

Approaches for testing herbivore effects on plant population dynamics

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Summary

1. As plant invasions pose one of the greatest threats to biodiversity, it is critical to improve both our understanding of invasiveness and strategies for control. Much research into plant invasions and their management, including biological control, assumes strong demographic effects by natural enemies, including herbivores. However, the importance of natural enemies in the regulation of plant populations remains controversial: some ecologists contend that they rarely affect plant populations, and others that they can strongly limit plant population sizes.

2. We briefly review the conflicting views and suggest that new approaches to gather and analyse data are needed before the effects of natural enemies on plant populations can be fully characterized.

3. We outline experimental and analytical approaches that incorporate density dependence into population models and thus provide a more complete test of the long-term effects of natural enemies on plant populations. We also introduce new methods for obtaining stochastic estimates of equilibrium density, which will provide a key test of enemy effects on plant population size.

4. *Synthesis and applications.* Designing effective strategies for invasive plant management requires information about the factors that limit plant population size. Together, the experiments and analyses we describe measure more clearly how natural enemies influence plant population dynamics. They will provide an important tool in evaluating the role of enemy release in plant invasions and for predicting the potential success of biological control. Such information should help to prioritize strategies that are most likely to control invasive plants effectively and will contribute to risk assessment when considering the release of non-native natural enemies as biological control agents.

Key-words: biological control, carrying capacity, density dependence, enemy-release hypothesis, invasions, matrix population models, plant–herbivore interactions, population regulation

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Introduction

Understanding the factors that determine population size is a long-standing problem in plant ecology that has important applications for the management of invasive

and weedy species. Extensive evidence supports the important role of resource competition in plant populations. For example, both resource availability and plant density have strong effects on plant population dynamics (Gustafsson & Ehrlén 2003) and performance (reviewed by Harper 1977; Silvertown & Doust 1993), especially during recruitment (Silva Matos, Freckleton & Watkinson 1999; Goldberg *et al.* 2001; Gustafsson & Ehrlén 2003; Blundell & Peart 2004).

The relative importance of natural enemies in plant population dynamics is more controversial (Maron & Crone, in press). Although many plant ecologists

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hold that competition is the dominant factor regulating plant population size (reviewed by Harper 1977; Silvertown & Doust 1993), a long history of fundamental (Janzen 1970; Connell 1971; Louda 1982, 1983; Clark & Clark 1984; Brown & Heske 1990; Silman, Terborgh & Kiltie 2003) and applied (reviewed by Harper 1977; Maron & Vilá 2001; Keane & Crawley 2002; Colautti *et al.* 2004) research is founded on the assumption that natural enemies can strongly suppress or regulate plant populations. For example, the practice of biological control is based on the assumption that natural enemies are important in suppressing plant populations in the native range (DeBach & Rosen 1991) and successful examples of biological control have been cited as evidence that natural enemies can strongly regulate plant populations (Harper 1977; but see caveats in Crawley 1989). Likewise, the enemy-release hypothesis argues that a lack of herbivores and pathogens in the introduced range accounts for the higher population size and density of invasive plants in the introduced than in the native range (reviewed by Maron & Vilá 2001; Keane & Crawley 2002). Again, this hypothesis is based on the assumption that natural enemies are responsible for substantially depressing or regulating plants in their native range, but this assumption is rarely tested. Note that population regulation occurs when the probability distribution of population densities through time is stationary (Turchin 1995), in other words when a population tends to return to a carrying capacity, K , rather than growing without bound or deterministically going extinct (Murdoch 1994).

Determining how often natural enemies do limit plant populations is of central importance to understanding the role of enemy release in plant invasions and to evaluating the potential success of biological control. We argue that prior tests of the effects of natural enemies on plant population dynamics are insufficient because they ignore two key issues in population dynamics: scaling up to population-level effects and incorporating density dependence. We briefly review these two issues, propose a combination of experimental and modelling approaches that would provide a more complete test of natural-enemy effects on plants, and describe the data and analyses needed to implement these methods. We focus on insect herbivores, but the ideas and approaches generalize to other natural enemies (such as pathogens).

