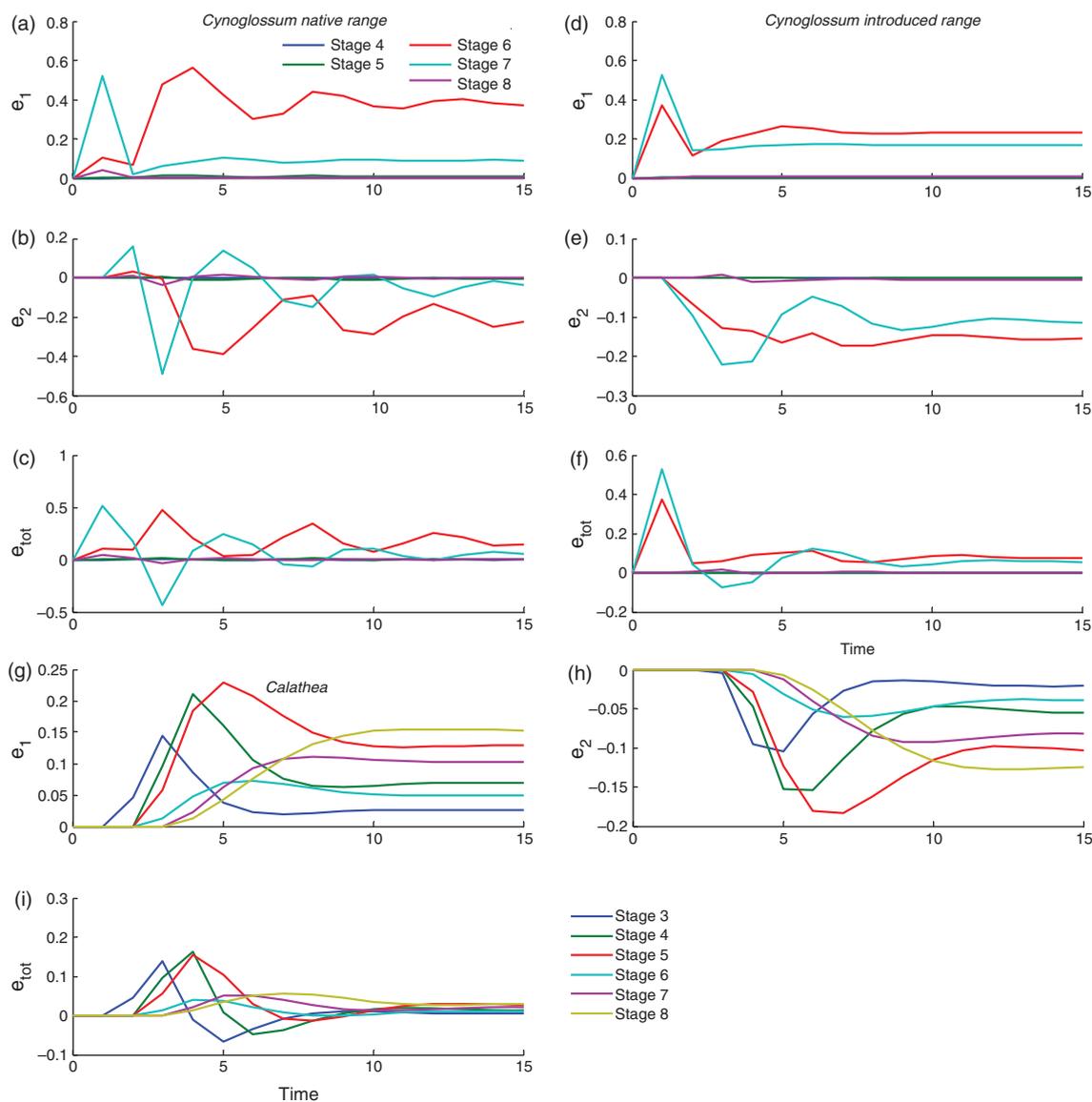


Fig. 4. Dynamics of transient elasticity for fertility of *Cynoglossum* in the native (a–c) and introduced (d–f) ranges for the matrices without herbivores and of *Calathea* (g–i) for the matrix with naturally occurring insects. Only stages contributing to next year's seeds are shown.

