

A proposal to use plant demographic data to assess potential weed biological control agents impacts on non-target plant populations

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Abstract Weed biocontrol programs aim to reduce the spread and population growth rate of the target plant while stabilizing or increasing populations of those native species considered under threat by invasive plants. This goal is not unique to weed biocontrol but applies to all other invasive plant management techniques, though such information is rarely collected. Without this information, success of management interventions can be ambiguous, and regulatory agencies, the public, policy makers, funders and land managers cannot be held accountable for chosen treatments. A fundamental reform, including use of demographic studies and long-term

assessments, are essential to guide weed biocontrol programs. We propose to add use of plant demography (an assessment of how environmental factors and ecological interactions, for example competition, disease or herbivory, may affect plant populations by altering survival, growth, development and reproductive rates of plant individuals) during host specificity risk assessments of potential biological control agents. Demographic models can refine assessments of potential impacts for those plant species that experience some feeding or larval development during host specificity testing. Our proposed approach to focus on impact on plant demography instead of attack on plant individuals is useful in appropriately gauging threats potential weed biocontrol agents may pose to non-target species after field release.

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Introduction

Biological weed control programs aim to find organisms able to reduce spread and population growth rate of target plants, while avoiding non-target impacts. The track record of weed biocontrol over the past century is decidedly mixed, since only a third of all weed biocontrol programs achieve at least partial

suppression of targets (Crawley 1989; Fowler et al. 2000; Moran et al. 2005). Many biocontrol agents fail to establish, or fail to control host plants (Crawley 1989; McFadyen 1998). On the other hand, while occasionally contested, the safety record of weed biocontrol is superior to other management methods, while economic and ecological benefits can be enormous and continue to accrue (Moran et al. 2005; Suckling and Sforza 2014).

Following publications of high profile cases of non-target attack by *Rhinocyllus conicus* Frölich (Curculionidae) and *Cactoblastis cactorum* Berg (Pyralidae), respectively, changes in decision making processes in regulatory agencies, particularly in the USA, shifted to a greater reliance on fundamental host-range data, a change that further threatens release even of highly specific agents (Hinz et al. 2014). The irony of this change in risk perception is that specific and successful agents of the past would have difficulties passing through current approval processes (Groenteman et al. 2011; Hinz et al. 2014). At a time when it is becoming increasingly evident that many invasive species control methods, particularly chemical management, are unable to achieve lasting control and may in fact threaten non-target species (Kettenring and Adams 2011; Pearson et al. 2016), we argue that it is time for fundamental reform of risk assessment and decision making processes in invasive plant management and weed biocontrol that is guided by appropriate scientific information and open dialogue, not fear (Blossey 2016b).

We propose that adoption of modern scientific tools focusing on demographic impacts of herbivores could constitute a breakthrough development in maintaining safety while increasing the ability to select effective herbivores. We consider it paramount to shift non-target risk assessments away from damage to individuals to population level effects expected after field releases. We envision that traditional reductionist approaches (no-choice, small herbivore confinements, followed by multiple-choice or potted plant experiments) will continue to be the mainstay of host specificity testing. These tests are valuable because the vast majority of test plant species will not be attacked even under constrained conditions (Fig. 1). However, in many programs often a few test plant species remain that may be fed upon, are accepted for oviposition, or even allow larval development (albeit at a greatly reduced rate compared to original host plants) by

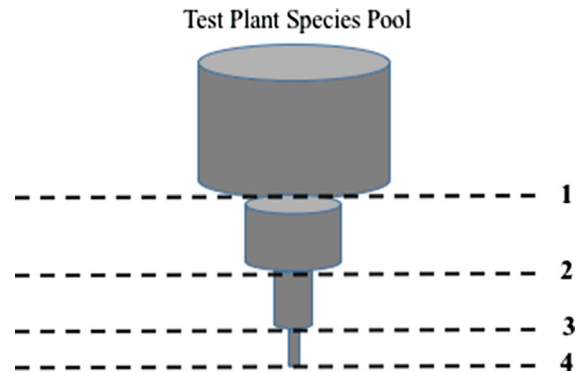


Fig. 1 Schematic design of typical proposed host specificity testing protocol for potential weed biocontrol agents. Depending on life history and feeding mode of the herbivore under consideration, test conditions may vary. Pool 1 includes all plant species proposed for host specificity testing that are tested using highly constrained no-choice conditions (Screen 1). Those species that could not be eliminated in the first screening step constitute pool 2 which are tested using more sophisticated designs, such as multiple-choice tests using potted plants or larger cages (screen 2). Species in pool 3 include plant species that were still attacked under the more sophisticated test conditions, or where larvae completed development. Tests utilized during screen 3 depend on herbivore feeding niches and logistical and regulatory considerations but include use of common gardens, multiple choice tests without containment, etc. Only those species that were still attacked under the most realistic conditions possible in a particular program would then be considered candidate species for demographic analyses (screen 4). Note that the pool of species shrinks with each test, while the realism of testing conditions and their ecological relevance increases

