

Tailoring biocontrol to maximize top-down effects: on the importance of underlying site fertility

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Abstract. The degree to which biocontrol agents impact invasive plants varies widely across landscapes, often for unknown reasons. Understanding this variability can help optimize invasive species management while also informing our understanding of trophic linkages. To address these issues, we tested three hypotheses with contrasting predictions regarding the likelihood of biocontrol success. (1) The *biocontrol effort* hypothesis: invasive populations are regulated primarily by top-down effects, predicting that increased biocontrol efforts alone (e.g., more individuals of a given biocontrol agent or more time since agent release) will enhance biocontrol success. (2) The *relative fertility* hypothesis: invasive populations are regulated primarily by bottom-up effects, predicting that nutrient enrichment will increase dominance by invasives and thus reduce biocontrol success, regardless of biocontrol efforts. (3) The *fertility-dependent biocontrol effort* hypothesis: top-down effects will only regulate invasive populations if bottom-up effects are weak. It predicts that greater biocontrol efforts will increase biocontrol success, but only in low-nutrient sites. To test these hypotheses, we surveyed 46 sites across three states with prior releases of *Galerucella* beetles, the most common biocontrol agents used against invasive purple loosestrife (*Lythrum salicaria*).

We found strong support for the fertility-dependent biocontrol effort hypothesis, as biocontrol success occurred most often with greater biocontrol efforts, but only in low-fertility sites. This result held for early stage metrics of biocontrol success (higher *Galerucella* abundance) and ultimate biocontrol outcomes (decreased loosestrife plant size and abundance). Presence of the invasive grass *Phalaris arundinacea* was also inversely related to loosestrife abundance, suggesting that biocontrol-based reductions in loosestrife made secondary invasion by *P. arundinacea* more likely.

Our data suggest that low-nutrient sites be prioritized for loosestrife biocontrol and that future monitoring account for variation in site fertility or work to mitigate it. We introduce a new framework that integrates our findings with conflicting patterns previously reported from other biocontrol systems, proposing a unimodal relationship whereby nutrient availability enhances biocontrol success in low-nutrient sites but hampers it in high-nutrient sites. Our results represent one of the first examples of biocontrol success depending on site fertility, which has the potential to inform biocontrol-based management decisions across entire regions and among contrasting systems.

Key words: *biological control; cattail, Typha spp.; Galerucella spp.; giant salvinia, Salvinia molesta; graphical model; herbivore tolerance; nutrient enrichment; purple loosestrife, Lythrum salicaria; secondary invasion; soil nitrogen; water hyacinth, Eichhornia crassipes.*

INTRODUCTION

Classical biological control uses specialist enemies imported from the invader's native range to control invasive species (Julien and Griffiths 1998, McFadyen 1998, Culliney 2005, Van Driesche et al. 2010). Biocontrol programs have been criticized for their inherent risks and low or unpredictable success rates (Simberloff and Stiling 1996, Louda et al. 1997, Thomas and Willis 1998, Callaway et al. 1999, Louda et al. 2003, Denoth and Myers 2005, Zangerl and Berenbaum 2005).

However, even for biocontrol agents with a record of successfully reducing populations of a target invasive species, substantial variation in biocontrol success across sites is often the norm (Louda et al. 2003, Lesica and Hanna 2004, Denoth and Myers 2005, Grevstad 2006, Van Driesche et al. 2010, Jamieson et al. 2012, Boag and Eckert 2013). The factors that underlie such variability in biocontrol success are poorly understood (Van Driesche et al. 2010), representing a serious weakness in the use of biocontrol for invasive species management.

Defining biocontrol success and determining the best metric by which to measure success can be difficult and sometimes contentious (McFadyen 1998, Syrett et al.

Manuscript received 1 November 2013; revised 7 May 2014; accepted 12 May 2014. Corresponding Editor: R. A. Hufbauer.

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2000, Carson et al. 2008, Morin et al. 2009). A successful biocontrol program should reduce the abundance of a target species below some threshold at which it no longer causes significant economic or ecological damage (Syrett et al. 2000, Hulme 2006). Yet in practice, many assessments of biocontrol success report only early stage proxies of invader reductions, such as biocontrol agent abundances and their per capita effects on the target species, rather than later-stage metrics, such as invader abundance (McClay and Balciunas 2005, Thomas and Reid 2007). Furthermore, biocontrol success is rarely evaluated by quantifying the desired postinvasion community (Denslow and D'Antonio 2005, Clewley et al. 2012), although this is improving (e.g., Barton et al. 2007, Stephens et al. 2009, Tipping et al. 2009, Butler and Wacker 2010). Many have argued that these late-stage, community-level outcomes should be prioritized for measuring biocontrol success (Denslow and D'Antonio 2005, Carson et al. 2008, Stephens et al. 2009). We take an inclusive approach, using multiple metrics of success that reflect a combination of both early and late-stage biocontrol outcomes.

Regardless of the metric used, the likelihood of biocontrol success is expected to increase as more agents are released and, once established, as agent populations persist over longer periods of time (Grevstad 1999, Van Hezewijk et al. 2010, Clewley et al. 2012). This represents an emphasis on top-down trophic effects, which should predominate as long as biocontrol agents are introduced without their own specialist enemies (McEvoy and Coombs 1999, Keane and Crawley 2002). However, strong top-down effects can be dampened or negated by the bottom-up effects of resource availability, both in native communities (Wise and Abrahamson 2007, Cronin et al. 2010) and within a biocontrol context (e.g., Room and Thomas 1985, Heard and Winterton 2000). We describe three hypotheses that make contrasting predictions regarding top-down and bottom-up effects on biocontrol success. We test these hypotheses using a geographically expansive survey of biocontrol release sites (extending from north-central Ohio to southeastern Pennsylvania and central New York), and using these findings, we attempt to reconcile conflicting patterns in the biocontrol literature regarding the dependence of biocontrol success on nutrient availability.

1) The *biocontrol effort* hypothesis states that invasive populations can be regulated primarily by top-down effects from biocontrol agents, in which case biocontrol success will be positively related to biocontrol efforts. This hypothesis reflects traditional expectations from much of the biocontrol literature (e.g., Huffaker and Kennett 1959, McEvoy et al. 1991, Grevstad 1999), as well as the enemy release hypothesis from the invasion literature (Keane and Crawley 2002, Mitchell and Power 2003). Where species introduced without their natural enemies have higher fitness, reintroducing those enemies as biocontrol agents is often seen as a viable manage-

ment strategy. To quantify biocontrol efforts, we use two key metrics that covary with success of a particular biocontrol agent: the number of individuals released and the length of time since their initial release. Greater numbers of a biocontrol agent make them more likely to overcome environmental and demographic stochasticity, minimize Allee effects, and reach densities sufficient to impact target invaders (Grevstad 1999). Increasing the time since release allows for lags in population growth rates (Huffaker and Kennett 1959, McEvoy et al. 1991, Van Hezewijk et al. 2010, Clewley et al. 2012) and enhances outcomes where biocontrol agent impacts result from damage occurring over multiple years (e.g., for plants with robust, perennial rootstocks; see Katovich et al. [1999]).