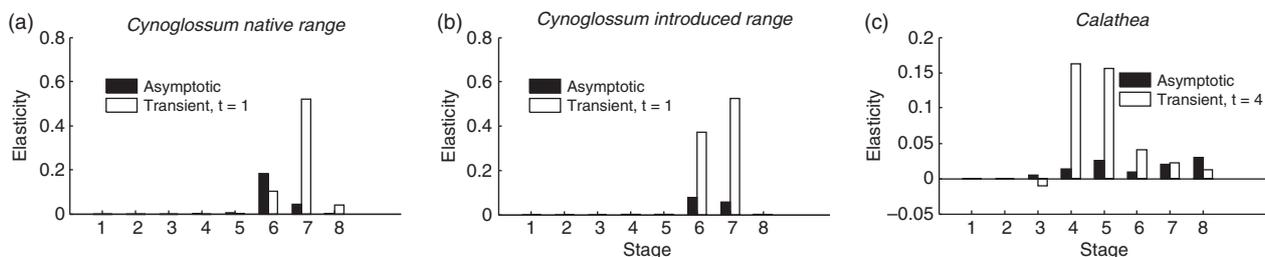


Fig. 5. Asymptotic and transient elasticities for fertility. Transient elasticity is illustrated at the point in time at which there was the largest effect of herbivore manipulation on transient λ ; for *Cynoglossum* this was at $t = 1$ in both the native and introduced range and for *Calathea* this was at $t = 4$ (see Fig. 1).

of the same vital rate for asymptotic λ (Fig. 5a,b). Similarly, there is a very high elasticity for seed production by stage-6 individuals in the introduced range but, in contrast, not in the native range, again underscoring that elasticity of stages 6 and 7 are out of phase in the native, but in phase in the introduced range.

For *Calathea*, contribution to next year's seeds by stage 3, 4 and 5 individuals have the largest fecundity elasticity early on, with contributions by stages 6, 7 and 8 individuals gradually rising and finally taking dominance over them (Fig. 4i). However, by the time these dominate, the overall fertility elasticity is quite low, thus the time of largest effect (Fig. 1i) coincides with when elasticity of contributions to seeds by stages 4 and 5 are both at their peaks, $t = 4$. The fertility elasticity at the time of the maximum effect of animals on transient λ , $t = 4$, is relatively high for contribution to seeds by stages 4, 5 and 6. For stages 4 and 5, it is perhaps an order of magnitude higher and for stage 6 about 4-fold higher than the elasticity of the same vital rates for asymptotic λ (Fig. 5c). In this case, it is not surprising for there to be lower elasticity for the larger stages at this time, because they are not yet well represented in this simulated colonizing population.

Discussion

Our analyses illustrate how population models can be used to extend the results from targeted experiments, thereby enabling one to examine how impacts of an interacting species on a particular vital rate translate to changes in plant population size and growth rate. For *Cynoglossum*, a 35% increase in seed production as a result of insect exclusion in the native range had somewhat limited projected impacts on both the asymptotic and time-averaged transient population growth rates. For *Calathea*, the estimated impacts of antagonists and mutualists on population growth were also somewhat muted in comparison with performance-level effects on reproductive success. However, even the small changes in λ caused by interacting species can translate to important effects on plant abundance. For example, in the case of *Cynoglossum*, if one started with a native population of 100 individuals (summed across all size classes), after 10 years (and with a $\Delta\lambda_{\text{transient}}$ of 0.08; $\lambda_{\text{transient}}$ with insects = 0.98, $\lambda_{\text{transient}}$ without insects = 1.06) there would be 82 individuals left in a herbivore-exposed population whereas there would be 179 individuals in an herbivore-free native population, a sizable difference.