Issue 1: scaling from individual responses to effects of herbivores on entire plant life cycles

Herbivory can strongly influence individual plant growth, survival and reproductive success (reviewed by Crawley 1989) but the effects on individual plants do not necessarily correspond to effects on plant populations. For example, changes in individual plant performance may alter population size and growth when seeds are limiting but are less likely to do so when safe germination sites are limiting (Louda & Potvin 1995; Maron & Gardner 2000; Bonsall, van der Meijden &

Crawley 2003). Estimating population-level effects of herbivory requires scaling up from individual plant responses to population changes over time, by means of either models or long-term series of data.

A few studies have estimated population-level effects of herbivores (including seed predators) experimentally. In several well-studied systems, the removal or addition of herbivores has substantially altered plant population densities. In the short term, experimentally excluding seed predators has led to higher population densities in the next generation in several perennial asters (*Asteraceae*) and legumes (*Fabaceae*) (Louda 1982, 1983; Louda & Potvin 1995; Maron & Simms 1997; Maron, Combs & Louda 2002). Long-term plant densities have also changed in response to herbivory. For example, Silman, Terborgh & Kiltie (2003) observed increases in *Astrocaryum murumuru* density during a decade-long local extinction of a major seed predator, and subsequent decreases when the predator recolonized the site. Similarly, changes in sea-urchin (*Strongylocentrotus* spp., *Diadema antillarum*) density have had enormous effects on algal densities in kelp forests and coral reefs (Estes & Palmisan 1974; Lessios 1988; Estes & Duggins 1995). Insects released for biological control of invasive plants have successfully reduced the population size and density of the target plants in a few well-known cases (reviewed by Harper 1977; Keane & Crawley 2002), such as that of *Cactoblastis cactorum* feeding on *Opuntia* spp. in Australia. However, biological control involves herbivores outside their native range, where they may be released from natural enemies and possibly competitors as well (Crawley 1989). Biological control examples may therefore exhibit herbivore effects stronger than those on plant populations in natural systems.

In addition, some recent studies have used density-independent matrix population models to estimate the effects of herbivores on the full plant life cycle and plant population dynamics. In these studies, herbivory often reduces predicted population growth (usually measured as the finite rate of increase, λ), although not always to the value of $\lambda < 1$ necessary for populations to decline (Bastrenta, Lebreton & Thompson 1995; Ehrlén 1995; Shea & Kelly 1998; Fagan & Bishop 2000; Parker 2000; Bishop 2002; Horvitz & Schemske 2002; Rooney & Gross 2003; Knight 2004; McGraw & Furedi 2005).

Issue 2: incorporating density dependence

Although density-independent factors can depress a population's rate of increase, only density-dependent factors can regulate population size. Therefore, answering questions about whether and how herbivores regulate plant populations requires accounting for density dependence. Plant density often has important effects on plant–herbivore interactions. For example, both herbivore damage levels (Root 1973; Turchin 1988; Kunin 1999; Shea *et al.* 2000; Sullivan 2003; reviewed by Rhainds & English-Loeb 2003) and the effects of damage on plants (Hartnett 1989; Parmesan 2000) can

vary with plant density. In addition, changes in damage levels across abiotic or successional gradients have been correlated with variation in plant population size or density (Louda 1982, 1983; Fagan & Bishop 2000; Maron, Combs & Louda 2002).

With some recent exceptions (Rees & Paynter 1997; Rees & Hill 2001; Buckley *et al.* 2005; Rose, Louda & Rees 2005), studies that have used models or long-term data sets to test herbivore effects at the scale of plant populations have not explicitly incorporated density dependence into their analyses, nor have they evaluated how herbivores affect plant density dependence. Similarly, although many plant ecologists have studied density dependence, and some have included density effects in population models (see examples below), no studies have used density-dependent population models to compare the relative importance of herbivory and competition in plant population dynamics. Because the long-term dynamics of a plant population will be determined by both density-independent and density-dependent factors, characterizing density dependence is crucial to an understanding of longer-term plant population dynamics (Bierzychudek 1999; Freckleton *et al.* 2003), including effects of herbivores on plant populations. Therefore, even the best studies to date cannot address directly how herbivores contribute to regulating plant populations.

Even with density-independent models, some aspects of density dependence can be explored through the use of a well-known set of tools, including elasticity analysis and life table response experiments (LTRE), to compare populations across a density gradient. For example, sites that differed naturally in plant density differed in the effects of herbivores on λ for both a native (Fagan & Bishop 2000) and an exotic (Parker 2000) species, suggesting that plant population responses to herbivory are density dependent.

