

## ARTICLE

## Vegetation Ecology

# From ecological menace to roadside attraction: 28 years of evidence support successful biocontrol of purple loosestrife

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**Abstract**

Introduction and spread of non-native plants provide ecologists and evolutionary biologists with abundant scientific opportunities. However, land managers charged with preventing ecological impacts face financial and logistical challenges to reduce threats by introduced species. The available toolbox (chemical, mechanical, or biological) is also rather limited. Failure to permanently suppress introduced species by mechanical and chemical treatments may result in biocontrol programs using host-specific insect herbivores. Regardless of the chosen method, long-term assessment of management outcomes on both the target species and associated biota should be an essential component of management programs. However, data to assess whether management results in desirable outcomes beyond short-term reductions of the target plant are limited. Here, we use implementation of a biocontrol program targeting a widespread wetland invader, *Lythrum salicaria* (purple loosestrife), in North America to track outcomes on the target plant over more than two decades in New York State. After extensive testing, two leaf-feeding beetles (*Galerucella californiensis* and *Galerucella pusilla*; hereafter “*Galerucella*”), a root-feeding weevil (*Hylobius transversovittatus*) and a flower-feeding weevil (*Nanophyes marmoratus*), were approved for field releases. We used a standardized monitoring protocol to record insect abundance and *L. salicaria* stem densities and heights in 1-m<sup>2</sup> permanent quadrats at 33 different wetlands and followed sites for up to 28 years. As part of this long-term monitoring, in 20 of these wetlands, we established a factorial experiment releasing either no insects (control), only root feeders, only leaf beetles, or root and leaf feeders. We documented reduced *L. salicaria* occupancy and stem densities following insect releases over time, irrespective of site-specific differences in starting plant communities or *L. salicaria* abundance. We could not complete our factorial experiment because dispersal of leaf beetles to root-feeder-only and control sites within 5 years invalidated our experimental controls. Our data show that it took time for significant changes to occur, and short-term studies may provide misleading results, as *L. salicaria* stem densities initially increased

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before significantly decreasing. Several decades after insect releases, prerelease predictions of significant purple loosestrife declines have been confirmed.

#### KEYWORDS

biological control, biological success, herbivory, invasion, long-term monitoring, *Lythrum salicaria*, management

## INTRODUCTION

Plant invasions constitute unplanned large-scale ecological and evolutionary experiments affecting both introduced and native species (Callaway et al., 2004; Colautti & Lau, 2015; Davis et al., 2019; Mack et al., 2000; Sakai et al., 2001). For ecologists, introduced species provide opportunities to address rapid evolution, influence of natural enemies, dispersal, food web dynamics, and competitive hierarchies in plant communities (Blossey & Nötzold, 1995; Keane & Crawley, 2002; Meisner et al., 2014). Conservationists and land managers, on the other hand, view spread of introduced plants as a serious management problem interfering with their ability to safeguard native biota (Vila et al., 2011). Enormous logistical and financial resources are expended in attempts to reduce established populations and limit spread into uninvaded areas (Foxcroft et al., 2014; Martin & Blossey, 2013b). Yet whether introduced species are drivers of ecosystem degradation or simply take advantage of disturbances remains contested (Davis et al., 2011; MacDougall & Turkington, 2005; Simberloff, 2012; van Kleunen et al., 2010).

Biological invasions and their impacts are long-term phenomena (Mills et al., 2003), as species disperse over decades or even centuries from initial introduction sites (Lankau et al., 2009; Stuckey, 1980). Lack of appropriate assessment methods and standardized long-term data to track spread and impacts of introduced plants contributes to divergent views about their importance as drivers of ecological impacts and threats to native species (Blossey, 1999; Boltovskoy et al., 2022; Essl et al., 2017; Martin et al., 2015; Martin & Blossey, 2013a). Because we typically lack long-term data, we also fail to understand how management activities affect not only populations of targeted plants but also their impact on other biota or ecosystem processes.

In the absence of long-term data, land managers instead often rely on a plant species' non-native origin and rapid spread and increase in local abundance as reasons to attempt control. Underpinning this philosophy are assumptions that increases in introduced species abundance create undesirable environmental conditions and that reducing local abundance of introduced species

should mitigate or reverse impacts while improving conditions for native species. Herbicide application (primarily glyphosate) is the most widespread control method (Wagner et al., 2017; Weidlich et al., 2020), but even if it reduces cover or abundance of target plants, this is not necessarily followed by increases in native plant diversity or abundance (Kettenring & Adams, 2011; Louhaichi et al., 2012; Rinella et al., 2009; Skurski et al., 2013). Replacement communities are often dominated by other introduced species, or the initially targeted introduced plants quickly recolonize managed areas, requiring repeat treatments.

Weed biological control (hereafter “biocontrol”), the introduction of host-specific natural enemies from the native range of an introduced plant, is often an option of last resort (McFadyen, 1998; Schwarzlander et al., 2018). Some biocontrol programs are spectacularly successful, such as the classic examples of suppression of prickly pear (*Opuntia stricta*) or giant salvinia (*Salvinia molesta*) in Australia, water hyacinth (*Eichornia crassipes*) in South Africa, and other introduced floating aquatic plants (Forno & Julien, 2000; Freeman, 1992). Indeed, not all biocontrol programs are so visibly successful—many even fail (McFadyen, 1998; Schwarzlander et al., 2018). However, about a third of biocontrol programs are considered successful, leading to declines in target plant populations and greatly reduced needs to use other management methods (McFadyen, 1998; Moran et al., 2005; Schwarzlander et al., 2018). Suppression of Klamath weed (*Hypericum perforatum*) in California; leafy spurge (*Euphorbia esula*) in the Western United States; musk thistle (*Carduus nutans*), ragwort (*Jacobaea vulgaris*), and heather (*Calluna vulgaris*) in New Zealand (Butler et al., 2006; Crawley, 1989; Fowler et al., 2024; Lesica & Hanna, 2009; Peterson et al., 2020) are such examples. Yet, despite an overwhelming safety record (e.g., Suckling & Sforza, 2014), biocontrol remains controversial (Havens et al., 2019a), often because of suspicion of the existence of undocumented nontarget effects (e.g., Louda & Stiling, 2004; Simberloff & Stiling, 1996) and poor quantification of efficacy (Havens et al., 2019a).