highly specific herbivores. We propose to utilize plant demography (an assessment of how environmental factors and ecological interactions, for example competition, disease or herbivory, may affect plant populations by altering survival, growth, development and reproductive rates of plant individuals) (Salguero-Gomez et al. 2015) to assess potential threats of candidate biocontrol agents to non-target species. This approach aims to provide a means by which to evaluate potential impacts to non-target plant populations. Our proposal constitutes a significant shift in the way weed biocontrol researchers, review panels and others may look at the approval and risk assessment process—but it is a scientifically valid and biologically meaningful one. We are not concerned by host use but by negative impacts to populations of non-target species. This is not a reduction in protections afforded to native species as it continues to safeguard all native species or valuable introduced species that

have attained cultural, ornamental or agricultural significance. We argue that to “safeguard” means that populations of non-target organisms are maintained and do not suffer demographic declines due to biocontrol agent introductions. Cosmetic damage or even substantial damage to, or death of, individuals does not necessarily indicate demographic or ecological consequences.

The shift we propose will find resistance based on risk perceptions regarding safety of non-target plants due to concerns that herbivores introduced to control introduced plants will (1) attack (rare) native species leading to declines in populations of these species; and (2) that diet restriction (i.e. specificity) of weed biocontrol agents are “fluid” and change over time, leading to attack and unintended negative consequences for native species. We will briefly review evidence for these concerns before further developing our proposal to use demography in host specificity risk assessments. However, we first provide a primer on terminology used to describe plant–herbivore interactions because we believe that some differences in perceived risk perception are semantic.

Terminology used in describing plant–herbivore interactions and weed biocontrol programs

Ecologists typically refer to diets of herbivores using terms like specialists or generalists (Smilanich et al. 2016) or more specifically monophagous (feeding on a single or few species within a genus), oligophagous (utilizing several plant species, typically in different genera), and polyphagous (using different plant species in different genera and families) (Bernays and Chapman 1994). In contrast, weed biocontrol researchers typically focus on herbivores using a single plant species. Furthermore, “use” in the ecological and evolutionary literature typically refers to plants chosen for oviposition and allowing larval development in the field, recognized as realized host range in weed biocontrol. Experimental host-specificity testing aims to (1) elucidate the fundamental host range (plant species acceptable for feeding, oviposition and larval development using no-choice tests in the absence of the original host), and (2) provide additional data using less constrained and increasingly ecologically realistic testing procedures to allow forecasting of realized host ranges. Realized field host

ranges are always narrower than experimentally determined fundamental host ranges.

Evidence for threats of weed biocontrol agents to (rare) native plant species

Reports of weed biocontrol agents attacking non-target species do exist, including spillover events with substantial temporary defoliation of non-target species (Blossey et al. 2001; Louda et al. 1997, 2003; Paynter et al. 2008; Pemberton 2000; Suckling and Sforza 2014). Comprehensive reviews assessing weed biocontrol outcomes (Blossey et al. 2001; Suckling and Sforza 2014), conclude that > 90% of all biocontrol agents never attack non-target species. The majority of non-target feeding is attributed to spillover events and Suckling and Sforza (2014) report such attacks on 128 non-target plants. Host specificity testing appears unable to predict identity of these species, but physical proximity may explain some of it (Blossey et al. 2001).

However, occasional or prolonged host use appears highly predictable using fundamental host range data (Paynter et al. 2015). Fewer than ten biocontrol agents have established populations on non-target species, a risk that was known, and accepted by regulatory agencies, at time of their introduction (Blossey et al. 2001). Of these, only three, *R. conicus*, *C. cactorum* and *Trichosirocalus horridus* (Panzer) (Curculionidae) may have effects that reduce populations and growth rates of non-target species (Louda et al. 1997; Suckling and Sforza 2014; Takahashi et al. 2009). None of these herbivores would be approved under current decision making frameworks (McFadyen 1998; Suckling and Sforza 2014).

Detailed documentation of non-target plant species occasionally attacked by biocontrol agents offer assurances that significant non-target effects have not gone unrecognized or unreported—in this case absence of evidence indicates evidence of absence of such effects and not just lack of effort. A recent literature survey of threats by insect herbivores to rare plants concluded that with exception of *R. conicus* and *C. cactorum*, “currently this threat is either seldom realized (perhaps because of extensive pre-release screening in modern biocontrol programs) or else seldom documented” (Ancheta and Heard 2011).