2) The *relative fertility* hypothesis states that invasive populations will respond primarily to bottom-up effects, in which case nutrient enrichment or relatively fertile sites will increase community dominance by invaders regardless of biocontrol efforts (e.g., Jamieson et al. 2012). Increasing rates of anthropogenic nutrient loading globally plus well-supported theory predicting that increased resource availability can enhance invasion success (Davis et al. 2000) make this a viable alternative to the biocontrol effort hypothesis. For example, nitrogen often limits productivity (Fenn et al. 1998, Bedford et al. 1999), but human-induced nitrogen availability has increased exponentially since the 1950s (Vitousek et al. 1997, Fixen and West 2002, Galloway et al. 2003) and now accounts for 45% of all nitrogen fixed globally (Canfield et al. 2010). Ecologists have long known that nutrient enrichment can enhance the relative abundance of one or a few highly productive species (Tilman 1987, Carson and Barrett 1988, Carson and Pickett 1990, Goldberg and Miller 1990, Rajaniemi 2002, Lamb et al. 2009, Isbell et al. 2013), and within the context of plant invasions, introduced species can often increase in abundance due to nutrient enrichment (Huenneke et al. 1990, Thompson et al. 2001, Leishman and Thomson 2005). If strong bottom-up effects from nutrient enrichment outweigh the effects of top-down suppression by biocontrol agents (e.g., by increasing an invader's tolerance of or resistance to herbivory), then nutrient enrichment alone may enhance invasiveness and thwart biocontrol success.

3) The *fertility-dependent biocontrol effort* hypothesis states that top-down effects of biocontrol agents can suppress invasive populations, but only where bottom-up effects due to fertility are weak (see also McEvoy and Coombs [1999], Knochel and Seastedt [2010]). This hypothesis predicts a strong interaction between site fertility and biocontrol effort whereby biocontrol success responds positively to biocontrol effort in nutrient-poor but not nutrient-rich sites. It is conceptually related to the resource-enemy release hypothesis (Blumenthal 2006), which states that invasive species most adapted to resource-rich conditions should experience the greatest degree of release upon introduction to

a novel region without their natural enemies and that the effects of enemy release should be maximal in resource-rich conditions (e.g., Blumenthal et al. 2009). In many plant species, nutrient enrichment can increase herbivore resistance or tolerance (Maschinski and Whitham 1989, Wise and Abrahamson 2007, Cronin et al. 2010; but note that enrichment can also increase susceptibility [Herms 2002]), thus we can expect nutrient availability to play a critical role for invasion and biocontrol success as well. Although interactions between resource availability and herbivory are not universal (Gruner et al. 2008), some examples from the biocontrol literature do exist (Room and Thomas 1985, Heard and Winterton 2000, Moran 2006). For example, eutrophication can reduce the success of biocontrol targeting water hyacinth (*Eichhornia crassipes*) by enhancing primary productivity to such an extent that herbivore populations fail to keep pace (Heard and Winterton 2000). This suggests that biocontrol success could be enhanced by reducing anthropogenic nutrient inputs or by focusing biocontrol releases on low-nutrient sites. However, the opposite pattern has also been shown, with nutrient additions to oligotrophic waters enhancing biocontrol success on *Salvinia molesta* (Room and Thomas 1985, Sullivan et al. 2011). Here, nutrient enrichment reduces resource limitation in the herbivore, making population establishment of the biocontrol agents more likely. Thus, although there are good reasons to expect that site fertility will impact biocontrol outcomes, contradictory findings raise questions about the directionality of any such effect. We propose a framework that addresses this apparent contradiction.

Assessing the relative importance of top-down, bottom-up, and interactive effects for biocontrol is a critical consideration, given significant increases in both nitrogen saturation (Canfield et al. 2010) and biocontrol releases (McEvoy and Coombs 1999, Syrett et al. 2000) in many parts of the world. Biocontrol can be a cost-effective option for managing species invasions (Fowler et al. 2000, van Wilgen et al. 2004, Clewley et al. 2012), but because of their significant ecological risks (e.g., Callaway et al. 1999, Louda et al. 2005, Pearson and Callaway 2008), biocontrol releases should be designed to account for key variation that can impact the likelihood of success. One dimension of among-site variation that may play a critical role in biocontrol success is site fertility. With this goal in mind, we surveyed 46 sites across a very large region (~100 000 km²) of the northeastern United States that had a history of biocontrol releases targeting the invasive purple loosestrife (*Lythrum salicaria*). We quantified multiple metrics of biocontrol success, and we used these data to test the three alternative hypotheses.

METHODS

Study species

Purple loosestrife (*Lythrum salicaria* L., hereafter *Lythrum*; see Plate 1) was introduced to North America

from Europe by the early 1800s and was considered a problem weed by the 1930s (Stuckey 1980). Since then, *Lythrum* has been shown to have widespread negative effects on wetland communities and ecosystems (Blossey et al. 2001, Farnsworth and Ellis 2001, Brown et al. 2006, Fickbohm and Zhu 2006, Schooler et al. 2006, Hovick et al. 2011). In the early 1990s, an extensive biocontrol program targeting *Lythrum* was developed (Malecki et al. 1993, Blossey et al. 2001), for which the most commonly introduced biocontrol agents have been the leaf-feeding chrysomelid beetles *Galerucella calmaricensis* L. (see Plate 1) and *G. pusilla* Duftschmidt. The relative abundances of these two species vary across their introduced range (Dech and Nosko 2002, Landis et al. 2003, Grevstad 2006), but they are similarly effective and difficult to distinguish (Blossey 1995). Our data on biocontrol releases did not distinguish which species was released, thus we refer to both species together as *Galerucella*.

Data collection

We selected 46 sites in New York, Pennsylvania, and Ohio where *Galerucella* had been released to control *Lythrum* populations (Appendix: Table A1). As with most postrelease biocontrol assessments (Carson et al. 2008), we lack vegetation data from before the *Galerucella* releases, but we buffer this limitation by including a large number of sites spread widely across three states. Key recommendations for selecting appropriate *Lythrum* biocontrol release sites are clear: *Lythrum* populations must be dense and at least 0.4 ha (1 acre) in size (Wilson et al. 2004). Moreover, based on historical photographs taken at nine of our Pennsylvania sites (56% of Pennsylvania sites, 20% of all 46 sites) *Lythrum* was abundant at every site, in contrast with the among-site differences we later quantified in our surveys (S. Hovick, *personal observation*). Importantly, our sites did vary widely in their biocontrol effort and site fertility, which was critical for testing our three hypotheses. We took advantage of detailed state archives to compile *Galerucella* release dates and the number of beetles released on each date for all sites.

We completed all surveys between 30 May and 25 June 2008, generally working south to north to coincide with *Lythrum* and *Galerucella* phenology. At each site, we assessed the areal extent of the *Lythrum* stand and established twelve sampling quadrats (1 × 1 m) spaced evenly across it. Wherever an elevation (water-depth) gradient existed, we ran transects along it, in most cases yielding a rectangular array of four quadrats in each of three transects. This sampling scheme was designed to capture within-population variation in plant and beetle abundances without subconsciously selecting either *Lythrum*-present or *Lythrum*-absent patches.