Public acceptance of biocontrol is also underwhelming in many regions of the world, including the United States

(Simmons et al., 2024). This lack of acceptance may reflect many unknowns in management: managers often operate without knowing the full impacts of targeted introduced species, and they either do not collect or do not publish information on long-term impacts of their management methods (which is not unique to biocontrol). For weed biocontrol programs, widespread implementation of outcome assessments is often prevented by logistical difficulties, the need to assess outcomes for extended time periods, and resistance to fund monitoring (Blossey, 1999; McFadyen, 1998). However, continued support for biocontrol, and other methods of introduced species management, relies on public trust and public resources, and decades-old calls to monitor long-term management impacts need to be answered (Huffaker & Kennett, 1959; Schroeder, 1983).

Implementing biocontrol for *Lythrum salicaria* (purple loosestrife), for example, showcased many of these social tensions and controversies. At the time of this program's initiation 30 years ago, overwhelming evidence suggested that (1) *L. salicaria* was negatively affecting native species and their habitats (Blossey et al., 2001), while (2) decades of unsuccessful management, particularly chemical treatments, were accelerating demise of native wetland species, furthering ecological dominance of *L. salicaria* (Blossey et al., 2001). Consequently, starting in 1992, four host-specific insect species attacking flowers, leaves, and roots were released and distributed across North America (Hight et al., 1995; Malecki et al., 1993). Managers embraced this program, but some academics opposed biocontrol (Hager & McCoy, 1998), arguing for more peer-reviewed publications quantifying *L. salicaria* impacts and more elaborate trials of mechanical, physical, or chemical control efforts before releasing herbivores.

We agree with the fundamental need for better and longer term assessments of impacts of invasions and impacts of different management methods (Blossey, 1999, 2016). To this end, we developed a standardized monitoring protocol (Blossey et al., 2015) to capture insect impact, response of *L. salicaria*, and response of the associated wetland plant community (including potential nontarget effects) over a period of up to 28 years. Here we focus on biological success, defined as reductions in the target population through management (Blossey, 2016). We ask the following question: did the released insects establish and then permanently suppress *L. salicaria* abundance? In our companion paper (Endriss et al., 2024), we address ecological success, defined as increases in native and overall plant diversity as a function of *L. salicaria* declines, and also address the fate of species considered to be at potential risk of attack by the introduced herbivores.

## METHODS

### Target species

*L. salicaria* is a long-lived perennial, and individuals may live for decades under seasonally moist to permanently flooded conditions. Annual shoots sprout from woody rootstocks in early spring and grow quickly (>1 cm/day) to 2 m or more by August. Plants develop large crowns with multiple stems bearing showy magenta flowers in long spikes. In New York State, plants can begin flowering in late June and may bloom into September.

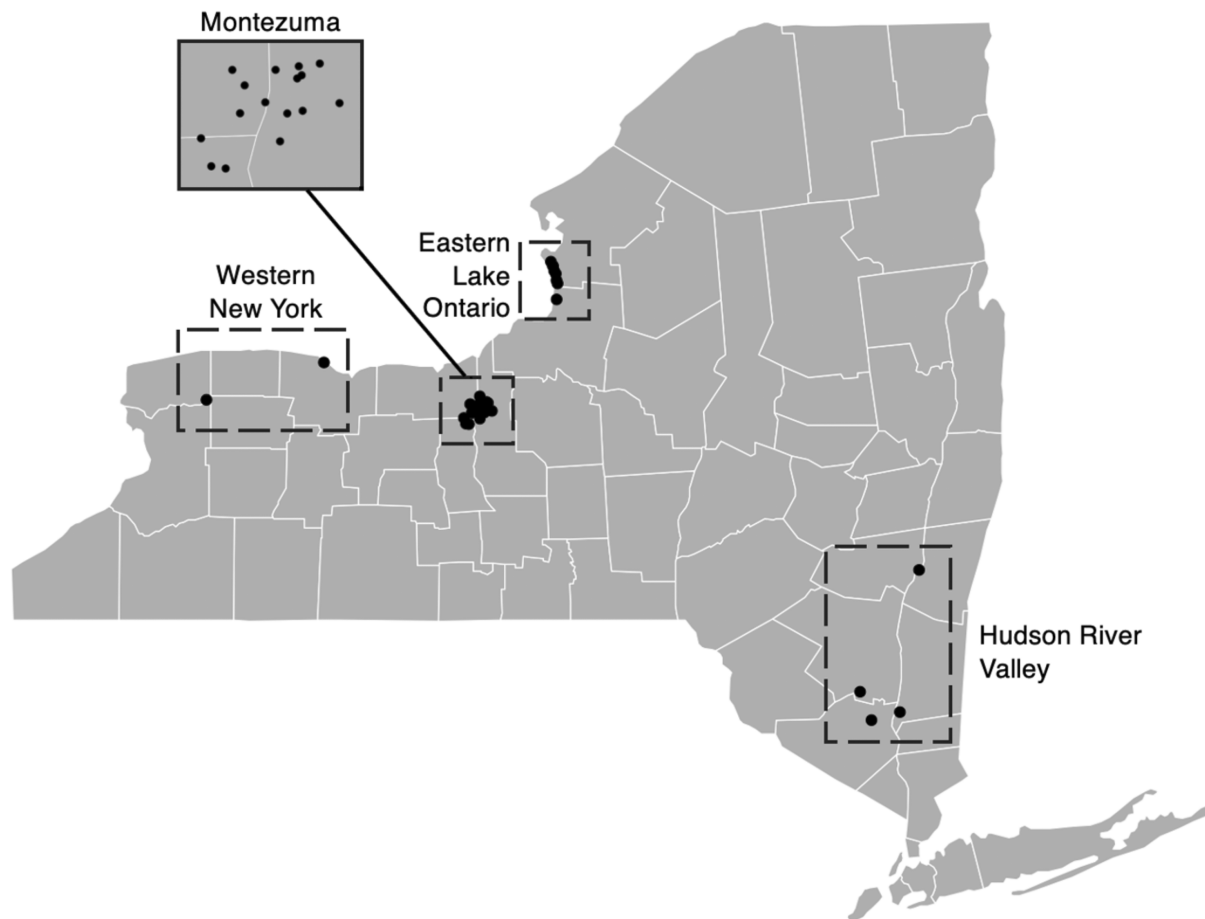
### Data collection and experimental design