Lack of evidence for evolution of dietary preferences in weed biocontrol agents

Permitting processes for biocontrol agent releases may differ widely among countries (Sheppard and Warner 2016), but host specificity tests are widely standardized (Wapshere 1974). Despite further refinements proposed and implemented in subsequent years (Briese 2005; Clement and Cristofaro 1995; Sheppard et al. 2005; USDA 2016), this sequence of testing has largely remained state-of-the-art, providing overwhelmingly safe weed biocontrol agents. There is no evidence that fundamental host ranges of biocontrol agents have evolved (Arnett and Louda 2002; Marohasy 1996; Paynter et al. 2004; Sheppard et al. 2005; van Klinken and Edwards 2002), despite dire warnings (Simberloff and Stiling 1996). There is, however, evidence for evolution of improved performance on non-target plants (McEvoy et al. 2012) and we acknowledge that few formal assessments have been made.

However, occasional use, even if predicted, of species that are not targets of weed biocontrol, and frequent citation of the few species with anticipated large negative impacts, appears to be registered by non-biocontrol scientists as evidence for a poor track record and evolutionary malleable diet breadth of insect herbivores used in weed biocontrol. We argue that the problem arises due to the disconnect between perception of labile or rapidly evolving host ranges in weed biocontrol agents and available evidence. Weed biocontrol researchers have increased efforts to improve testing procedures to mitigate constraints of laboratory conditions that affect insect behavior to improve predictions of realized host ranges (Clement and Cristofaro 1995; Fowler et al. 2012; van Klinken and Edwards 2002). While such improvements are essential to increase reliability of predictions regarding realized host ranges, the focus on improving testing conditions appears to have prevented a discussion among scientists and regulatory agencies regarding the appropriate meaning of safeguarding other species (Hinz et al. 2014).

Clearly, diets of insect herbivores change over time and both generalists and specialists may acquire new hosts (Futuyma and Agrawal 2009). Range expansions through human aided introduction of novel plants or insects provide enormous ecological and evolutionary opportunities for herbivores to adopt new hosts.

Species accumulation curves on novel host plants plateau in approximately 100 years for generalists and 500–10,000 years for specialists (Bernays and Graham 1988). However, the vast majority of phytophagous insects show “phylogenetic conservatism” retaining their association with plant taxa over millions of years with < 10% of speciation events including a shift to a different plant family (Winkler and Mitter 2008). Biocontrol agents passing through host range testing, as far as we can tell from decades of observation and study, appear particularly “conservative”.

We now return to our argument that use of demographic models should be a desired and required tool during risk assessment of biocontrol agents. We are not the first to propose such new tools (Louda et al. 2005a; Raghu et al. 2006; Sauby et al. 2017), although we believe we are the first to ask that this becomes part of pre-release risk assessments. We will briefly introduce concepts of demographic modeling and then provide examples how demography has, and can be utilized in weed biocontrol. To the best of our knowledge, no biocontrol program has used demographic information to assess risks to non-targets before field releases, so we will rely on post-release analyses and a hypothetical scenario involving a current target of biocontrol research, water chestnut, *Trapa natans* L. (Lythraceae) to illustrate our proposal.

Using demography to evaluate biocontrol agent risks to non-target plants

Demography and matrix population models (Caswell 2001) are now common tools in biology (Caswell and Salguero-Gomez 2013) and their use in invasion biology and weed biocontrol is increasing (Carvalho et al. 2008; DeWalt 2006; Eckberg et al. 2014; Kerr et al. 2016; McEvoy and Coombs 1999; Shea and Kelly 1998; Swope et al. 2017). Technical background is provided elsewhere (Caswell 2001; Caswell et al. 2011; Caswell and Salguero-Gomez 2013; Williams et al. 2001), but briefly development of demographic models requires estimating vital rates, the transition probabilities from one life stage to another. For plants with clear developmental stages, a stage-based model requires estimation of transitions from seed, to seedling, to rosette to flowering plant, to seed output,

back to seed and seed bank (Davis et al. 2006; Shea and Kelly 1998). Local abiotic conditions, competition, herbivores, stochasticity, density dependence and other processes may affect survival and the probability that an individual will transition from one stage to the next. Vital rates can be inferred in the field by monitoring cohorts of marked individuals.