At each quadrat we recorded *Lythrum* size and abundance and *Galerucella* abundance and percentage of leaf damage using a modified protocol developed for postrelease monitoring of *Lythrum* biocontrol (Wilson

et al. 2004). We assessed *Lythrum* plant size by recording stem density (the number of stems rooted within the 1-m² quadrat), the heights of the five tallest stems, and the diameter of the largest genet that was at least partially rooted within the quadrat. We assessed *Galerucella* abundance using three 1-minute scans, one each for its three distinct life stages (adults, larvae, and egg masses). Where there were too many *Galerucella* to complete the count within one minute, we determined what proportion of the plot had been assessed within that time and extrapolated to estimate whole-plot abundances (Lindgren 2003). For analysis, the abundances of each life stage were summed to account for among-site differences in the timing of *Galerucella* development (counting each egg cluster as one rather than counting individual eggs to account for expected substantial prelarval mortality [Matos and Obrycki 2007]). We estimated percentage of leaf damage by *Galerucella* on *Lythrum* for three leaves per stem (young, middle, and old) on three haphazardly selected stems in the quadrat. We used templates with known leaf damage for comparison (Carson and Root 2000), and each leaf was assessed independently by two people who then agreed on a consensus damage estimate.

We assessed plant abundance at the quadrat scale by visually recording percent cover for *Lythrum* and three other common dominant plant species (*Phalaris arundinacea*, *Phragmites australis*, and *Typha* spp., hereafter referred to by genus only); each estimate reflects the consensus of two individual observers. The *Typha* we observed across our sites included *T. latifolia*, *T. angustifolia*, and their hybrid *T. × glauca*, but we did not attempt to differentiate them. We also estimated percent cover at the transect and site scales. Transect-scale cover was estimated by two people, encompassing a 2 m wide swath centered on the transect and running its entire length. Site-scale cover estimates were based on the consensus of all four members of our field crew.

A single core of mineral soil (2 × 5 cm) was collected from below the organic layer of each quadrat (12 per site) and refrigerated until all samples could be air dried and processed. Once dried, they were pooled to yield three samples per site for nutrient analyses (generally a low-, middle-, and high-elevation sample). The pooled samples were then divided for two separate analyses. One set was analyzed by the University of Georgia Agricultural and Environmental Services Laboratories using their routine soil test (we report P, K, and Ca concentrations because they are particularly critical for wetland plants [Boyd and Hess 1970]). For the second set, we removed small rocks and root fragments and ground the soil using a 8000D Mixer Mill ball mill grinder (Spex Industries, Metuchen, New Jersey, USA); these samples were then analyzed by the University of Georgia Soil, Water and Plant Analysis Laboratory for percentage of N using the micro-Dumas combustion assay.

We wanted to ensure that *Lythrum* size and *Galerucella* abundance and leaf damage data were collected even in sites where *Lythrum* was uncommon, thus if *Lythrum* was absent from a given quadrat, we recorded *Lythrum* cover as zero, collected a soil core, and then relocated the quadrat over the closest *Lythrum* clone perpendicular to the transect. This new location was used only to record data on *Lythrum* size (clone diameter, stem density, and stem heights), *Galerucella* abundance, and percentage of leaf damage.

Statistical analyses

Our unit of replication is the site, thus data recorded from multiple quadrats or transects per site were averaged ($n = 46$ sites for all analyses). We assessed three different predetermined sets of predictor variables to test our three hypotheses regarding biocontrol success (Johnson and Omland 2004). We tested the biocontrol effort hypothesis using two predictors: age (in years) of the first *Galerucella* population introduced to a site (AGE) and the total number of *Galerucella* individuals released over time (GAL). We tested the relative fertility hypothesis using measurements of soil N, P, K, and Ca as predictors. Lastly, we tested the fertility-dependent biocontrol effort hypothesis using eight predictors: AGE, GAL, soil N, soil P, and all two-way interactions between N or P and the biocontrol effort variables. We only included interactions with N and P because these soil resources are most likely to limit both plant and insect growth (Chapin 1980, Mattson 1980, Aerts and Chapin 2000). Post hoc tests to investigate interactions with additional soil nutrients were not significant and did not change our interpretation (data not shown). In testing each of the three hypotheses, we used a backward variable elimination procedure where all terms were initially included in the model and the least-significant parameter in each successive run was eliminated (Murtaugh 2009). We retained hierarchical structure within our models so if an interaction term was included, both component main effects were as well. We repeated this procedure either until all variables had been excluded (indicating no support for that hypothesis) or until all remaining variables had $P \leq 0.10$ (excepting main effects from a significant interaction). The P values and test statistics we report are from the final models following this procedure. In all cases, our results were consistent with model comparisons based on bias-corrected Akaike information criterion (AIC_c). When multiple hypotheses were supported by the data we compared models using AIC_c and Akaike weights (w_i) (Burnham and Anderson 1998). Akaike weights derive from AIC_c and sum to 1.0, giving the plausibility of a given model relative to all other models under consideration.

Within this model-comparison context, we used general linear models (GLM) to assess each of our three alternative hypotheses, using as response variables a range of early and late-stage metrics to quantify

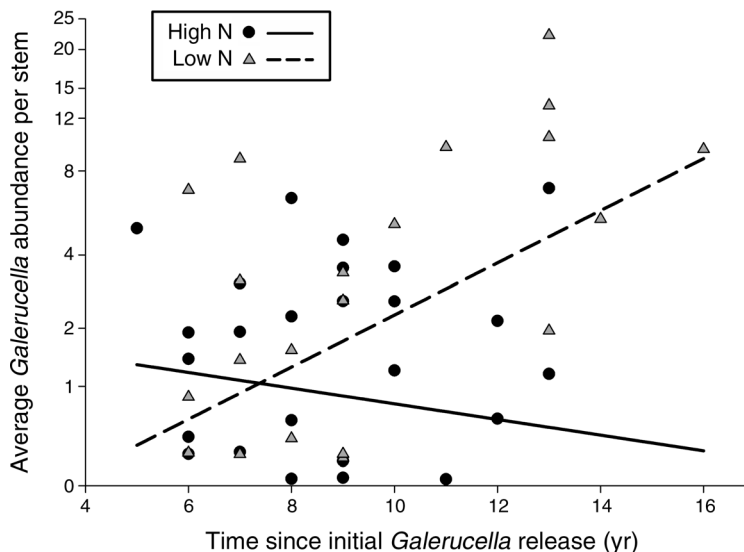


FIG. 1. *Galerucella* density increases with the age of the *Galerucella* population but only in low-nitrogen sites (significant age in years [AGE] \times N interaction), illustrating the fertility dependence of biocontrol efforts. To facilitate visualization of significant interactions between biocontrol effort and soil N (which are both continuous variables), general linear model (GLM) solutions are plotted at either high or low values of soil N (evaluated at mean N \pm SD) and sites are labeled as either high N or low N relative to the mean ($n = 25$ or 21 sites, respectively). *Galerucella* density (abundance per *Lythrum* stem) is shown on a \log_{10} -transformed scale.

biocontrol success. Specifically, our responses of interest were *Galerucella* densities (abundance per *Lythrum* ramet), percentage of leaf damage on *Lythrum*, *Lythrum* plant size (clone diameter, stem density, and stem height), and percent cover of *Lythrum* and *Typha*. We limited our analyses to percent cover at the quadrat scale, because for both *Lythrum* and *Typha*, this was highly correlated with transect- and site-scale cover estimates ($r > .85$). Because *Phalaris* occurred in only 21 of our 46 sites, we used logistic regression to assess predictors of *Phalaris* presence rather than using GLM to assess cover. *Phragmites* only occurred in nine sites, thus we excluded it from all analyses.