We worked at 33 sites (mix of federal, state, and private ownership) varying in size from a few hundred square meters to >10 ha across New York State (Figure 1; Appendix S1: Table S1). Initially, most sites (old fields, wetlands, marshes, and impoundments) were dominated by *L. salicaria*, although some releases occurred where managers documented only small patches. Water levels varied through time, reflecting natural variation in precipitation patterns, beaver activity, and intentional manipulations by wetland managers and private landowners.

We monitored each site for a period of 15–28 years, starting the year insects were first released (Appendix S1: Table S1). Releases included one or several of the following species: two leaf-feeding beetles (*Galerucella californiensis* and *Galerucella pusilla*), a root-feeding weevil (*Hylobius transversovittatus*), and a flower-feeding weevil (*Nanophyes marmoratus*). Detailed information of the insects, their life cycle, and current distribution in North America is available in Blossey and Endriss (2023).

We released *Galerucella* adults from May to July and *H. transversovittatus* adults throughout the growing season in accordance with seasonal activity patterns (Blossey, 1993, 1995). We released initially at two sites in western New York (1992 and 1995), followed by four sites in the Hudson River Valley (1995–1998), 15 sites in the Montezuma Wetlands Complex in central New York (1999–2000) and at eight sites along eastern Lake Ontario (2006) (Appendix S1: Table S1). Montezuma releases were part of a factorial study (20 sites, at least 2 km apart) where we assessed independent and interactive effects of leaf and root feeders. We randomly assigned five sites each to *Galerucella* only, *Hylobius* only, *Galerucella* plus *Hylobius*, or no insects (control). Unfortunately, we lost one control site to development.

At each site, we established 1–15 1-m<sup>2</sup> permanent quadrats spaced 5–50 m apart along a predetermined



**FIGURE 1** Location of 33 long-term monitoring sites across four regions in New York State, USA.

transect. While the presence of *L. salicaria* was a prerequisite for initial quadrat placement, we rigorously adhered to a random placement of quadrats, only selecting another random placement if the first quadrat location did not contain purple loosestrife. In our region, *L. salicaria* is well established and wetlands have long-term presence of populations that are stable and not undergoing short-term fluctuations. We were not attempting to assess local or regional spread since locating areas without *L. salicaria* presence at our sites was rare, except for some sites along Lake Ontario. Here, we found only a few isolated patches limiting our ability to place quadrats, but plants were mature with well-developed rootstocks. The number of quadrats and distance between quadrats was dictated by *L. salicaria* population size. We used 1.5-m tall PVC (2.53 cm diameter) poles to mark each corner of each quadrat and recorded GPS position and hand-drew maps indicating distance and azimuth to help relocate quadrats. Over the 28 years, individual poles and occasionally all poles of a quadrat disappeared; we used GPS and field notes to reestablish quadrats as close to the original position as possible.

Using a slightly expanded monitoring protocol, we recorded detailed data about *L. salicaria* growth and reproduction, the presence and abundance of released insects and co-occurring plant species at each site. We initially visited all sites twice annually. In June, we counted *L. salicaria* stem density, estimated *L. salicaria* cover (in percentage) and recorded *Galerucella* abundance using timed counts (1 min each for eggs, adults, and larvae) and made visual assessments of leaf area removed (in percentage). We did not record the presence for *H. transversovittatus* as larvae feed in roots, and adults are night active, preventing detection without destructive sampling. We also did not record the presence of *N. marmoratus*. However, during our last sampling in 2019, we recorded the presence of flower-feeders and assessed root feeder presence at all sites, except those that were permanently flooded, by excavating rootstocks and checking for larval feeding damage.

In September, in each quadrat, we recorded *L. salicaria* stem density and cover (in percentage) and, for the five tallest stems, height, number of inflorescences, length of the tallest inflorescence, and number of flower buds in the central 5 cm of that inflorescence.

Depending on insect releases, we recorded data for variable time periods at each site between 1996 and 2007 (Appendix S1: Table S1), and again at all 33 sites in August and September 2019. We anticipated that measuring the five tallest stems would be a time-efficient way to assess growth and reproductive activity while increasing participation by non-academics. A similar method was used to assess outcome of wolf (*Canis lupus*) releases reducing elk (*Cervus elaphus*) browse intensity at Yellowstone National Park on aspen (*Populus tremuloides*) recovery (Ripple & Beschta, 2007). To assess if measuring only the five tallest stems accurately reflected *L. salicaria* performance, we measured height and flowering status of all *L. salicaria* stems at Montezuma sites in all years, and at all sites in September 2019.