Demographic models can aid in assessments of potential impacts of proposed biocontrol agents on non-target plants that could not be excluded using traditional testing sequences (Fig. 1). We propose use of experiments, for example by manipulating herbivore access or attack rates and then measuring stage specific reductions in survival, recruitment, growth, biomass, or seed output of non-target plants, which can be done in common gardens, or other confinements when insects are not approved for release. Constructing and populating models with data, and analyzing model performance under different scenarios (often referred to as perturbation analysis) allows comparisons of contributions made by different vital rates for overall population growth rates (Caswell 2000). The outcome of these exercises is the ability to forecast population growth rates (λ), population fluctuation and potential extinction risk, and the sensitivity of growth rates to small changes in vital rate values, regardless of which management action is applied (Kerr et al. 2016). We recognize that demographic approaches during evaluation of potential biocontrol agents will have to contend with many different obstacles, the smallest among them may be lack of familiarity of biocontrol scientists with demographic modeling (Blossey 2016b). But this is a small price to pay for the ability to improve predictability of impacts to targets or risks to non-target organisms. Furthermore, a fast growing and increasingly utilized open access database, COMPADRE, provides a potentially important resource to inform construction of appropriate models for species of interest (Salguero-Gomez et al. 2015).

Retrospective demographic analyses for target and non-target effects in weed biocontrol

Demographic modeling has been used to understand success or failure of weed biocontrol programs in reducing target plant population growth rates (Buckley et al. 2004; DeWalt 2006; Shea and Kelly 1998;

Shea et al. 2005; Swope et al. 2017). These examples are important in recognizing that demographic approaches are already an important part of the evaluation process in weed biocontrol. We will not review these here but focus instead on efforts to help assess demographic impacts of weed biocontrol agents on non-target plants after release. Twenty years have passed since the initial widespread criticism regarding safety of (weed) biocontrol (Louda et al. 1997; Pemberton 2000; Simberloff and Stiling 1996). At least ten biocontrol agents have established populations on non-target species and > 120 non-target plants are reported to be attacked (Blossey et al. 2001; Suckling and Sforza 2014), thus we expected to find numerous publications outlining demographic consequences, or at least attempts to evaluate consequences of such attacks. Our Web of Science searches uncovered few studies, which may indicate that they either were not conducted, did not get published, or were deemed unimportant to conduct or fund. We therefore focus on *R. conicus* and *C. cactorum*, species that according to categorization by Suckling and Sforza (2014) have “massive” non-target impacts, plus post-release evaluations of *Mogulones crucifer* Pallas (Curculionidae), a species approved for release against houndstongue (*Cynoglossum officinale* L.) (Boraginaceae) in Canada (Catton et al. 2016). Apparently, studies evaluating demographic effects of *T. horridus* beyond documentation of attack on a non-target plants do not exist, therefore we exclude this species.

A high-profile paper regarding non-target effects of *R. conicus* (Louda et al. 1997) tabulated attack rates on native thistles, but fell short of documenting demographic effects, which were strongly implied due to seed limitation and large demographic impacts by native seed feeders on *Cirsium altissimum* (L.) Spreng (Asteraceae) (Guretzky and Louda 1997). Additional investigations clearly documented demographic threats by *R. conicus* (Louda et al. 2005b) based both on field and laboratory data. But effects appear context-dependent and do not occur every year and in every location (Rand and Louda 2004; Rose et al. 2005). In addition, some native thistles show positive population growth rates even in the presence of and attack by *R. conicus* (DePrenger-Levin et al. 2010). Furthermore, results of demographic models to assess population growth rates for Platte thistle, *Cirsium canescens* Nutt. concluded that impacts may be

substantial, but variable in space and time and not as catastrophic as previously feared (Rose et al. 2005). While *R. conicus* should have never been approved for release, current evidence is of widespread attack on native *Cirsium* species, but evidence for predicted massive negative demographic non-target effects (sensu Suckling and Sforza 2014) has not been presented at this time.

The accidental introduction of *C. cactorum* to North America (Pemberton 1995) raised concerns over safety of native North and Central American *Opuntia* spp. (Cactaceae) (Viguera and Portillo 2001), particularly for rare endemics, such as *Opuntia corallicola* Small where only 12 known individuals existed in the Florida Keys (Johnson and Stiling 1996). Follow-up work, including using plant demography, over the past two decades has delivered a more refined view of realized threats. While initial introductions to Nevis and St. Kitts in the Lesser Antilles to control weedy native *Opuntia* spp. was ill advised, a survey 50 years after *C. cactorum* releases showed that the targeted native species *Opuntia triacantha* (Willd.) Sweet and *Opuntia stricta* (Haw.) Haw. remain under biological control while the native tree pear *Consolea rubescens* (Salm-Dyck ex DC) Lem. (Cactaceae) was not attacked and the cultivated and naturalized *Opuntia cochenillifera* (L.) Mill showed limited feeding by *C. cactorum* (Pemberton and Liu 2007). In the Southeastern USA, *C. cactorum* has spread rapidly, resulting in variable impacts depending on cactus species, often resulting in size decreases and reduction in relative growth rates (Sauby et al. 2017). Jezorek et al. (2012) summarized these findings as follows: “although *C. cactorum* should still be considered a threat, particularly for rare opuntoids, overall survival along the west central Florida coast is currently high and plants that are able to survive *C. cactorum* attack are not being reduced in size, possibly because they possess traits that render them more tolerant of *C. cactorum* damage. Our findings suggest that an assumption of severe negative effects of an invasive species, based on its effects in other regions or over short periods of time, may not always be justified”. In the case of the rare endemic *O. corallicola*, detailed studies and restoration efforts revealed that salinity, moisture conditions, hurricanes, trampling by deer, and stem rot over the past two decades were more important demographic threats than *C. cactorum* (Stiling et al. 2000). Only by developing detailed