Soil nutrient concentrations, the number of *Galerucella* introduced (GAL), all three measures of *Lythrum* size, and *Galerucella* density were \log_{10} transformed. For *Lythrum* size and *Galerucella* density, we added 1 prior to taking the log. Percentage of leaf damage and percentage of plant cover were square root transformed. All of our final models had normally distributed residuals. Analyses were conducted in SAS v 9.3 (SAS 2009), and unless otherwise noted, we report untransformed means \pm SE. To facilitate the visualization of significant interactions between biocontrol effort and soil nutrients (which are both continuous variables), we used parameter estimates from the final interaction model to plot the relationship between biocontrol effort and biocontrol success at high and low values of site fertility (evaluated at mean \pm SD across all sites; see Figs. 1–3). In the figures, we also label individual sites as high or low relative to the mean ($n = 25$ or 21 sites, respectively) to help interpret significant interactions,

but we reiterate that in all analyses soil fertility was treated as a continuous variable, not a dichotomous one.

RESULTS

At the quadrat scale, average *Lythrum* cover ranged from 0–46% (mean, $11.2\% \pm 1.5\%$), whereas estimates at the transect- and site-wide scales ranged from 0–75% (transect mean, $19.2\% \pm 2.5\%$; site, $20.8\% \pm 2.5\%$; see Appendix: Table A1 for details). *Typha* and *Phalaris* had a similar range of abundance as *Lythrum* (Appendix: Table A1), although the cover of both species tended to be lower (*Typha* quadrat $8.9\% \pm 2.0\%$, transect $16.7\% \pm 3.2\%$, site $20.5\% \pm 3.6\%$; and *Phalaris* quadrat $8.6\% \pm 2.5\%$, transect $11.6\% \pm 3.0\%$, site $12.6\% \pm 3.4\%$).

Sites varied widely in our metrics of biocontrol effort and in relative fertility (Appendix: Table A1). Initial *Galerucella* releases were between five and 16 years old in 2008, and although there were only one or two release events at most sites, one site had received six separate *Galerucella* releases. The median total number of beetles released over time was 2705, with two sites having $>75,000$ beetles released in the 13 years since biocontrol began. Percent N in our soil samples ranged from 0.06–1.63% (mean, $0.33\% \pm 0.04\%$), which is at the upper end of the range found in our region ($\leq 0.35\%$; Brady 1990) and on par with high-fertility wetland sites elsewhere in the United States (Bartodziej et al. 2011). In addition, soil P ranged from 2.9–125.5 mg P/kg soil (mean, 27.6 ± 3.4 mg P/kg soil), soil K ranged from 25.8–150.7 mg K/kg soil (mean, 79.3 ± 3.6 mg K/kg soil), and soil Ca ranged from 354–10,323 mg Ca/kg soil (mean, 3624 ± 340 mg Ca/kg soil).

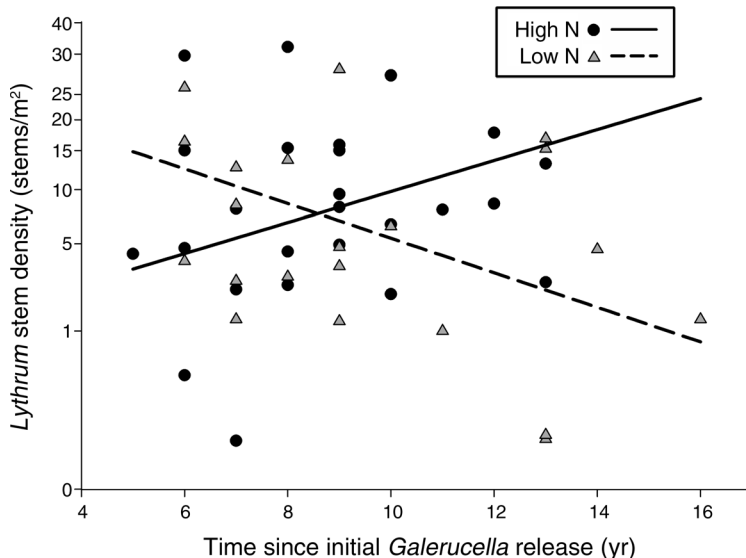


FIG. 2. *Lythrum* stem density decreases with increasing biocontrol effort but only in low-nitrogen sites, consistent with fertility-dependent biocontrol efforts. The significant interaction is visualized as in Fig. 1. *Lythrum* stem density is reported on a square-root-transformed scale.