DRIVERS OF TRANSIENT DYNAMICS

Although assessing the asymptotic growth rates and the elasticities that govern the effects of particular vital rates to plant population growth has long been of interest, there is a growing recognition that many plant populations may not be at equilibrium and thus interest has also been growing in analysing transient dynamics (Fox & Gurevitch 2000; Haridas & Tuljapurkar 2007; McMahon & Metcalf 2008; Stott *et al.* 2010). For some species, transient elasticities can be very different from asymptotic elasticity (McMahon & Metcalf 2008). As such, the impacts of an interaction on *per capita* population growth may be more (or less) important across a transient phase than one might estimate based on asymptotic analyses. Our results show that $\Delta\lambda(t)$ is quite dynamic despite demographic rates and impacts of consumers being held constant in the model.

The dynamics of $\Delta\lambda(t)$ are driven by the underlying demographic structure of the population, and the fact that elasticities of particular matrix elements are also changing through time. In particular, transient elasticities are dictated by two components, e_1 and e_2 . Elasticities are calculated by making small proportional changes to matrix elements and determining the effects on $\lambda(t)$. $e_1(t)$ and $e_2(t)$ estimate how perturbations create two effects having to do, respectively, with how, at each time step, the perturbations in matrix elements act on the unperturbed structure and the original matrix elements act on the perturbation of structure.

Since $\Delta\lambda(t)$ fluctuates over the transient phase, we also took the time-averaged sum of these values in an attempt to integrate the impacts of consumers on plant population growth over this phase. This integrative measure of how population growth rate is affected by an interaction can then be contrasted with the asymptotic value or compared among different types of interactions. In making these calculations, we recognize, however, that depending on the question of interest, one could examine $\Delta\lambda(t)$ values time-averaged over only a portion of transient time and the results might differ from when $\Delta\lambda(t)$ values were time-averaged over the entire transient period. Moreover, $\Delta\lambda(t)$ values will clearly converge on $\Delta\lambda_{\text{asymptotic}}$ as t approaches the year a SSD is reached. There is no convention for deciding exactly how close a stage distribution must be to the SSD to determine the 'end' of the transient period.

One of the drivers of differences between near-term projected population responses and those predicted at equilibrium

is the difference between the initial stage distribution and the SSD. Depending on how different these two distributions are, and which stages are over- or under-represented in the initial distribution, the magnitude and length of the transient dynamics can vary quite widely. This underscores the need to explicitly 'capture' the starting age or stage structure of the reference population, which could be done by using a sample distinct from the plants marked for long-term monitoring. Special efforts and techniques may be needed to estimate the abundances of cryptic life stages, such as the number of dormant seeds in the soil. In situations where quantifying the existing stage or age structure of a population is difficult (for example in conservation contexts), Townley *et al.* (2007) and Stott *et al.* (2010) outline a technique for calculating the outer bounds of transient dynamics without the need to know initial population structure.

Because insect herbivores affect only fecundity of *Cynoglossum* and *Calathea*, the changing elasticity of fecundity through the transient phase underlies the changes in $\Delta\lambda$. Thus, consumers that influence vital rates with low asymptotic elasticities can have potentially large transient effects on $\lambda(t)$ if transient elasticities of those vital rates are larger. Moreover, as illustrated for *Cynoglossum*, differences in demography between regions lead to differences in reproductive values and SSD (Fig. 2), which, in-turn, influence the predicted results of species interactions in new locations. Such regional differences in demography have been demonstrated for other species (Grigulis *et al.* 2001; Hyatt & Araki 2006; Jongejans *et al.* 2010).