## Statistical analyses

Generalized additive mixed models (GAMMs) can accommodate nonlinear relationships between predictor and response variables via smoothing splines (Hastie & Tibshirani, 1990). As initial plots of raw data indicated nonlinear annual fluctuations in metrics of *L. salicaria* performance, we used the `gamm4` function (Wood & Scheipl, 2017) in R v. 4.1.3 (R Core Team, 2022) to fit GAMMs to data of the proportion of quadrats occupied by *L. salicaria* (binomial) and stem density of *L. salicaria* within occupied quadrats (negative binomial) for 29 monitored sites where insects were released (Appendix S1: Table S1). For the five tallest *L. salicaria* stems within each quadrat, we also fit GAMMs to evaluate changes in stem height (Gaussian) and fertility (binomial) and—if stems were fertile—number of inflorescences per stem (log-transformed and Gaussian), length of the longest inflorescence (square-root-transformed, Gaussian), and flower density (square-root-transformed, Gaussian). In all full models, we included random intercept effects of calendar year and quadrat nested within site as well as fixed effects of longitude, latitude, and (except for GAMMs fit to occupancy data) *L. salicaria* stem density at start of monitoring (log-transformed). We also included a fixed effect of stem height for full models fit to proportion of fertile stems, number of inflorescences, and flower density, as well as a fixed effect of inflorescence length (square-root-transformed) in our full model fit to flower density.

For each performance metric, we fit candidate models two ways: with a single thin plate regression spline for number of years after biocontrol agents were first released (hereafter “time”) across all sites or with a separate spline for time for each sampling region. We then

used stepwise selection with corrected Akaike information criterion ( $AIC_c$ ) to identify the most parsimonious (hereafter “best”) model from a set of candidate models (Burnham & Anderson, 2002). Prior to running analyses, we used variance inflation factors (VIFs) to confirm our fixed effects did not exhibit strong collinearity ( $VIF < 5$ ) (Zuur, 2009). We fully report all candidate models and summaries of the best models in Appendix S1: Tables S2–S10. We summarize the best models in Table 1.

To test whether the five tallest stems were a reliable proxy of all stems, we used the R function `aictab` to select the “best” of our linear mixed-effects models (Gaussian distributions) evaluating whether change in mean *L. salicaria* stem height over time was influenced by whether we tracked all *L. salicaria* versus only the five tallest *L. salicaria* stems per quadrat. We fit models to a reduced dataset including only sampling period by site combinations where data on all *L. salicaria* stems per quadrat were recorded. We included random intercepts of calendar year and quadrat nested within site for all models. In our full model, we included fixed effects of the measurement method (all stems vs. five tallest stems), time, and stem density (log-transformed).

## RESULTS

*Galerucella* established rapidly at most release sites, often within a single year (Appendix S1: Table S1). Within Montezuma (the only region with “no insect” control sites), *Galerucella* quickly dispersed to control sites, on average spreading ~1 km per year (Figure 2a). Yet, herbivory was still initially higher for sites where *Galerucella* and/or *H. transversovittatus* had been released compared with neighboring control sites (Figure 2b). Across all Montezuma sites, herbivory levels doubled within 1–4 years following insect releases, even at control sites (Figure 2), which paralleled increased *Galerucella* abundance over time (Figure 3). Across all regions, *Galerucella* was detected within 1 year at 19 of 24 release sites and was detected at all but two sites over time (Appendix S1: Table S1). *L. salicaria* was also more likely to be damaged if we detected *Galerucella* eggs within the quadrat (Appendix S1: Figure S1).

When we began monitoring (1996–2007), all 340 quadrats across 33 sites contained *L. salicaria*. However, by 2019, *L. salicaria* occupied only 60% of 329 remaining quadrats and was absent across all permanent quadrats for four of the 33 sites (this does not necessarily indicate complete eradication in these sites). Stem densities on average had declined 85% across sites (Figure 4). In line with these data, our best models (Table 1) indicated that

**TABLE 1** Summary of best models fit to data of biological success.

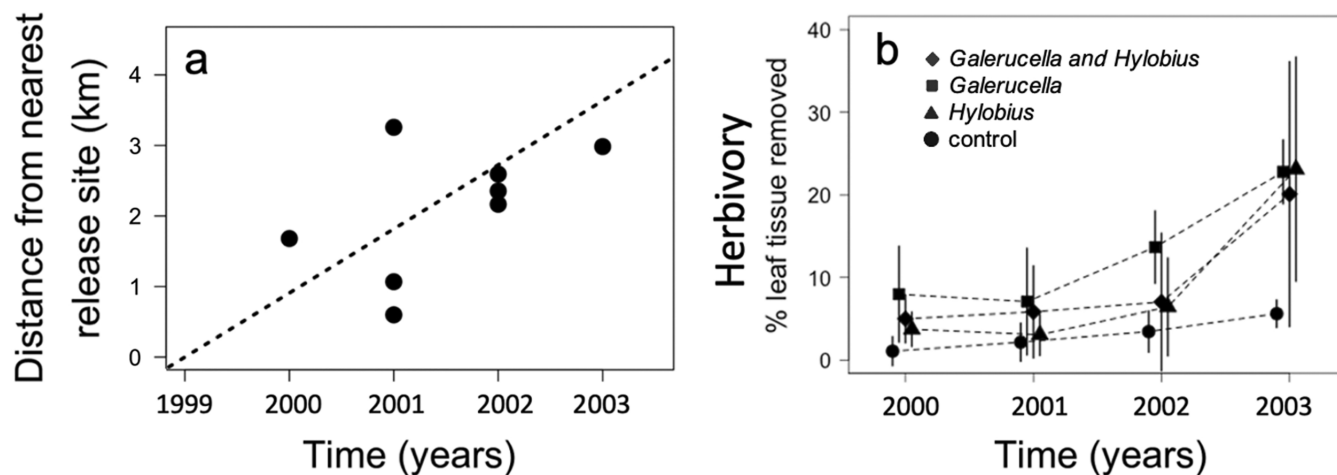
Response	Best model	Adj. $R^2$	Adj. $w_i$	Model interpretation	Figures and tables
All stems					
Occupancy	Single spline + latitude	0.35	0.68	Across all regions, the proportion of quadrats occupied by <i>Lythrum salicaria</i> initially increased then decreased over time ( $p < 0.001$ ); fewer quadrats were occupied the further north the site ( $p = 0.01$ ).	Figure 4c; Appendix S1; Table S2
Stem density	Single spline + initial stem density + longitude	0.49	0.67	Across all regions, stem density initially increased then more strongly decreased over time ( $p < 0.001$ ); stem density was higher the further east the site ( $p < 0.001$ ) and the higher the initial stem density ( $p < 0.001$ ).	Figure 4d; Appendix S1; Table S3, Figure S2
Five tallest stems					
Stem height	Single spline + initial stem density + longitude + latitude	1.53	0.96	Models are a poor fit—factors other than time, stem density, and location likely influence changes in stem height.	Appendix S1; Table S4
Proportion of fertile stems	Splines by area + stem density + stem height + longitude	0.35	0.55	The manner in which the proportion of fertile stems changed over time was regionally variable; stems were more likely to be fertile the taller they were ( $p < 0.001$ ) and the further east the site ( $p < 0.01$ ).	Appendix S1; Figure S3, Table S5
No. inflorescences	Splines by area + stem height + initial stem density	0.30	0.50	Whether and the manner in which the no. inflorescences changed over time varied by region; the no. inflorescences decreased as stem height decreased ( $p < 0.001$ ) and initial stem density increased ( $p < 0.001$ ).	Appendix S1; Figure S3, Table S6
Inflorescence length	Splines by area + stem height + initial stem density + latitude	0.37	0.62	Inflorescence length did not change over time in three regions, but became longer then shorter over time within one region; inflorescence length decreased as stem height decreased ( $p < 0.001$ ), initial stem density increased ( $p < 0.01$ ), and the further north the site ( $p < 0.001$ ).	Appendix S1; Figure S3, Table S7
Flower density	Splines by area + inflorescence length + stem height + longitude + latitude	0.18	0.59	The manner in which flower density changed over time varied by region; flowers were less dense; the shorter the stem ( $p < 0.001$ ), the shorter the inflorescence ( $p < 0.001$ ), and the further west the site ( $p < 0.01$ ).	Appendix S1; Figure S3, Table S8