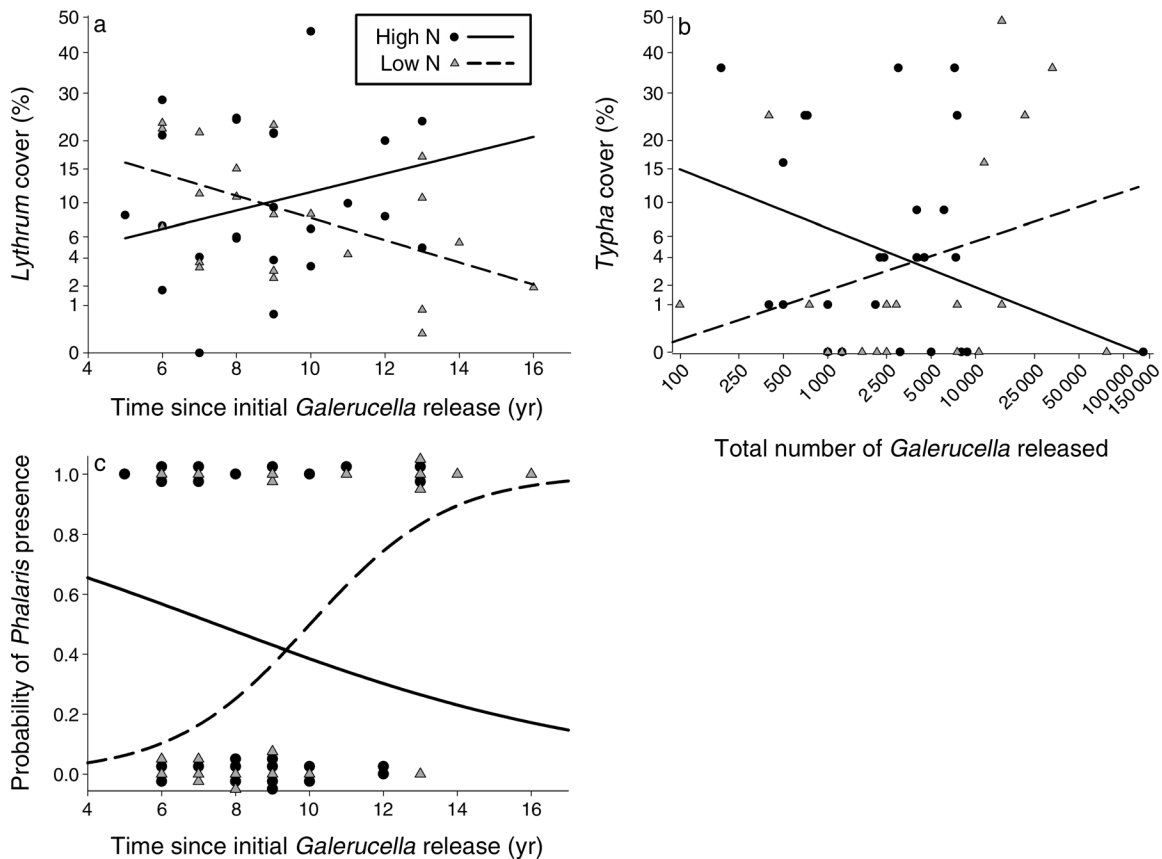


FIG. 3. The fertility dependence of biocontrol histories explains percent cover of *Lythrum* and *Typha*, plus the presence of *Phalaris*. The significant interaction is visualized as in Fig. 1. Percent cover is reported on a square-root-transformed scale and the total number of *Galerucella* released are reported on a log₁₀-transformed scale.

TABLE 1. Test statistics and parameter estimates (β , with SE in parentheses) for the selected model predicting *Galerucella* density, which supports the fertility-dependent biocontrol effort hypothesis.

Parameter	df	MS	F	P	β (SE)	R^2
Full model	3, 42	0.56	10.26	<0.001		0.423
AGE	1	0.26	4.81	0.034	-0.08 (0.04)	
N	1	0.45	8.15	0.007	1.39 (0.49)	
AGE \times N	1	0.7	12.8	0.001	-0.19 (0.05)	

Notes: AGE is age in years of the first *Galerucella* population introduced to a site and N is nitrogen content. The full model and all parameters are statistically significant ($P < 0.05$).

Galerucella density and damage

Our observations of *Galerucella* population density (abundance per *Lythrum* stem) support the fertility-dependence of biocontrol effort. *Galerucella* densities were significantly higher in older populations, but this pattern only held in low-nitrogen sites (Table 1 and Fig. 1). The biocontrol effort and the relative fertility hypotheses were also supported by our data, although based on their low Akaike weights ($w_i < 0.01$) neither is a plausible alternative to the fertility-dependence hypothesis (fertility-dependence AIC_c is -127.7, w_i is 0.995; biocontrol effort AIC_c is -115.7, w_i is 0.004; relative fertility AIC_c is -112.1, w_i is 0.001).

Percentage of leaf damage on *Lythrum* was highest in sites where *Galerucella* populations were the most dense ($r = 0.66$, $P < 0.001$); however, the fertility-dependent biocontrol model was not supported because the reduced model included only AGE as a significant predictor. In support of the biocontrol effort hypothesis, leaf damage was highest in sites with the oldest *Galerucella* populations ($\beta \pm SE$, 0.34 ± 0.14 ; $F_{1,44} = 6.44$; $P = 0.015$; $R^2 = 0.13$). Consistent with the relative fertility hypothesis, percentage of leaf damage also decreased with soil nitrogen concentrations ($\beta \pm SE$, -3.94 ± 1.56 ; $F_{1,43} = 6.37$; $P = 0.015$) and increased with soil calcium ($\beta \pm SE$, 2.84 ± 1.32 ; $F_{1,43} = 4.59$; $P = 0.038$; $R^2 = 0.14$). However, based on Akaike weights, the biocontrol effort hypothesis fit our leaf damage data better than the relative fertility hypothesis did (biocontrol effort AIC_c is 85.2, w_i is 0.685; nutrient loading AIC_c is 86.7, w_i is 0.315).

Lythrum plant size

Variation in *Lythrum* stem density (stems/m²) could only be explained by the fertility dependence of biocontrol effort. *Lythrum* stem density was lowest in sites with the oldest *Galerucella* populations, as long as soil nitrogen was also low (Table 2 and Fig. 2). We found the same pattern for *Lythrum* clone diameter (data not shown), which was significantly and positively correlated with stem density ($r = 0.762$, $P < 0.001$). In contrast, our data on *Lythrum* height supported only the relative fertility hypothesis, indicating that plants grew tallest in sites with abundant soil nitrogen and low potassium (Table 2).

Dominant plant cover

In support of the fertility-dependence of biocontrol efforts, older *Galerucella* populations led to reductions in *Lythrum* cover but only in low-nitrogen sites (Table 3 and Fig. 3a). Neither the biocontrol effort nor the relative fertility hypotheses explained significant variation in *Lythrum* abundance.

Although *Typha* abundance was inversely related to *Lythrum* abundance (Fig. 3b), and the fertility-dependent biocontrol effort hypothesis was supported by our *Typha* abundance data (Table 3), the relative fertility hypothesis was clearly the most plausible model based on Akaike weights (relative fertility AIC_c is 71.6, w_i is 0.910; fertility dependence AIC_c is 76.7, w_i is 0.073; biocontrol effort AIC_c is 79.7, w_i is 0.017). *Typha* cover was highest in sites that had high calcium and phosphorous concentrations and low potassium concentrations in the soil (calcium $\beta \pm SE$, 4.12 ± 1.18 ,

TABLE 2. Selected statistical models for *Lythrum* plant size following backward variable elimination support the fertility-dependent biocontrol effort hypothesis for stem density and the relative fertility hypothesis for maximum height.

Models	df	MS	F	P	β (SE)	R^2
Stem density						
Full model	3, 42	0.25	3.44	0.025		0.197
AGE	1	0.42	5.8	0.021	0.10 (0.04)	
N	1	0.56	7.71	0.008	-1.55 (0.56)	
AGE \times N	1	0.65	8.97	0.005	0.18 (0.06)	
Maximum height						
Full model	2, 43	0.09	4.06	0.024		0.159
N	1	0.09	4.08	0.05	0.18 (0.09)	
K	1	0.16	7.44	0.009	-0.46 (0.17)	

Notes: Parameter estimates (β) and their standard errors (in parentheses) are also given. Both models and all parameters are statistically significant. K is potassium level. See Table 1 for definitions of other abbreviations.

TABLE 3. Selected statistical models for *Lythrum* and *Typha* cover (general linear models) and *Phalaris* presence (logistic regression) following backward variable elimination support the fertility-dependent biocontrol effort hypothesis (although see *Results: Dominant plant cover* for details regarding relative fertility as a better predictor of *Typha* cover).

	df	MS	<i>F</i> or χ^2	<i>P</i>	β (SE)	<i>R</i> ²
<i>Lythrum</i> cover						
Full model	3, 42	4.69	2.15	0.109		0.133
AGE	1, 42	7.57	3.47	0.07	0.43 (0.23)	
N	1, 42	10.8	4.94	0.032	-6.80 (3.06)	
AGE × N	1, 42	12.15	5.56	0.023	0.78 (0.33)	
<i>Typha</i> cover						
Full model	3, 42	4.52	2.62	0.063		0.158
GAL	1, 42	20.26	4.48	0.04	-2.49 (1.17)	
N	1, 42	32.22	7.13	0.011	14.92 (5.59)	
GAL × N	1, 42	26.74	5.92	0.019	-4.17 (1.72)	
<i>Phalaris</i> presence						
Full model	3		9.1	0.028		
AGE	1		2.24	0.134	-0.58 (0.39)	
N	1		4.81	0.028	12.38 (5.65)	
AGE × N	1		4.45	0.035	-1.32 (0.63)	

Notes: Parameter estimates (β) and their standard errors (in parentheses) are also given. For logistic regression, the likelihood ratio χ^2 is reported for the full model and Wald χ^2 for tests of individual parameters. Significant results ($P < 0.05$) are shown in bold and marginally significant ones ($P < 0.10$) in italics. GAL is the total number of *Galerucella* individuals released over time. See Table 1 for definitions of other abbreviations.