The most powerful method for characterizing density dependence, however, would measure demographic parameters across a range of experimentally manipulated densities (Harrison & Cappuccino 1995; Fowler, Overath & Pease 2006). Functions describing how these parameters change with density can be incorporated into density-dependent matrix population models. These models allow a complete description of population dynamics, including population growth, regulation and equilibrium behaviour, although not all types of analyses available for density-independent matrices (e.g. LTRE) are possible. Integral projection models are an alternative framework for using experimental data to examine the role of density dependence in interactions between plants and natural enemies (see below; Easterling, Ellner & Dixon 2000). Although density-dependent plant population models are less common, they have led to important insights about which life-cycle stages make the greatest contribution to population growth (Stokes, Bullock & Watkinson 2004) and how different harvest (Freckleton *et al.* 2003) or control (Taylor & Hastings 2004) strategies affect plant population dynamics.

Analysing time series from plant populations exposed to different densities of herbivores is an alternative approach because model fitting can be used to examine both population growth and density dependence in time-series data. Time series are rarely long enough for robust tests, however, and are even more rarely replicated across different environments, such as herbivore treatments. Furthermore, methods for examining density dependence in time-series data other than model fitting, such as autocorrelation analyses, have been controversial (reviewed by Turchin 1995). Finally, relatively long time series still may not detect density dependence even when it is acting strongly in a system (Fowler, Overath & Pease 2006).

Methods

ASSESSING THE INFLUENCE OF HERBIVORES ON PLANT POPULATION DYNAMICS

We suggest that a combination of manipulative density experiments and structured matrix population models will provide better tests of herbivore effects on plant populations. Together, these approaches can answer questions such as (i) whether the demographic transitions that contribute most to plant population regulation change in the presence of herbivores, (ii) how herbivores affect the strength of density dependence in a plant population, and (iii) whether herbivores can change a plant population's equilibrium density. They will also allow direct tests of assumptions about how herbivores affect plant population dynamics, as well as an evaluation of the relative importance of herbivory and competition in regulating populations of plants. For specific problem plants, these methods can help determine whether natural enemies released for biological control are likely to have the desired effects on plant population size over the long term. We have focused on the effects of herbivores in general on plant population dynamics; studies characterizing both plant and herbivore population dynamics would be useful for plants with narrow specialist herbivores (as in biocontrol) to address additional questions such as the stability of the interaction (Buckley *et al.* 2005).

EXPERIMENTAL DESIGN

The data for the population models should come from factorial experiments that manipulate both herbivore and plant densities. Although they are labour-intensive, density manipulations add the strengths of an experimental approach (i.e. decoupling factors, clear causality) to the matrix models' ability to project long-term population dynamics. A minimum of two different plant densities is necessary to reveal whether density has an effect, and a minimum of three densities would be necessary to reveal whether or not this effect is linear; five levels of plant density balance the ability to distinguish non-linear from linear density functions with diminishing

returns on effort (B. Inouye, unpublished data). The minimum number of herbivore densities would be two: present and absent. Additional herbivore densities would permit description of density functions for herbivore effects but are likely to lead to prohibitively large experiments when crossed with multiple plant density levels. For each combination of plant and herbivore densities, standard demographic data would be needed on the growth, survival and reproduction of individual plants in different age or stage classes (Caswell 2001). The necessary level of replication within and among treatments will vary with the experimental system.

The measure of plant density is an important choice in the design of such an experiment. Most commonly, population density has been measured as the number of individuals, sometimes divided among different size or age classes, but phenomena such as self-thinning, compensatory growth and the resulting changes in plant architecture may decouple individual numbers from density dependence. For example, Parker (2000) found that estimated biomass was a much better surrogate for plant density than number of individuals for *Cytisus scoparius*. If alternatives to individual counts (such as percentage cover or biomass) are found to be better density measures, transition matrices can be based on these alternative measures (Tanner 1999).