Note: Following Burnham and Anderson (2002), we identified the best model as the model with the lowest corrected Akaike information criterion value. Tables and figures labeled with an “S” are found in Appendix S1.

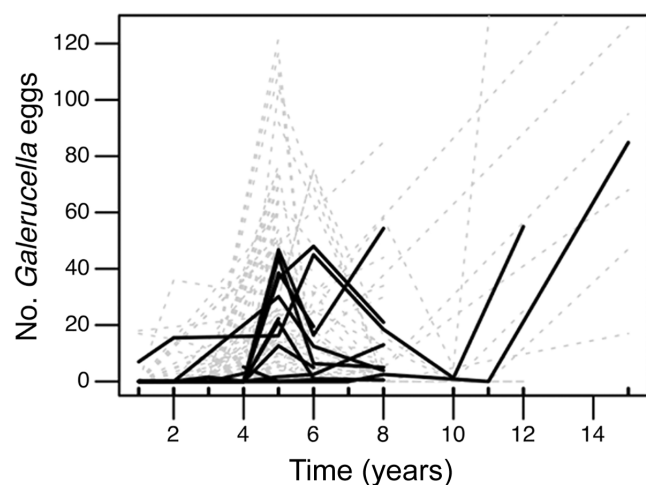
Abbreviation: Adj., adjusted.

both proportion of quadrats occupied and *L. salicaria* stem density per quadrat briefly increased the first few years following insect releases, and then declined over longer periods of time (Figure 4). Declines were only significant more than a decade after initial insect releases (Figure 4), a pattern that was consistent across regions (Table 1, that is, the best models included a single spline for time;  $p < 0.001$  for both occupancy and stem density).

In contrast, the best models suggested that how the performance of the five tallest *L. salicaria* stems per quadrat changed over time was regionally variable; models performed better with separate splines for each region versus a single spline for time across all sites (Table 1). Despite regional variation, performance of the five tallest *L. salicaria* stems per quadrat either did not change over time, or typically mirrored how *L. salicaria* presence and



**FIGURE 2** (a) Annual *Galerucella* dispersal distance as a function of distance to the nearest release site. The dotted line depicts a linear line of best fit with a fixed intercept of zero. *Galerucella* are capable of dispersing more than a kilometer per year and individuals were detected at all 19 sites by 2003, including at control and *Hylobius transversovittatus*-only sites. (b) Herbivory on *Lythrum salicaria* over time at 19 sites at Montezuma where either *Galerucella* ( $N = 6$ ), *H. transversovittatus* ( $N = 5$ ), both species ( $N = 4$ ), or neither species (control,  $N = 4$ ) were released starting in 1999 and 2000, respectively (Appendix S1: Table S1). Herbivory data were first collected in 2000. Data are means  $\pm$  1 SD.



**FIGURE 3** Number of *Galerucella* eggs detected within 1-m<sup>2</sup> quadrats over time, starting with the year of release (not all sites had the same length of observation period). Gray dotted lines connect actual values across time for each quadrat. Dark, solid lines connect mean values (averaged across quadrats) over time for each site where *Galerucella* were released singly or in combination. The tick marks on the inner margin of the x-axis show when data were collected.