$F_{1,42} = 12.2$, $P = 0.001$; phosphorous $\beta \pm$ SE, 1.77 ± 0.85 , $F_{1,42} = 4.27$, $P = 0.045$; potassium $\beta \pm$ SE, -5.31 ± 2.57 , $F_{1,42} = 4.26$, $P = 0.046$; full model $R^2 = 0.245$).

The likelihood of the invasive grass *Phalaris arundinacea* occurring in our sites was only explained by the fertility dependence of biocontrol efforts. Where soil nitrogen was low, *Phalaris* was most likely to occur in sites with older *Galerucella* populations, but in high nitrogen sites, *Phalaris* presence was only weakly related to *Galerucella* population age (Table 3 and Fig. 3c). This pattern suggests that one unintended outcome of reduced *Lythrum* abundance due to *Galerucella* herbivory in our region may be secondary invasion by *Phalaris*.

Correlations among early and late-stage metrics of biocontrol success

Galerucella population density was negatively related to both *Lythrum* stem density and cover (stem density, $r = -0.58$, $P < 0.001$; cover, $r = -0.41$, $P = 0.004$). However, when high- and low-nitrogen sites were analyzed separately, these relationships only held in low-nitrogen conditions, reflecting a decoupling of *Galerucella* densities from biocontrol success in high nitrogen sites (*Lythrum* cover, low N, $r = -0.52$, $P = 0.011$, $n = 23$; *Lythrum* cover, high N, $r = -0.28$, $P = 0.199$, $n = 23$; *Lythrum* density, low N, $r = -0.73$, $P < 0.001$; *Lythrum* density, high N, $r = -0.37$, $P = 0.084$). Percentage of leaf damage was unrelated to *Lythrum* stem density, and cover across all sites and when high- and low-nitrogen sites were considered separately (all $P > 0.35$). Across all sites, soil nitrogen was not significantly correlated with *Lythrum* cover ($P = 0.47$) or height ($P = 0.40$), although stem density was higher overall in high-nitrogen sites ($r = 0.51$, $P = 0.012$).

DISCUSSION

Our data support the fertility-dependent biocontrol effort hypothesis, indicating that although increasing *Lythrum* biocontrol efforts can enhance biocontrol success, such success is less likely to occur in high- vs. low-nutrient sites. Thus, although both top-down and bottom-up effects influence *Lythrum* biocontrol, significant interactions between these processes appear to be important and may help explain at least some of the variation in *Lythrum* biocontrol success that is commonly reported. This is one of the first studies in any system to show that relative site fertility can impact all stages of biocontrol success, from proximate responses (biocontrol agent density) to ultimate outcomes, such as declines in the target invader's size and abundance and increases in neighboring vegetation (see also Coetzee et al. [2007] and Heard and Winterton [2000] for examples with purely aquatic invaders). We realize that by sampling in only a single year we are unable to quantify year-to-year *Lythrum* population dynamics, a common limitation of sampling schemes that substitute space for time. Likewise, because we did not experimentally manipulate site fertility, additional factors we did not consider may have contributed to our findings. However, by surveying a large number of sites across an extensive geographic area, we were able to capture substantial variation in both biocontrol effort and relative site fertility, doing so with sufficient statistical power to test for interactions between them. Given the prevalence of anthropogenic eutrophication (Canfield et al. 2010) and the often scarce resources available for managing invasions using biocontrol, our findings have implications for the optimal selection, management, and monitoring of future *Lythrum* biocontrol release sites. Specifically, our data suggest that *Lythrum* invasions in



PLATE 1. (Left) Characteristic herbivore damage on purple loosestrife (*Lythrum salicaria*) by the biocontrol agent *Galerucella calmariensis*. An adult *G. calmariensis* can be seen in focus on the left side of the image. (Right) A healthy flowering stem of purple loosestrife (*Lythrum salicaria*) in the absence of herbivore damage by *Galerucella* biocontrol agents. Photo credits: S. M. Hovick.

low-nutrient sites be prioritized for biocontrol releases over invasions in high-nutrient ones and seeded with large numbers of biocontrol agents. Alternatively, if high-value sites are strongly eutrophied, then mitigation of anthropogenic nutrient enrichment should be a priority to facilitate biocontrol success (Driscoll et al. 2003, Cherry et al. 2008).

The patterns we found relating *Lythrum* abundance to site fertility and biocontrol effort appear robust and may even be conservative. Although we lack prebiocontrol vegetation data, the absence of a correlation between *Lythrum* abundance and soil nitrogen suggests that our findings do not simply result from larger initial *Lythrum* invasions in the most nitrogen-rich sites. Moreover, qualitative assessments from historical photographs, showing that *Lythrum* abundance was consistently high across sites before *Galerucella* releases, also supports this interpretation (see *Methods*). Furthermore, ours may be a conservative estimate of the degree to which biocontrol success depends on site fertility because of how we measured soil nitrogen. Combustion assays measure all nitrogen including compounds that are metabolically unavailable to plants, a fraction that is often substantial in wetland soils (Brady 1990). And although wetland soils do comprise by far the largest pool of nitrogen in wetlands (Bowden 1987), percent nitrogen in soil is one of the metrics least responsive to nitrogen inputs (Aber et al. 2003, Lu et al. 2011). Thus, with a measure that better captured variability in plant-available nitrogen, we may have explained an even greater degree of variation in biocontrol success than we did. Of course, it is also possible that our measure of soil nitrogen is more closely related to important environmental factors that we failed to measure than it is to plant-available nitrogen, which could weaken our inferences. Future

efforts should therefore focus on measuring plant-available nutrients to better elucidate the patterns we have identified here.