models incorporating more than presence of herbivore attack and other “stressors” are we able to gauge impacts appropriately. As in the case of *R. conicus*, anticipated “massive” impacts of *C. cactorum* are, according to published studies, not currently materializing in the field.

Risk assessment after release of *M. crucifer*, a root feeding weevil that attacked some Boraginaceae, including some US native and rare plants, during host specificity testing (De Clerck-Floate and Schwarzländer 2002), provides a good example of an application of matrix population models. Canadian authorities granted release permits and *M. crucifer* established and began to spread in British Columbia, prompting fears about non-target attacks upon arrival in the USA (Andreas et al. 2008). Additional host specificity testing, including field tests in British Columbia, also documented non-target attack by *M. crucifer* but found minor adult feeding and infrequent larval development, despite ability of the weevil to complete development under no-choice conditions (De Clerck-Floate and Schwarzländer 2002).

Subsequent monitoring showed that *M. crucifer* did not establish at sites where *C. officinale* was absent (Catton et al. 2015) and attack of non-target species tapered off within a few meters (Catton et al. 2014), including during spillover events. Furthermore, detailed demographic work on *Hackelia micrantha* (Eastw.) J. L. Gentry (Boraginaceae), a native plant species regularly attacked in the field, demonstrated that while population growth rates for *C. officinale* were reduced below replacement rates ($\lambda < 1$), *H. micrantha* benefitted from *C. officinale* reductions (Catton et al. 2016). These results indicate that while individual *H. micrantha* are being attacked and allow larval development of *M. crucifer*, the species is safe and suffers no harm at the population level (Catton et al. 2016). Similar demographic experiments with rare plants that are part of the fundamental host range of *M. crucifer* could help evaluate real (vs. feared) threats to other US native Boraginaceae.

These examples showcase the value of detailed demographic studies to assess how attack by biocontrol agents may, or may not, contribute to harm, or endangerment of non-target species. Only through such detailed work are we able to separate anecdotal observation of attack from contributions of many factors (habitat loss and fragmentation, inbreeding depression, succession, disturbance, climate, abiotic

conditions, competition, other natural enemies, etc.) that affect plant demography simultaneously.

To the best of our knowledge, no biocontrol program has used a demographic analysis to assess herbivore impact on non-target plants pre-release or as part of a release petition. Raghu et al. (2006) proposed to use modeling a priori, but this recommendation followed rejection of a herbivore by Australian authorities due to minor feeding on a non-target plant. We believe weed biocontrol researcher should strive to make this standard practice when promising species fail traditional testing sequences (Fig. 1). Embracing this approach can lead to important collaborations with those concerned about native species and academics with specialized knowledge (Clewley et al. 2012).

To further develop our proposal to use plant demography models in pre-introduction risk assessments, we now turn to *T. natans*. We present data collection procedures used to develop a demographic model for *T. natans*. For the sake of argument, we assume *T. natans* to be a non-target species, and we further assume that two different chrysomelid beetles are potential biocontrol agents that failed to be cleared in traditional host specificity screening. We incorporate the feeding impacts of each herbivore into the demographic model to evaluate the risk each agent may pose to plant demography.

Evaluation of two herbivores attacking *T. natans*

The Eurasian *T. natans* is a floating aquatic annual plant invasive in North America where it is attacked by the native water lily leaf beetle, *Galerucella nymphaeae* L. while the extremely similar *Galerucella birmanica* Jacoby (Chrysomelidae) attacks *T. natans* in Asia (Ding and Blossey 2005; Ding et al. 2006a, b). Both herbivores are multivoltine and while *G. nymphaeae* is oligophagous with multiple host races (Cronin et al. 1999), *G. birmanica* is host-specific to *T. natans*, although it occasionally lays a few eggs on water shield, *Brasenia schreberi* J. Gmelin (Cabombaceae), the only other plant reported to be attacked in the field (Ding et al. 2006a) (natural histories of *T. natans*, *B. schreberi*, *G. nymphaeae* and *G. birmanica* are provided in Supplementary Materials, Section 1). Both herbivores were evaluated as potential biocontrol agents in experiments that assessed their impact on