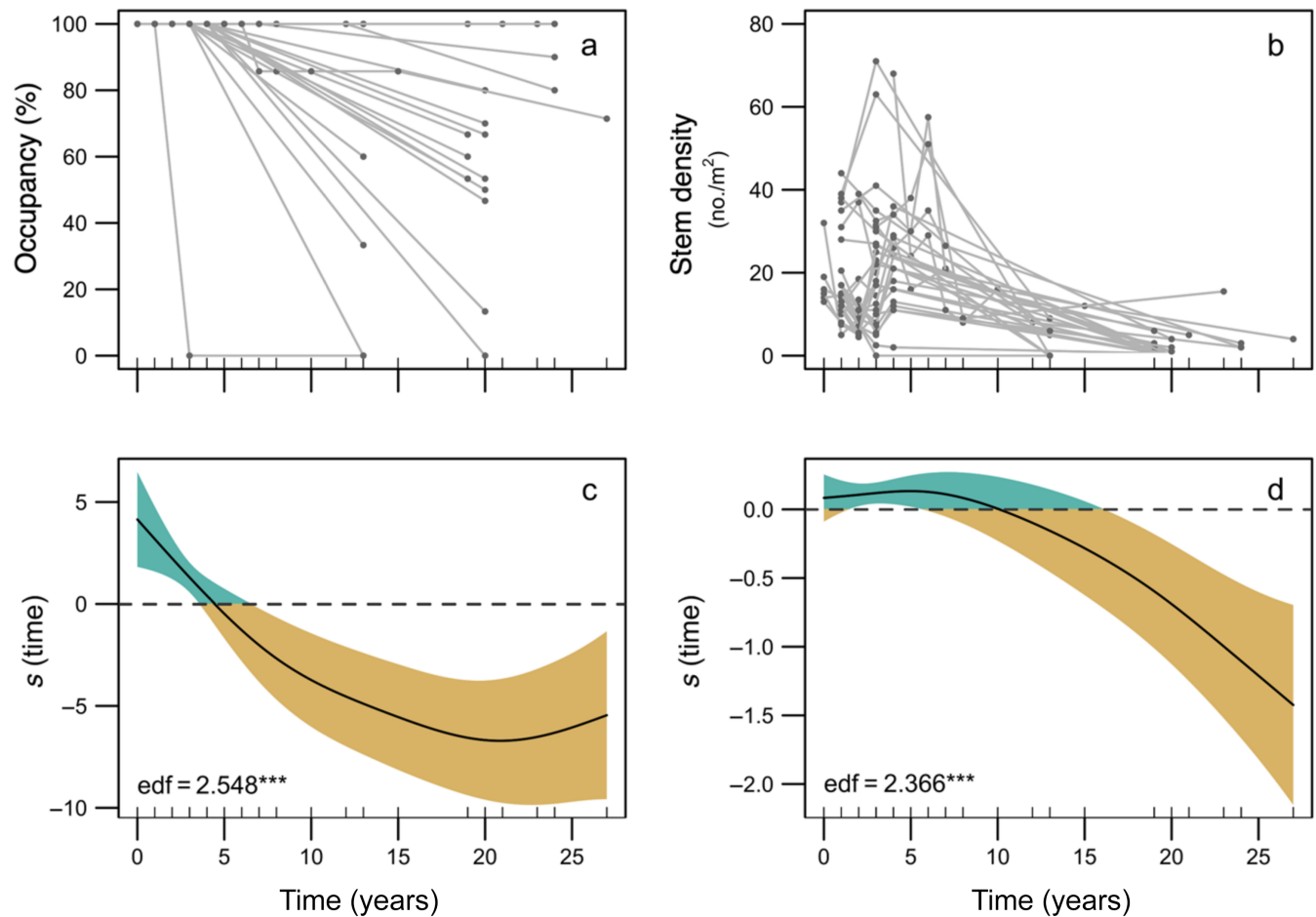
stem density changed over time (Appendix S1: Figure S3). Stem height was a significant predictor for all measured metrics of performance of the five tallest stems (Table 1), yet this relationship between stem height and stem density was mediated by whether we fit our model to data of the five tallest versus to all stems within a quadrat

(Figure 5; stem density  $\times$  method (five tallest vs. all stems) interaction:  $p < 0.001$ ).

## DISCUSSION

We report strong evidence that biocontrol herbivores quickly established, spread, and over time significantly reduced *L. salicaria* stem densities. We observed consistent sustained suppression following herbivore releases across 33 diverse wetlands in New York State, despite among-site variation in location, plant communities, and a diversity of other factors (Table 1: best abundance models include a single spline rather than multiple splines by “area”). Our data support similar evidence in the *L. salicaria* system that regional differences do not appear to reduce the potential for biological success despite site-to-site variation in the impact of biocontrol, insect predators, diseases, and site conditions (Boag & Eckert, 2013; Britton et al., 2014; Dávalos & Blossey, 2010; Hunt-Joshi et al., 2005; Landis et al., 2003; McAvoy et al., 2016; Piper et al., 2004; Skinner et al., 2006). However, our analyses are especially powerful given the spatial and temporal breadth of our data. While funding and logistical constraints often limit length of long-term studies (Agrawal & Maron, 2022; Blossey, 1999; McFadyen, 1998), we were able to monitor herbivores and the fate of more than 30 *L. salicaria* populations for 13–28 years.

Our evidence at the field site level complements and extends previous experimental work demonstrating