Mechanisms underlying fertility dependence of biocontrol outcomes

Our results may have been driven by the ability of *Lythrum* to tolerate substantial herbivore damage, particularly in high-nutrient conditions. The amount of leaf damage caused by *Galerucella* was not closely related to *Lythrum* abundance, and *Galerucella* abundances were related to *Lythrum* stem density and cover only in low-nitrogen sites. Thus, as has been demonstrated in both biocontrol and nonbiocontrol contexts (Carson and Root 1999, Schmitz et al. 2000, Halaj and Wise 2001, McClay and Balciunas 2005, Cronin et al. 2010), the number of herbivores or the amount of damage does not always correlate well with declines in plant hosts, indicating these early-stage metrics are poor indicators of ultimate biocontrol success. In contrast, the ability to tolerate herbivore damage has been repeatedly associated with invasiveness (Rogers and Siemann 2004, Stastny et al. 2005, Ashton and Lerda 2008, Hovick et al. 2012, Gard et al. 2013), and tolerance often increases with fertilization because of enhanced regrowth made possible by additional resources (Hawkes and Sullivan 2001, Rogers and Siemann 2004, Wise and Abrahamson 2007, Cronin et al. 2010, Sun et al. 2010). We note that we cannot exclude the possibility of resistance mechanisms in *Lythrum* (e.g., defense chemicals or leaf toughness) also increasing in response to site fertility; however, the lack of a significant relationship between leaf damage and site fertility across our sites does suggest that resistance to herbivory has played at most a minor role in our system

(see also Ashton and Lerdau [2008] and Chun et al. [2010]). Despite the potential impact on biocontrol outcomes, few studies have assessed whether highly fertile sites may enable invasives to better tolerate or resist damage from biocontrol agents (but see Sun et al. [2010], Wang et al. [2010]). Such assessments could be critical for the success of biocontrol programs and should be implemented more broadly.

Generalist predation on *Galerucella* could also contribute to our findings, particularly with respect to *Galerucella* abundances. The quarantine testing that occurs prior to any introduction of biocontrol agents, including *Galerucella*, should prevent the presence of their specialist enemies, thereby maximizing the top-down effects of biocontrol agents on target invaders as predicted by the biocontrol effort hypothesis. However, generalist predation on *Galerucella* does occur (Wiebe and Obrycki 2004, Hunt-Joshi et al. 2005, but see Dávalos and Blossey [2010]), and if predators increase with underlying nutrient availability (Oksanen et al. 1981, Sarnelle 1992, Fraser and Grime 1997), then *Lythrum* could be released from top-down herbivore effects in high nutrient sites. If so, this could explain why we observed *Galerucella* abundances increasing (Fig. 1) and *Lythrum* abundances decreasing (Fig. 3a) with increased biocontrol efforts only in low-fertility sites, as well as significantly higher *Galerucella* abundances in lower-fertility sites on average (see Fig. 1 and significant effects of soil N in Table 1). Our data cannot directly address any impact that predation may have had across our sites, and future efforts should attempt to do so; however, we note that even if predation on *Galerucella* underlies the patterns we observed, management implications would likely be identical to those outlined under the fertility-dependent biocontrol effort hypothesis.

As predicted by the relative fertility hypothesis, bottom-up effects best explained variation in *Typha* cover; its abundance was greatest in sites that were high in calcium and phosphorous, resources known to limit *Typha* abundance (Boyd and Hess 1970). However, more so than *Lythrum* abundances (which were likely high across all sites before biocontrol releases), our *Typha* data reflect a combination of preinvasion abundance patterns and postbiocontrol increases that may have occurred following *Lythrum* declines. Thus, we note that although the relative fertility hypothesis fit our data best (based on AIC_c), the fertility-dependent biocontrol effort hypothesis also explained significant variation in *Typha* abundance (Fig. 3b). This suggests that although site fertility is probably the most important consideration, increasing biocontrol efforts in low-nitrogen sites may also contribute to recovery of this important wetland species. More work is clearly needed to assess postbiocontrol responses by this and other nontarget native vegetation. Whole-community recovery should be the ultimate goal of *Lythrum* biocontrol, yet whether the response by *Typha* is indicative of patterns in other species is unknown.

Putting it in context: reconciling contrasting patterns of biocontrol success in response to site fertility

Our results suggest that the likelihood of biocontrol success will decrease as site fertility increases, but how general are these findings? The degree to which they apply broadly will depend on how often top-down control of invaders by biocontrol agents diminishes with increasing site fertility. Where this has been well studied for purely aquatic plant invaders, the results are equivocal: depending on the setting, nutrient enrichment can either reduce biocontrol success (on water hyacinth, see Moran [2006], Coetzee et al. [2007]) or enhance it (on giant salvinia and water hyacinth, see Room and Thomas [1985], Heard and Winterton [2000], Sullivan et al. [2011]). In nutrient-poor sites, moderate nutrient enrichment tends to enhance biocontrol success, relieving insect herbivores from nutrient limitation and enhancing their survival and/or fecundity. Indeed, nutrient enrichment has been used in nonaquatic systems to enhance mass-rearing programs and the establishment of newly introduced biocontrol agents (on *Tripleurospermum perforatum*, see Hinz and Muller-Scharer [2000], and on *Linaria dalmatica* see Van Hezewijk et al. [2008]). In contrast, nutrient enrichment tends to limit biocontrol success above some threshold or in nutrient-rich sites when those nutrients enhance the plant invader's ability to compensate for damaged tissue or better tolerate herbivory (as in our system). There are now well documented cases where biocontrol in eutrophic aquatic systems is thwarted by additional nutrient enrichment (water hyacinth invasions in South Africa, see Coetzee and Hill [2012]), as well as biocontrol success on *Centaurea stoebe* being reduced with nitrogen enrichment manipulations in the field (Knochel and Seastedt 2010). Small-scale experiments with biocontrol agents on the invasives *Alternanthera philoxeroides* and *Hydrilla verticillata* also confirm the pattern illustrated by these latter findings (Wheeler and Center 2001, Sun et al. 2010).

Such opposing patterns of biocontrol success in response to nutrient enrichment across broad gradients in site fertility might be reconciled if there exists a unimodal relationship between site fertility and the likelihood of biocontrol success. We present a graphical model to illustrate this idea in Fig. 4. This hypothesized unimodal relationship is consistent with much ecological theory from studies on how herbivory impacts native plant communities (Oksanen et al. 1981, Sarnelle 1992, Fraser and Grime 1997), in addition to empirical assessments of how herbivore control on dominant plant species varies with nutrient enrichment in both nutrient-rich (*Solidago canadensis* dominated oldfields, see Cronin et al. [2010]) and nutrient-poor environments (*Calluna vulgaris* dominated heath uplands, see Hartley and Mitchell [2005]). If this hypothesis is upheld, we expect that different plant species will vary substantially regarding the range of site fertility at which biocontrol success is more or less likely; thus the *x*-axis in Fig. 4 should be regarded as a relative measure of site fertility