growth and reproduction of *T. natans* at different larval densities (0–50 L_1 per rosette) (Ding and Blossey 2005; Ding et al. 2006b). We combine herbivore impact data with demographic plant data obtained in outdoor aquatic mesocosms to build demographic models that project future plant population dynamics under different beetle herbivory scenarios. These data were initially collected and the demographic model built to assess utility of each herbivore as a biocontrol agent. By considering, for sake of argument, *T. natans* as a non-target species, we can show how biocontrol programs can use demography in risk evaluation for non-target species. Full descriptions of the herbivore impact studies are available elsewhere (Ding and Blossey 2005; Ding et al. 2006b) and results and details of our experimental design to collect demographic data in aquatic mesocosms using four different plant populations collected in Massachusetts (MA), Rhode Island (RI), New York (NY), and Virginia (VA), USA are detailed in Supplementary Materials, Section 2.

Model development

We evaluated differences in population growth rate of *T. natans* with periodic matrix population models. Periodic matrix models are suited to explore within year transitions of annual organisms, such as *T. natans* (Caswell 2001). These models partition life history transitions into m phases defined by a matrix (\mathbf{B}_h) that projects the population into the next phase (h ; where $h = 1 \dots m$). Population over entire cycles is given by the product of period matrices: $\mathbf{A} = \mathbf{B}_m \mathbf{B}_{m-1} \dots \mathbf{B}_1$; where \mathbf{A} is the annual transition matrix. We partitioned *T. natans* life cycle into three phases (Fig. 2): fall-spring (seedbank or new seeds germinate), spring-summer (rosettes grow small or large), and summer-fall (reproduction). We classified individuals in each life stage as seedbank, seeds, small or large plants and determined plant size as a function of surface area. We used census data from the common garden to estimate transition and germination rates and published data to calculate seedbank longevity (Kunii 1988) (Supplementary Materials, Table S3). We calculated annual population growth rate (λ) given by the dominant eigenvalue of \mathbf{A} and used bootstrap methods to estimate 95% confidence intervals for each population (defined as the 2.5 and 97.5% quantiles from a distribution based on resampling values with

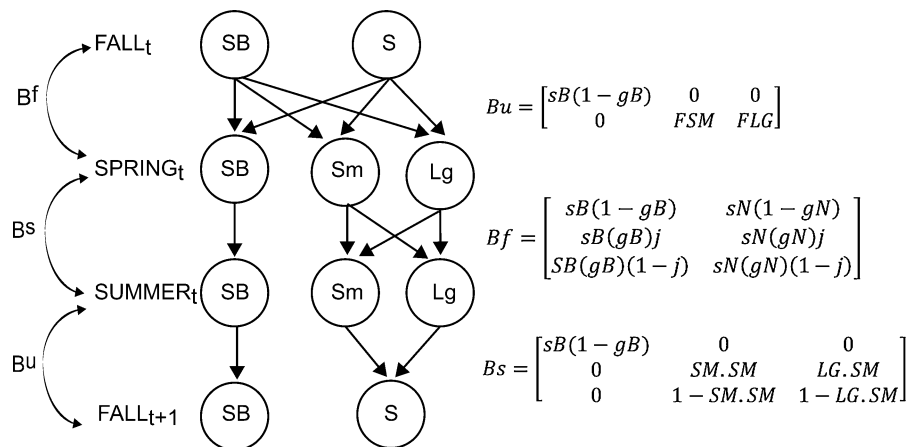


Fig. 2 Seasonal life cycle diagram and periodic matrices for *T. natans*. Each row represents a season and each circle a life stage (SB: seedbank, S: seed, Sm: small plant, Lg: large plant). Periodic matrix Bf represents germination of seeds from

seedbank or previous fall until spring, Bs plant survival and growth from spring to fall in the same year and Bu reproduction of small and large plants. Parameters are defined in Supplemental Materials, Table S3

replacement holding sample size constant for 1000 iterations) (Caswell 2001). We also conducted elasticity analyses on each periodic matrix to evaluate which transition most influenced growth rate (Caswell 2001; Smith et al. 2005).