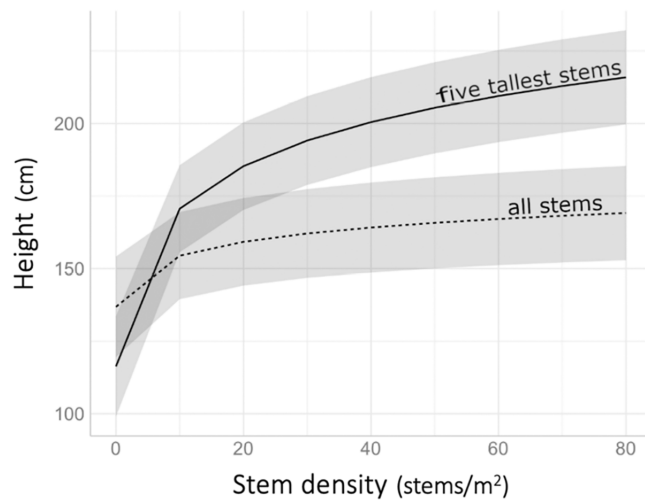
**FIGURE 4** (a) Probability that quadrats are occupied by *Lythrum salicaria* and (b) *L. salicaria* stem density over time. Gray lines connect mean or median quadrat values (for occupancy vs. stem density, respectively) for each sampled year within each unique site. (c, d) Corresponding derivative curves (i.e., generalized additive mixed model splines) for models evaluating (c) occupancy and (d) stem density. Solid black lines represent model estimates for the slope of the relationship between occupancy or stem density over time, while shading represents 95% credible intervals—green for when *L. salicaria* is predicted to increase with time (i.e.,  $y > 0$ ) and orange for when *L. salicaria* is predicted to decline with time (i.e.,  $y < 0$ ). Estimates are significant if 95% credible intervals do not overlap with the x-axis (i.e.,  $y \neq 0$ ). The estimated df (edf) represents the “wiggleness” of the curve—edf values increase the more “turns” in the derivative curve. Edf values approaching one represent an increasingly linear relationship between the derivative and time (\*\*\* $p < 0.001$ ; splines are considered significant if  $p < 0.02$ , as per Wood, 2006). The tick marks on the inner margin of the x-axis show when data were collected.

impacts of leaf- and/or root herbivory on individual plant performance (Hunt-Joshi & Blossey, 2005; Nötzold et al., 1998; Schat & Blossey, 2005), and on plant populations (Hunt-Joshi et al., 2004). We were unable to disentangle the relative impact of individual herbivores, or herbivore combinations, in driving this success; our experimental set-up at Montezuma was overwhelmed by rapid dispersal of leaf beetles to both control and root-feeder-only sites (Figure 2a), thus rendering our design obsolete. We did not quantify the presence of root-feeding *Hylobius* and flowering-feeding *N. marmoratus*, but we observed both species at most sites in 2019 (the last year of monitoring), and they can now be found across New York, sometimes even on isolated plants. We consider our

evidence that the released insects drove observed declines in *L. salicaria* persuasive.

Some suggest experimental “no insect” controls are essential to document biological success in weed biocontrol programs, as other factors (such as climate, weather, density dependence, and other natural enemies) also could drive population declines over time (Havens et al., 2019a, 2019b). We agree that experimental control to assess impacts of insect herbivores on plant populations can be an important part of well-designed biocontrol programs, but it is not essential. We caution, for example, that some experimental control methods suitable for laboratory settings are not appropriate for field studies. For example, sometimes insecticide applications fail to reduce





**FIGURE 5** Estimated marginal means and 95% confidence bands for the height of the five tallest *Lythrum salicaria* stems versus all *L. salicaria* stems as a function of *L. salicaria* stem density. Above a certain stem density ( $\sim 25$  stems/m<sup>2</sup>), sampling only the five tallest *L. salicaria* stems overpredicts average *L. salicaria* stem height.

herbivory by biological control agents on the target plant (Paynter, 2005). Furthermore, nonselective pesticides target all insects, resulting in reduced herbivore, predator, or pollinator loads on nontarget plant species, with unintended consequences that make interpreting outcomes difficult (Agrawal & Maron, 2022; Lonsdale & Farrell, 1998). Treatments would also need to be continued at large scales for many years, in our case decades. We consider this unnecessary, ecologically inappropriate due to the nontarget effects, and logistically difficult given financial costs and difficulties in permitting pesticide use in wetlands. Furthermore, while we explored caging plants as an alternative to insecticide exclusion for assessing interactions between leaf and root feeders of *L. salicaria* (Hunt-Joshi et al., 2004), caging can affect insect dispersal (both herbivores and their predators), pollinators, as well as plant growth and plant demography. We do support using demographic models in biocontrol programs (Blossey, 2016; Blossey et al., 2018) to forecast insect impacts, but for a plant species able to live for decades, with a long-lived seedbank, and seedling recruitment dependent on disturbances, we believe the utility of such models in this or similar systems is limited.

Further evidence for the crucial role of herbivores in driving the decline in *L. salicaria* abundance versus influences of changes in climate, hydrology, or other unknown potential factors, come from thriving roadside populations (Rogers et al., 2022). While unintentional, mowing or herbicide treatments during the growing season effectively remove food for adults and larvae,

particularly for the leaf and flower feeders. This results in a local crash of herbivore populations, while *L. salicaria* quickly resprouts and plants even flower late into the season, which is particularly obvious along roadsides. Similarly, *L. salicaria* continues to thrive in the Fraser and Columbia Rivers in the Pacific Northwest, where tidal influences limit the capabilities of specialized insects to suppress *L. salicaria* populations by flushing eggs and larvae of biocontrol herbivores away (Denoth & Myers, 2005).

While negative soil feedback can over time cause declines in some introduced plant populations (van der Putten et al., 2013), such suppressive effects by soil microbiota have never been reported for *L. salicaria*. Seedlings rapidly establish after drawdowns or disturbances but are then quickly eliminated by dispersing biocontrol herbivores. A strong indication that plants are more sensitive to short-term fluctuations in insect herbivory rather than negative soil feedback processes is the quick resprouting of defoliated individuals as soon as leaf beetles cease feeding, typically in late July or August in our region. This late flush of stems does not exclude other species or reverse the negative impacts of the herbivores on plant populations, but probably is slowing population reductions. Taken together, we find no evidence for other alternatives that could explain the population reductions we observed, despite the absence of control sites.