One important feature of transient analyses is that until all stages are 'filled' (i.e. non-zero), observed transient effects are partly driven by the absence of some plant stages. Transient elasticities for vital rates that influence stages with 0 individuals will themselves be zero until those empty stages are filled. This was the case for our *Calathea* example, which started with a population comprised only of seeds, representing a population in a colonizing phase. This case is applicable and interesting for disturbance-driven species and for species invading a new range. At the edge of the wavefront, stage structure may differ considerably from that in the central part of the species' distribution and such differences are crucial to understanding the sensitivity of invasion speed to demographic parameters (Neubert & Caswell 2000). Thus, for *Calathea*, from time $t = 0$ to 3, dynamics are influenced by the fact that some stage classes are empty. Transient dynamics are not only influenced by the starting stage structure, but also by other 'context-dependent' effects. For example, in soil mites, maternal age can influence egg quality, with complicated effects on transient population dynamics (Plaiستow & Benton 2009). Such cross-generational maternal effects have been documented for plant-animal interactions (Agrawal, Laforsch & Tolrain 1999), but their population dynamic consequences have not been fully explored.

ASSESSING THE IMPACT OF SPECIES INTERACTIONS

One advantage of combining demography, experiments and population models is that it enables one to perform 'what if

exercises. While the impacts of particular management actions have often been inferred based on the elasticities of particular vital rates (Morris & Doak 2002), these exercises are less frequently applied to assessing the consequences of novel species interactions (but see Parker 2000; Shea & Kelly 2004; Davis *et al.* 2006). In our case, based on experimental results from the native range and demographic rates in the introduced range, we can investigate the potential impacts that the native specialist insect could have if introduced into North America as a biocontrol agent. Our results suggest insects that damage plants equally in the introduced range as in the native range would have similarly weak effects on this plant's population growth in the introduced range. A similar result was obtained when demographic data from two additional introduced populations and two additional years were included in the analyses (Williams, Auge & Maron 2010). An important caveat, however, is that here we make the key assumption that the negative effects of insects will be the same in the introduced and native range. This assumption would be incorrect if insects were substantially more damaging as biocontrol agents, either because they attained greater population numbers or because they influenced other vital rates besides fecundity.

What types of interactions might be suitable for studying with our approach? The interactions that would be easiest to quantify with this methodology would be those where a particular interaction only influenced a limited number of demographic transitions. Examples of these might include pathogens that only attack seedlings, pollinators that may only influence the probability of seed set, or post-dispersal seed predators that influence only the probability of a seed becoming a seedling. In these instances, a targeted experiment could quantify how an interaction of interest affected the relevant demographic transition. All other demographic rates could be estimated within unmanipulated 'control' or 'reference' populations, thus eliminating the need to collect a full set of demographic data on both 'control' and 'treatment' populations. It therefore potentially helps overcome what we suspect has been a major factor inhibiting ecologists from using these models to extend results from individual-level experiments, which is that an onerous amount of demographic data is required before matrix models can be employed.

Although experimental data on individuals can be profitably combined with demographic models to quantify interaction strength over transient or asymptotic time scales, it is important to realize that there are also inherent limitations in the approach we have outlined. In our examples, we found that experimental treatments affected one type of matrix element only and did not have covarying effects across the life cycle. As such, it was a straightforward exercise to alter a single type of matrix element and investigate the simulated population-level consequence using the matrix. However, there are many cases in which complex feedbacks occur between how an interaction influences one vital rate and how that altered vital rate in turn influences other vital rates in a plant's life cycle. These feedbacks can create covariation between vital rates that might be missed unless one collected a full set of demographic data from 'control' and 'manipulated' populations rather than control

and manipulated individuals. In such cases, the whole population is considered the experimental unit (as opposed to individuals) and the whole life table is the response variable. Any and all elements and their covariance could be altered by the experimental manipulation. Life table response experiments (LTREs) are used to find out how multiple parameters that responded to the experiment each contribute to observed variation in asymptotic λ between treatments. Covariation between vital rates is accounted for in these analyses (Caswell 2000; Van Tienderen 2000). Such an approach has been profitably used in cases where: (i) herbivores simultaneously influence multiple vital rates (Ehrlén 2003) and (ii) environmental factors, such as disturbance, interact with biotic interactions, like herbivory, to influence plant population growth (Eldred & Doak 2006). LTREs for transient analyses would certainly be interesting to pursue, but rather complex to present. At each time step, the contributions of each stage to population growth could change.