ANALYSING STRUCTURED MATRIX POPULATION MODELS

When both density-independent and density-dependent matrix population models are employed, the data from this factorial experiment can answer several questions about herbivore effects on plant populations (Fig. 1). Matrix population models have the general form $N_{t+1} =$

AN_t , where N_{t+1} and N_t are vectors of individuals in each stage, A is a matrix of transitions between stages (survival and growth rates and fertilities) and N_t is the total population size at a given time step (sum of the elements of N_t). Integral projection modelling, which treats plant size as continuous or piecewise continuous instead of using discrete size classes (Easterling, Ellner & Dixon 2000), is a related alternative approach that has some advantages, including requiring fewer parameters (for a directly relevant example see Rose, Louda & Rees 2005) and the ability to incorporate density easily as a covariate in survival growth or fecundity functions. Analyses analogous to some of those described below have been developed in an integral projection model framework (Childs *et al.* 2004) and others can be applied as they become available (Ellner & Rees 2006).

For both density-independent and density-dependent models, the first step in analysis is constructing the population matrix, A . For density-independent models, matrices of fixed demographic transition probabilities and fecundities should be calculated separately for each combination of plant and herbivore densities (Caswell 2001). Constructing density-dependent matrix models is a two-stage process. The first stage involves identifying demographic transitions that respond to plant density. The data for these analyses are the fixed probabilities and fertilities from the density-independent matrices for each plant density–herbivory treatment combination (Tanner 1999). Linear and non-linear density-dependent and density-independent functions can be fitted to these data by maximum likelihood and the best-fitting function identified with the Akaike information criterion (Burnham & Anderson 1998). Note that when transition probabilities are a function of the numbers of plants in particular stages rather

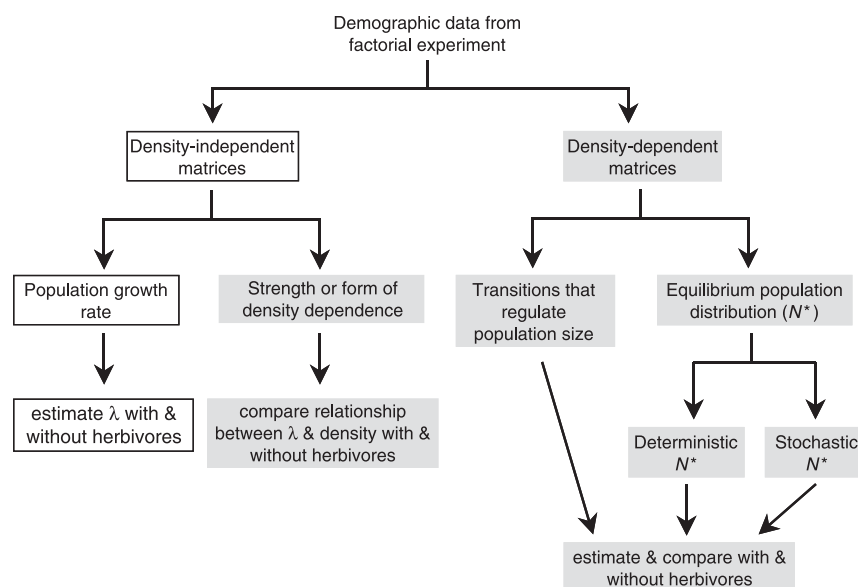


Fig. 1. Flow chart of analyses using data from a factorial experiment manipulating plant and herbivore densities. Analyses in shaded boxes account for density dependence; those in white boxes do not. λ is population growth rate; N^* is equilibrium population density.

than of total density, the density functions in the matrix can reflect that observation (Freckleton *et al.* 2003). The second stage involves incorporating these density functions into a stage-structured matrix and analysing the population dynamics this model predicts. When density influences a transition, fixed probabilities or fertilities are replaced by the best-fit functions (Morris & Doak 2002). When density does not influence a transition, the matrix entry remains a fixed probability or fertility, estimated as the mean probability or fertility across all densities. These calculations result in a single density-dependent matrix for each herbivory treatment composed of a mixture of fixed probabilities and density functions. If the experiment is maintained for multiple years, density-dependent transitions and matrices from each year can be constructed for use in stochastic population projections (Caswell 2001).

Herbivores may affect both population growth rate (λ) and density dependence. Because most demographic studies have focused on measuring population growth rates, we will not discuss those analyses in depth here. Briefly, a deterministic λ can be estimated by numerical methods as N_{t+1}/N_t for any particular time step for both density-dependent and density-independent matrices, or as the eigenvalue of **A** once **N**_{*t*} has reached the stable-stage distribution for density-independent matrices (Caswell 2001). A stochastic λ , which takes into account temporal variation in population growth rate, can also be estimated if some measure of temporal variance in transition rates is available (Caswell 2001; details below).