Non-target threat simulation

We examined how presence and typical attack of *G. nymphaeae* or of *G. birmanica* affects demography of *T. natans* (Ding and Blossey 2005; Ding et al. 2006b). We modeled effects of each scenario on *T. natans* populations over ten time steps (t) and 10,000 iterations (i) and parametrized the model with values estimated from the common garden and the literature (Supplementary Materials, Table S3). We modeled stochastic variation following a two-step procedure in order to incorporate temporal variation and parametric uncertainty in model predictions (McGowan et al. 2011). We modeled temporal variation in survival rates and transition terms for each realization i and time step t as a beta distributed random variable with parameters α_i and β_i derived from the mean survival (or transition) rate, μ_i , such that $\mu_i = \alpha_i / (\alpha_i + \beta_i)$ and $\sigma_i = \mu_i (1 - \mu_i) / (\alpha_i + \beta_i + 1)$. We incorporated parametric uncertainty in the replication loop by sampling μ_i from a beta distribution, and σ_i from an inverse Gaussian distribution with mean m (m = 0.001) and shape parameter λ ($\lambda = 0.0001$). We followed the same two-step approach for fertility

parameters (FSM and FLG, fertility for small and large plants, respectively), but in this case fertility values were drawn from a Poisson distribution.

To account for density dependent effects, which result in decreased *T. natans* fertility and plant size (Groth et al. 1996), we modeled fertility values as a density-dependent parameter, such that number of seeds produced by small (FSM) or large (FLG) plants was dependent on the number of *T. natans* plants (P) in the previous season (s)

$$F_s = \frac{e^{(1-(zP_{s-1}))}}{1 + e^{(1-(zP_{s-1}))}}$$

we set z, the regression parameter, to 0.0005, indicating weak density-dependent effects. To model effects of management scenarios, we estimated average number of seeds produced by small or large plants (FSM or FLG, respectively) and weighted the value by rate of fertility decrease according to scenario. At each time step we estimated annual growth rate (λ) as ratio between population size at current year (N_{t+1}) and previous year (N_t). Values of $\lambda > 1$ indicate increasing populations while values of $\lambda < 1$ indicate declining populations. We conducted all analysis using package popbio (Stubben and Milligan 2007) in R Core Team (2016).

Results of demographic analyses

Plant area, seed output and germination varied significantly among populations and number of seeds per plant was positively correlated with plant area (Supplementary Materials, Fig. S1; Tables S1, S2). Asymptotic population growth rates varied significantly across populations (Supplementary Materials, Section 3). Elasticity analyses indicated that matrix elements representing germination of new seed and growth into large plants had the greatest influence on λ (Supplementary Materials, Fig. S3).

Results from modelled simulations

Our model predicted that *T. natans* populations will continue to grow until carrying capacity or habitat requirements do not allow further expansion, despite continued attack by *G. nymphaeae* (Fig. 3). This indicates that if *T. natans* were a non-target species, *G. nymphaeae* would not constitute a demographic threat to *T. natans* populations despite regular feeding, oviposition and larval development. In contrast, our model predicts that *T. natans* populations will be greatly reduced when attacked by *G. birmanica*. After ten years simulated populations increased from 1000 plants to > 40,000 plants when attacked by *G. nymphaeae*, but declined to near zero individuals under *G. birmanica* attack (Fig. 3). Thus, under our

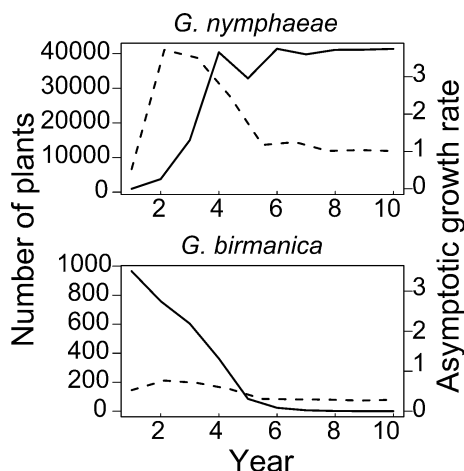


Fig. 3 Simulated population size (continuous line) and population growth rate (dashed line) of a *T. natans* population under attack by either the leaf beetle *G. nymphaeae* or *G. birmanica*. Model data are integrated means derived by collecting demographic data for four different *T. natans* populations

hypothetical scenario of *T. natans* as a potential non-target, *G. birmanica* would be a grave threat to continued existence of the species. If the goal were to safeguard *T. natans*, our results show that of these two extremely similar herbivores, *G. nymphaeae* would be a safe biocontrol agent while releases of *G. birmanica* should not be considered.