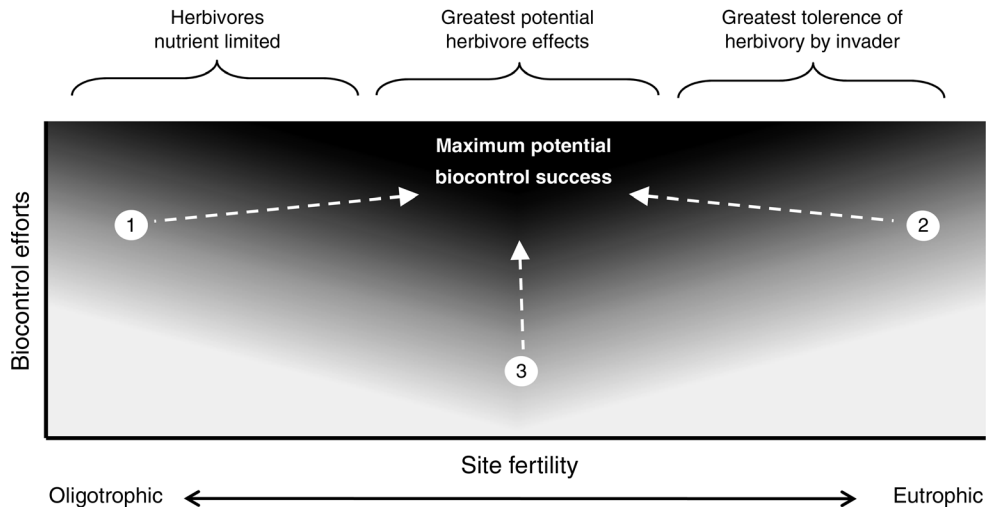


FIG. 4. Generalizing the fertility-dependent biocontrol effort hypothesis to account for conflicting patterns in the literature. In this graphical model, the combination of site fertility and biocontrol effort conditions predicted to yield maximum potential biocontrol success is indicated with darker shading. For any given degree of biocontrol effort (i.e., number of biocontrol agents released, elapsed time since release, etc.), biocontrol success is predicted to respond unimodally to a continuum of site fertility with success most likely at intermediate fertility. Best management practices for enhancing biocontrol outcomes would therefore depend to some extent on where sites are located along a site fertility gradient. For example, in the nutrient-poor conditions encountered by floating aquatic plants that invade oligotrophic waters, nutrient additions can enhance biocontrol success by reducing nutrient limitation in herbivorous biocontrol agents (path 1). In contrast, under eutrophic conditions, such as those commonly encountered by *Lythrum* populations, increasing biocontrol success may require site fertility reductions that impede the invader's ability to tolerate substantial herbivore damage (path 2). Under any site fertility regime, increased biocontrol efforts should enhance possible biocontrol success (path 3), thus both axes could be manipulated independently or in combination to maximize biocontrol success. Note that although this model predicts a unimodal relationship between site fertility and biocontrol success across pest species, we expect a large degree of species-specific variation regarding which values of site fertility may be considered high or low (thus the x -axis represents a relative scale of site fertility and not an absolute one).

and not an absolute one. In practice, the among-species variability we expect would suggest that quantitative estimates of site fertility should be recorded as a standard component of pre- and postrelease assessments in many biocontrol systems, in order to help identify key factors underlying biocontrol success generally. We emphasize that the relationships proposed in Fig. 4 are not well tested and that doing so will require planned experimental manipulations, focusing on meaningful late-stage metrics of biocontrol success and their response to broad variation in nutrient availability.

Implications for *Lythrum* biocontrol

Among invasive plants in the United States, *Lythrum* invasions are some of the most widespread and control costs are among the highest (Pimentel et al. 2005). Although *Lythrum* biocontrol is successful in some sites (e.g., Lindgren 2003, Albright et al. 2004), little is known about what limits success more broadly (Dávalos and Blossey 2010). For example, a survey of 36 *Galerucella* release sites in New York ten years following their initial introduction found that, averaged across all sites, *Lythrum* stem densities and abundances had not decreased over time (Grevstad 2006). Similar to our study, increased biocontrol efforts (number of beetles released) made *Galerucella* population persistence more

likely, yet this did not lead to *Lythrum* reductions (Grevstad 2006). Grevstad postulated that insufficient time had passed for biocontrol to succeed, but because some wetlands did see *Lythrum* reductions, we suggest instead that many sites were simply too nutrient rich for *Galerucella* to control *Lythrum* populations. Variation in water depth may also affect biocontrol outcomes, with deeper water leading to reduced predation on *Galerucella* and increased palatability of *Lythrum* leaf tissue (Denoth and Myers 2005, Dávalos and Blossey 2010). Our data do not permit a robust test of this hypothesis, but the importance of water depth (either independently or in conjunction with site fertility effects) should be assessed in the future. Variable success is common for *Lythrum* biocontrol (Landis et al. 2003, Denoth and Myers 2005, Boag and Eckert 2013), and *Lythrum* is often associated with nutrient-rich soils (Ketterer and Abrahamson 2006); yet the data needed to link *Lythrum* biocontrol success with site fertility have not previously been reported. Our data clearly indicate that variation in site fertility is an important factor for *Lythrum* biocontrol, thus we suggest that future efforts strive to incorporate site fertility measurements into all stages of *Lythrum* biocontrol releases, from prerelease planning to postrelease monitoring.

Ideally, successful *Lythrum* biocontrol should result in rebounding native communities, but an unfortunate outcome that has received increasing attention recently is secondary invasion following the decline of a target invader (e.g., Campbell and McCaffrey 1991, Symstad 2004, Story et al. 2006, Butler and Wacker 2010). In our system, the invasive grass *Phalaris arundinacea* occurred most often in the same conditions that lead to low *Lythrum* abundance, consistent with the secondary invader hypothesis. Anecdotal evidence from three of our sites points to similar increases in *Phragmites australis* abundance following *Lythrum* declines (see also Blossey et al. [2001]). Further study is needed to determine whether these secondary invasions are in fact facilitated by biocontrol-based declines in *Lythrum* (versus other factors such as drought). If so, then successful *Lythrum* biocontrol could potentially lead to invasions that are even more ecologically damaging and difficult to control than the original.

CONCLUSIONS

Our findings indicate that biocontrol effectiveness targeting *Lythrum* may depend not only on sufficient biocontrol efforts but also on local conditions of site fertility, which are increasingly affected by anthropogenic inputs. Given limited resources for invasive species control in governmental and other organizations, it may therefore be sensible to quantify nutrient availability prior to initiating biocontrol releases, account for variation in site fertility when prioritizing sites for biocontrol-based management and postrelease monitoring, and, to the extent possible, modify nutrient inputs where biocontrol releases are common. Previous reports on the effects of nutrient enrichment for biocontrol success have been inconsistent, thus we also propose a general model that may help reconcile these differences and, we hope, inform biocontrol-based management of invasive species across diverse landscapes and divergent systems.

ACKNOWLEDGMENTS

This research was supported by the Mid-Atlantic Panel for Aquatic Invasive Species, the National Science Foundation (DEB-0807817), and the USDA Weedy and Invasive Plants Program (PENR-2000-00885). For assistance in the field and the lab, we sincerely thank Michelle Degnin, Angela Rousch, Michael Dzwonek, Adam Ewing, Andrea Glassmire, David Bacher-Hicks, L. Peter Butz III, Andy Stiff, Sam Miles, and Juli Barron. We thank the editor and the anonymous reviewers for constructive comments and suggestions on earlier versions of the manuscript. Finally, this work would not have been possible without data, permissions, and logistical assistance from many individuals and organizations, including Buckhorn Island State Park, Heritage Conservancy, John Heinz National Wildlife Refuge, Jacobsburg Environmental Education Center, Marsh Creek State Park, Ottawa National Wildlife Refuge, PPL Susquehanna Riverlands, Presque Isle State Park, Silver Lake Nature Center, Wildwood Lake Nature Center, the Ohio Department of Natural Resources, the New York Department of Environmental Conservation, the Pennsylvania Departments of Agriculture and Conservation and Natural Resources, and numerous private landowners.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: <http://dx.doi.org/10.1890/13-2050.1.sm>