The effect of herbivores on plant population dynamics can be examined in several ways. Below we focus on three specific questions.

DO THE TRANSITIONS THAT CONTRIBUTE MOST TO PLANT POPULATION REGULATION CHANGE IN THE PRESENCE OF HERBIVORES?

For matrix models that incorporate density dependence, a simulation approach can reveal which transitions contribute to population regulation (Tanner 1999). These simulations measure the effect of removing density dependence from a single transition (i.e. replacing a density function with a fixed probability) on the predicted population dynamics. If the replacement leads to a continuously growing population, density dependence in that transition is critical for population regulation (Tanner 1999). Using data from experimental manipulations of plant and herbivore densities (described above), these simulations can identify regulating transitions at different herbivore densities. Differences in the identity of these important transitions between populations with and without herbivores would be evidence that herbivores change the form of density dependence (and thus population regulation) operating in the system.

Although these analyses alone will not directly estimate herbivore effects on plant population size, they can provide information about whether herbivores

affect the mechanism of population regulation. They also might suggest target stages for management in both the presence and the absence of herbivores.

HOW DO HERBIVORES AFFECT THE STRENGTH OF DENSITY DEPENDENCE IN A PLANT POPULATION?

One way to estimate the strength of density dependence is to use density-independent models to examine the relationship between instantaneous population growth rate (λ) and density (Agrawal, Underwood & Stinchcombe 2004). This relationship can be characterized from estimates of λ across an experimental plant-density gradient. This approach involves calculating a separate stochastic or deterministic λ for populations at each density, plotting λ against density separately by herbivore treatment, and fitting linear or non-linear relationships to these points. Likelihood-ratio tests can be used to determine whether populations with and without herbivores differ in the parameters describing slope or curvature across densities. Differences in these parameters would provide evidence that herbivory affects the strength or form of density dependence.

This analysis has the advantage of allowing an examination of herbivore effects on density dependence without parameterization of a full density-dependent matrix model, which could provide preliminary information for management of plants using natural enemies. This approach has limitations, however, because the relationship between λ and total population density is likely to be non-linear when density dependence acts differently for different life stages, even when density dependence is linear for any particular transition. Consider, for example, the simplest case of a two-stage population model with a single transition that changes with density:

$$\begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_{t+1} = \begin{pmatrix} a & b \\ c & d \end{pmatrix} \begin{pmatrix} n_1 \\ n_2 \end{pmatrix}_t$$

For this model,

$$\lambda = N_{t+1}/N_t = (an_{1,t} + bn_{2,t} + cn_{1,t} + dn_{2,t})/(n_{1,t} + n_{2,t})$$

If fecundity (b) is a function of density $f(n_{1,t}, n_{2,t})$, then

$$\lambda = [(a + c)n_{1,t} + (f(n_{1,t}, n_{2,t}) + d)n_{2,t}]/(n_{1,t} + n_{2,t})$$

Note that a quadratic term in the numerator [$n_{2,t}^2$, arising from the product of $f(n_{1,t}, n_{2,t})$ and $n_{2,t}$] creates non-linearity in the relationship between λ and total population density ($n_1 + n_2$) even when the density function for this particular transition is linear. Simulations (see Appendix S1 in the supplementary material) suggest that the non-linearity increases in magnitude if the density function itself is non-linear (see Fig. S1 in the supplementary material). Such non-linearity seems likely to be generated in most cases

where density dependence does not act the same way in all life stages.

This result has two implications. First, it emphasizes the difficulty of extrapolating from components of the population cycle to overall population dynamics. In this case, density effects may be linear in a single life-history stage but change to non-linear in overall population dynamics, so extrapolations from the former would be incorrect. This result provides additional evidence that effective management based on an understanding of the target's population dynamics will require information on the complete life cycle (Fowler, Overath & Pease 2006). Secondly, it argues for caution in a possible extension of the analysis of density-independent matrices across densities. Because population size will not change at equilibrium, the density at which $\lambda = 1$ could provide an estimate of equilibrium density and could be estimated from a linear fit of λ vs. density. The expectation that this relationship is non-linear means, however, that a linear fit would result in an inaccurate estimate of equilibrium density, especially if the empirical values of λ do not bracket 1 or if estimates of λ have high variance.

DO HERBIVORES CHANGE A PLANT POPULATION'S EQUILIBRIUM DENSITY?