Implications for demographic assessments of non-target effects

We considered a hypothetical example of *T. natans* as a non-target plant and evaluated potential threats by two herbivores that can successfully feed, oviposit and develop on the species. Under current decision making processes, biocontrol scientists or regulators would not consider *G. nymphaeae* a safe biocontrol agent because fundamental and field host range include *T. natans*. Field evidence from > 100 years of association with *T. natans* in North America, and results from our demographic modeling efforts, however, clearly indicate that *G. nymphaeae* is no demographic threat to *T. natans*. Furthermore, there is no evolutionary tendency, despite enormous opportunity, to improve larval performance on the novel host, and female choice retains its preference for oviposition on the original host, even when larvae developed on *T. natans* (Ding and Blossey 2009). The traditional risk assessment process, as currently being implemented, would eliminate a potentially important biocontrol agent due to safety concerns regarding attack on *T. natans*, but this would be fundamentally unjustified given the realized demographic impact of *G. nymphaeae*. Our demographic assessments correctly predict what is evident in the field: *G. nymphaeae* does not affect *T. natans* populations, while *G. birmanica* attack can lead to rapid and severe population growth rate declines.

Discussion

Reports of non-target attack by weed biocontrol agents after their release has a chilling effect on agent approvals in ongoing programs, funding and recruitment (Moran and Hoffmann 2015). Land managers, ecologists, conservationists and weed biocontrol scientists spent enormous amounts of time discussing implications, focusing on the two high profile cases of

R. conicus and *C. cactorum*, while critics implied that non-target impacts are potentially widespread, but not recognized (Louda et al. 2003). Almost 20 years have passed since the initial publications and while we have been provided with some evidence for negative demographic consequences by *R. conicus*, the same cannot be said for *C. cactorum*. Importantly, there is not a single publication documenting negative population level impacts on any other non-target plant species by weed biocontrol agents. Observation of herbivorous biocontrol agents feeding on other plants are widespread, indicating that evidence of their non-target feeding is being recognized, collected and reported, but their attack appears inconsequential at the population level.

Unless there are unrecognized, or unpublished data on more widespread negative demographic consequences by approved weed biocontrol agents, the feared threats to native plants currently do not appear to exist. This is entirely overlooked by regulators, conservationists and ecologists who may equate feeding on non-target plants with demographic threats. The reliance on data about fundamental host range tests has been called risk-averse, but it ignores the increasing realized impacts of invasive plants on native biota (Downey and Paterson 2016), and increasing herbicide use by land managers that result in widespread and documented detrimental long-term effects to species of conservation concern (Kettenring and Adams 2011). We emphasize that society and citizens are entitled to have questions regarding performance of invasive species management methods answered to make informed decisions about priorities, risk acceptance and funding (Blossey 2016a, b), but this requires appropriate assessments and interpretation, not fear mongering and it should apply to all management methods (Kerr et al. 2016; Pearson et al. 2016).

Use of herbivore impact studies and demographic models in the way we have described here would be an important tool to evaluate efficacy and safety of potential biocontrol agents, yet it is completely unutilized despite its promise (Blossey 2016b). Use of plant (and herbivore) demography would be an important advancement in improving scientific rigor and predictability of weed biocontrol programs, albeit we acknowledge it will not be an easy transition. For far too long, the focus has been narrowly on fundamental host ranges and not allowing any attack on

native plants. Pivoting to new risk assessment procedures and lines of evidence will take some time but we argue it is essential and well justified.

We acknowledge that biological control, like every other management technique, is not risk free and that ecological surprises may occur. For example, it appears that identity of plant species attacked during outbreak or spillover events is unpredictable (Blossey et al. 2001). But these are temporary events with no demographic consequences for attacked plant species and do not constitute host shifts. Assessing potential non-target effects is the ethical thing to do, but without use of demographic information on targets and non-targets biocontrol scientists and practitioners are vulnerable to accusations of inappropriate conduct and may get blamed for population declines or extinctions, whether these accusations are true or not. We argue that we should acknowledge our responsibilities for safeguarding the continued existence of populations of native or non-target species, and that demographic approaches provide a powerful tool for evaluating ecological risk. To the best of our knowledge, with the exception of *R. conicus* or *C. cactorum*, there is no weed biocontrol agent that has negatively affected populations of non-target plants. Given that hundreds of control agents have been released over 100 years across the world, this track record is exemplary (Winston et al. 2014). But we also may miss out on very promising herbivores, because the current regulatory climate makes scientifically questionable and poorly justified decisions (Cristofaro et al. 2013; Fowler et al. 2012; Groenteman et al. 2011; Hinz et al. 2014).

Our proposal to utilize demographic approaches in forecasting agent efficacy, and potential impacts on non-target species, would go a long way in improving the standing of the discipline—one grounded in theory and applying modern tools—while retaining our exemplary track record in safeguarding native species. This does not make weed biocontrol inherently more risky. On the contrary, we would be able to focus on effective agents with a proven track record of impact on demography of invasive plants, and lack of demographic impact on non-targets. Delivering this information to society and decision makers and regulators will constitute part of the accountability we should require from all of those engaged in invasive species management and stewardship (Blossey 2016a, b; Hare and Blossey 2014).

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