Our results may appear to contradict earlier, shorter investigations in New York. Hovick and Carson (2015) used snapshot assessments during a single visit to sites in three states to conclude that *L. salicaria* suppression by *Galerucella* was more likely in low-fertility sites. Grevstad (2006) visited *Galerucella* release sites 10 years after initial releases and reported some plant height reductions for *L. salicaria* but no change in abundance. Sites selected by Grevstad (2006) included many roadside populations, which, as discussed earlier, often experience maintenance operations that constitute high disturbance events and may decrease biocontrol efficacy. However, in our investigations, stem density declines only became statistically significant 7–15 years after initial insect releases (Figure 4d). Thus, similar to our study using large walk-in cages over 4 years (Hunt-Joshi et al., 2004), Grevstad's resampling after a decade may have been too early to capture the long-term changes we report. Single visits to gauge biological success cannot capture long-term dynamics and may be strongly biased by herbivore and plant abundance fluctuations during the first decade after releases (Figure 3). These fluctuations may be driven by local factors or metapopulation dynamics and are therefore not synchronized across the landscape. Yet, we show biological success was consistently achieved across sites irrespective of pronounced differences in

hydrology, plant communities or other environmental gradients.

Our understanding of herbivory in this system is supported by our models. Increases in insect abundance paralleled increases in herbivory (Figure 3), indicating that herbivory by biocontrol herbivores drove the observed changes in *L. salicaria* abundance. Spring or early summer defoliation events cause *L. salicaria* stems to lose their apical dominance, in turn increasing branching (and thus stem density) of *L. salicaria* in fall. Additionally, defoliation events rarely spell the immediate demise of perennial plants, which can reallocate resources from their rootstocks to support aboveground growth, leading to pronounced time lags between herbivory and the impacts of that herbivory on plant performance. Taken together, this may explain the predicted increase in *L. salicaria* stem density and occupancy 1–6 years following insect releases (Table 1, Figure 4), with declines in *L. salicaria* abundance and occupancy only becoming statistically significant many years after initial insect releases.

At the initiation of the biocontrol program, Malecki et al. (1993) predicted that quick establishment of all insects, rapid dispersal specifically of the leaf beetles, and spectacular defoliations by leaf beetles will garner widespread attention. Three decades later, we can confirm that the authors were correct in their anticipation. We are unable to confirm or reject a further hypothesis that a combination of root and leaf feeders would be more effective because our Montezuma experiment failed to keep experimental treatments as designed for a sufficiently long period due to rapid dispersal of leaf feeders (Figure 2a). We also did not closely follow populations of *H. transversovittatus*, and we know comparatively little about its distribution and abundance in North America (Blossey & Endriss, 2023). While not as obvious, the slow destruction of root reserves likely contributes substantially to the overall biological success and should not be disregarded. Mesocosms and caged field experiments suggest an important role for root feeders (Hunt-Joshi et al., 2004).

We also found strong support for the claim that biocontrol would dramatically decrease the regional abundance of *L. salicaria* populations, perhaps even surpassing initial predictions by Malecki et al. (1993) of a 90% decline in *L. salicaria* abundance over time. Our study was not designed to assess a reduction in *L. salicaria* dispersal, although that is another important aspect of success in biocontrol programs. However, at the end of our nearly three-decade monitoring period, we found *L. salicaria* was absent in 40% of the monitored quadrats. Additionally, for the quadrats where *L. salicaria* did persist, its stem densities declined, on average, by 85%, and were still predicted

to be in decline by the end of monitoring in 2019 (Figure 4d). Surveys of roadside populations also support that both leaf-feeding *Galerucella* and flower-feeding *N. marmoratus* are strong dispersers often observed on single isolated *L. salicaria* plants. Overall, we therefore find unprecedented support that specialized herbivores have successfully reduced *L. salicaria* abundance across decadal timescales and diverse environmental conditions. Although we do not know of similar long-term assessments elsewhere, we expect that our results from New York extend through much of the range of *L. salicaria* in North America. However, there are many remaining unknowns, especially surrounding the establishment and spread of *Galerucella* in the Southeast and in areas where purple loosestrife is less abundant (Endriss et al., 2022).

Overall, establishing standardized long-term monitoring protocols is key to interpreting whether our management actions (or inaction) result in the desired outcomes over ecologically relevant periods of time. Yet, selecting appropriate metrics to accurately evaluate predefined metrics of success is equally critical to investigating ecological outcomes over time. For example, we developed a standardized monitoring protocol that suggested measuring only the five tallest stems within a quadrat, to reduce sampling effort to encourage participation by land managers and citizen scientists. We expected this could retain scientific rigor but found that the common method of measuring only the five tallest stems may overexaggerate long-term trends, especially declines in plant performance over time (Figure 5). Our findings mirror those of Brice et al. (2022) who documented that nonrandom sampling of the 10 tallest *P. tremuloides* saplings in Yellowstone National Park overestimated reductions in elk browse intensity. The five tallest stems within each quadrat were therefore an unreliable proxy for estimating changes in target plant populations. These are important insights into best practices when developing other standardized long-term assessment protocols.

We followed long-standing recommendations to remove uncertainty of biocontrol outcomes by evaluating biological success of agent releases. Here, we take the first step in documenting biological success, that is, reductions in target plant abundance. We expand on these findings in our companion paper (Endriss et al., 2024), providing evidence that *L. salicaria* abundance reductions (i.e., biological success) leads to plant community recovery (i.e., ecological success), indicating that increased abundance and dominance of *L. salicaria* was responsible for ecological deterioration in North American wetlands. We recommend that (1) future long-term monitoring methods avoid using the “five tallest” method of tracking changes in plant performance over time and (2) short-term studies should be interpreted with caution, as only long-term

studies can discover the true dynamics that shape invasions, their impact, and their control. We strongly emphasize this is not solely applicable to biocontrol but should be the standard for all introduced plant management methods.

### AUTHOR CONTRIBUTIONS

Bernd Blossey and Victoria Nuzzo conceptualized and designed the experiment and collected data. Stacy B. Endriss analyzed data, prepared graphics, and wrote the statistical analyses and results drafts. All authors contributed to various drafts and played major roles in finalizing this manuscript.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data and code (Blossey et al., 2024) are available from Dryad: <https://doi.org/10.5061/dryad.8pk0p2nt9>.

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### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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