By definition, when populations are regulated by any factor, an equilibrium population distribution (*sensu* Turchin 1995) or carrying capacity exists. Because populations cannot increase infinitely, a carrying capacity will exist for a plant population even in the absence of herbivores. If herbivores contribute to regulating plant populations, however, they should reduce the plant's equilibrium population density (N^*). Determining whether herbivores affect N^* is therefore the most important step in trying to understand the role of herbivores in plant population regulation generally and the role of enemy release in plant invasions specifically.

Density-dependent matrices can be used to determine the effect of herbivores on plant N^* in both deterministic and stochastic contexts. A deterministic N^* can be found by iteration of a density-dependent matrix until the population size reaches equilibrium (Alvarez-Buylla 1994; Tanner 1999; Freckleton *et al.* 2003) or, in rare cases, N^* might be found analytically (Caswell 2001). To our knowledge, previous studies using density-dependent matrices have not calculated a stochastic version of N^* (carrying capacity) but incorporating temporal changes in N^* should be possible by techniques analogous to those used to estimate stochastic λ from density-independent matrix models. For reference, stochastic λ can be obtained in several ways (Tuljapurkar 1997; Tuljapurkar, Horvitz & Pascarella 2003). One common approach is to create a separate matrix for each year (or other temporal partition) and then to use simulations that randomly select among these matrices for each iteration to estimate a long-term stochastic growth rate (Tuljapurkar 1997; Pascarella & Horvitz 1998;

Tuljapurkar, Horvitz & Pascarella 2003). Alternatively, the data from different years can be used to construct a single matrix with probability distributions around each vital rate or transition (Morris & Doak 2002). Each iteration of the model then draws transitions or vital rates from appropriate probability distributions. Each of these methods has strengths and weaknesses (for discussions see Morris & Doak 2002; Tuljapurkar, Horvitz & Pascarella 2003).

We suggest using analogous methods to calculate stochastic N^* . As with estimating stochastic λ from a density-independent matrix, one could construct either separate matrices for each data partition (e.g. year) or a single matrix with probability distributions surrounding each transition probability or function. Stochastic N^* would then be estimated by drawing a new matrix at each time step and continuing this process until a stationary equilibrium distribution has been reached. The long-term stationary equilibrium distribution could be summarized by its probability distribution [e.g. mean (the stochastic N^*) and its variance or confidence intervals]. Comparing these distributions of N^* among populations with different herbivore densities would test the effect of herbivores on plant N^* . A tempting third method for estimating a stochastic N^* would be to use simulations to find the deterministic equilibrium population density of matrices from different years. The stochastic N^* could then be estimated as the average value of the equilibria for these matrices, and the variance could also be estimated for significance tests. The geometric process of population growth means that this method of averaging the equilibria of temporally static models, although simpler to implement than having matrices change over time, is likely to be incorrect, just as averaging λ across density-independent matrices is not an appropriate estimate of stochastic λ (Caswell 2001).

In either the deterministic or the stochastic context, a decrease in N^* in the presence of herbivores is strong evidence that herbivores contribute to regulating plant population size. The advantage of the stochastic over the deterministic approach is that it provides a mechanism for testing the significance of the decrease in N^* . In application, the magnitude of the decrease offers information on the probable role of enemy release in a particular plant's invasiveness or on the likely success of biological control.

Discussion

Effective management of invasive species requires better information about the demographic consequences of potential control strategies. The experimental and analytical approaches we describe would provide powerful, more complete tests of the effect of one strategy (natural enemies) on plant population dynamics by addressing the question at an appropriate scale (long-term dynamics of populations) and incorporating the critical biological reality of density dependence.

The approach is challenging, requiring analyses that are computationally intensive and experimental density manipulations that are time and labour intensive, but we believe the challenges are worth facing for two reasons. First, using this approach will help provide answers to important empirical questions, including the long-standing controversy over the relative importance of herbivores in plant population dynamics. Secondly, the results of such analyses will provide vital information needed for management of plant invasions. This information would improve general understanding of the role of natural enemies in plant invasions. It could also be used in specific cases to predict better the likelihood of success if biological control agents are introduced. Such information could help balance the costs (i.e. risks of host switching) and benefits (i.e. control) of this important but controversial management strategy.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>.

Appendix S1. Simulations.

Figure S1. Density and lambda.