Other limitations of our proposed methods include the fact that they cannot capture cascading indirect effects that arise from an interaction. Long-term empirical experiments at the community level must be employed to capture indirect effects that propagate through a food web. Finally, the analyses we have outlined here employ density-independent models. However, perturbations of one vital rate by an interaction can often have complex effects on other vital rates, including changing the nature of density dependence. For example, if seedling herbivory reduces adult plant establishment, this reduction in adult density might lower future competition between adults and newly recruited seedlings (Kauffman & Maron 2006). Thus, density dependence could partially compensate for the negative impacts of an interaction. Although density dependence can in theory be incorporated into such models (Halpern & Underwood 2006; Kauffman & Maron 2006), the goal of such an approach would be to determine how an interaction influenced equilibrium population size as opposed to population growth rate. Moreover, in a density-dependent model sensitivities cannot be determined.

A general challenge in many demographic models is capturing spatial or temporal stochasticity in demographic rates (Boyce *et al.* 2006). Here, we have only used demographic data from a single year and either pooled data across sites (for *Calathea*) or used one site in the native and introduced range (for *Cynoglossum*). While we are interested in the importance of characterizing spatiotemporal variation in vital rates and single-stage effects of plant–animal interactions (Horvitz, Ehrlén & Matlaga 2010), such variability is not the focus of this paper. Our point here was to simply illustrate how, even with a constant demographic environment and a constant single-stage effect of animals, the strength of the effect of an animal on a plant population undergoes dynamics and even oscillations simply because of the inherent demographic transients in stage-structured populations. Methods for estimating stochastic transient sensitivities are currently in development (C. Haridas, personal communication) and a worthy future goal is to determine how various interactions influence plant transient dynamics in variable environments. Our primary goal here is

simply to introduce the idea that interaction strength can be estimated using experimental results, demography and population models and that one metric of interaction strength using this methodology ($\Delta\lambda(t)$) is dynamic. Just as with an empirical experiment, the demographic performance of plants during the years in which the experiment takes place will shape the real (or model-estimated) population response. The longer-term response will, of course, be influenced by longer-term temporal variation in vital rates, which may not be captured in a 4- or 5-year study.

The metrics of interaction strength we have discussed ($\Delta\lambda(t)$, $\Delta\lambda_{\text{asymptotic}}$ and $\Delta\lambda_{\text{transient}}$) all have a common currency. As such, they can be easily compared both among different types of interactions and for a particular interaction across ecological contexts. Although plants interact with many different competitors, mutualists and enemies, and although these interactions have been well studied, we still have remarkably limited insight into their relative importance in affecting plant population abundance or dynamics (Ashman *et al.* 2004; Howe & Miriti 2004; Maron & Crone 2006; Horvitz, Ehrlén & Matlaga 2010; Bricker, Pearson & Maron 2010). We see the combination of experiments, demography and population models as a complementary approach to classic longer-term enclosure studies and one that promises to make plant demography less of an observational endeavour and more experimental.

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Supporting Information

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

Appendix S1. MATLAB code for calculating transient elasticities.

Appendix S2. Stage projection matrices for *Cynoglossum* from one native (top panel) and one introduced (bottom panel) population.

Appendix S3, Fig. S1. Dominant and subdominant eigenvalues for *Cynoglossum* in the complex plane (top panel) native range, with and without insects and (bottom panel) introduced range, with and without herbivores.

Appendix S3, Fig. S2. Dominant and subdominant eigenvalues for *Calathea* in the complex plane (a) natural insects (b) without *Eurybia*, with ants, and (c) with *Eurybia*, without ants.

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