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Return of diversity: Wetland plant community recovery following purple loosestrife biocontrol

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Abstract

Spread of non-native species can be important drivers of biodiversity declines, leading to precautionary management based on assumptions that (1) non-native biota have negative impacts and are "guilty" of causing harm and (2) reducing a non-native species' abundance will reduce these negative impacts, in turn, benefiting native species. However, we frequently lack data to gauge both negative impacts of non-native species and success or failure of chosen management interventions to benefit native species. Addressing these knowledge gaps is critical to improving management outcomes for native species while maintaining public trust to sustain funding of management activities. Here, we investigated the response of *Lythrum salicaria* (purple loosestrife) and associated plant communities to implementation of biological control in more than 10 wetland sites in New York State for up to 28 years. Introduced to North America from Europe in the 1800s, *L. salicaria* is a prime example of a non-native species with a continent-wide distribution that could not be suppressed by mechanical and chemical treatments. In the 1980s, waterfowl biologists, wetland managers, and conservationists alike worried about the loss of diverse wetland plant communities associated with the rapid expansion of *L. salicaria*. In response, after careful assessments of safety, and potential costs and benefits, four highly host-specific insect herbivores were released in North America in the early 1990s to reduce *L. salicaria* abundance and its negative ecological impacts. In a companion paper, Blossey et al. documented reduced *L. salicaria* occupancy and stem densities following insect releases over time (i.e., biological success), irrespective of site-specific differences in starting plant communities or *L. salicaria* abundance. Here, we show that reduced abundance of *L. salicaria* leads to the ultimate goal of non-native plant management: increased cover, abundance, and diversity of species, often of native species (i.e., ecological success). We also conduct analyses to provide inference about which plant species are most sensitive to *L. salicaria*, including changes in *L. salicaria* stem density. Overall, we provide an important conservation success story: our findings emphasize that biocontrol of non-native plants can be effective and safe, allowing native species to recover as a dominant non-native species gradually declines.

KEYWORDS
biological control, community recovery, conservation, ecological recovery, ecological success, invasion, long-term monitoring, *Lythrum salicaria*, management

INTRODUCTION

Anthropogenic stressors, such as climate change, habitat loss, overharvesting, and non-native species, are responsible for unprecedented biodiversity declines (Isbell et al., 2017; Jaureguiberry et al., 2022; Johnson et al., 2017). Collecting, standardizing, and increasing accessibility of data is essential to recognizing changes in biodiversity and for mitigating species losses (León et al., 2023; Stephenson, 2020). However, despite valuable progress, mechanistic understanding of what factors or specific actions impact long-term trajectories of ecological communities often remains elusive or relies on extrapolations from only a few years of data. This challenge is exemplified by invasive species management. Research about the impacts and management of non-native species has exploded (Mack et al., 2000; Novoa et al., 2020; Stevenson et al., 2023; Woodworth et al., 2023), yet too often we are left with the question: did management make a lasting difference?

Answering this question is critical to addressing the inherent controversy of non-native plant management. Different people perceive risks associated with species introductions and of management differently (Estevez et al., 2015; Köhler & Triebskorn, 2013; Loss et al., 2022; Shackleton et al., 2019; Simberloff & Stiling, 1996), meaning that decisions to manage or to leave non-native populations unchecked continue to fuel scientific disputes and social conflicts (Crowley et al., 2017; Davis et al., 2011; Dickie et al., 2014; Woodford et al., 2016). However, these conflicts are also perpetuated because data on ecological, social, and economic impacts do not exist for the vast majority of non-native species (Vilà et al., 2024). What data do exist produce undeniably valuable insights on specific impacts of select non-native plants, for example, changes to hydrology, soil biota, or water chemistry. Yet extrapolating these data to predict "invasiveness" and impacts of other non-native species, or biotic introductions in general, may unintentionally exaggerate (or understate) potential harm to biodiversity and to rare or endangered species (Davis et al., 2011; Duenas et al., 2018). Thus, we urgently need more and higher quality data on impacts of non-native plant species and of non-native plant management, especially their long-term impact on plant community composition.

Greater data on impacts of non-native plants, such as their role in driving biodiversity declines, would be especially beneficial given that decisions to intervene—that is, to reduce the abundance of non-native plants—are motivated by the belief that (1) current or potential future negative impacts by these species outweigh their beneficial impacts and that (2) management will reduce or eliminate these negative impacts. Indeed, when mechanisms responsible for species declines are discovered, appropriate interventions may reverse declines. For example, when the thinning of eggshells that threatened many bird species was linked to widespread DDT use, banning these chemicals led to remarkably quick recovery. However, while government agencies, NGOs, and private landowners continue to invest significant resources to reduce established non-native plant populations and limit spread into uninvaded areas, these efforts often fail to result in permanent suppression (Foxcroft et al., 2014; Hiatt et al., 2019; Martin & Blossey, 2013), or only suppress very small populations (Quirion et al., 2018). Even when the abundance of non-native plants is reduced, other non-native species may take over vacated space (Seastedt et al., 2008), or suppressed species may re-invade (Martin & Blossey, 2013). Furthermore, the targeted non-native plant species may not even be a driver of a perceived ecosystem deterioration (Dávalos et al., 2014; MacDougall & Turkington, 2005) and instead may respond to ecological opportunities provided by poor land use such as eutrophication or overgrazing by livestock (Seabloom et al., 2015), large deer populations (Dávalos et al., 2015), or even other non-native species (Frelich et al., 2019). Thus, non-native species management is a "wicked problem" (Woodford et al., 2016): a multidimensional challenge with no easy solution. Long-term assessments are therefore desperately needed to confirm whether assumptions of impacts and benefits of management match reality (Blossey, 1999; Downey, 2011).

Purple loosestrife (*Lythrum salicaria*) in North America is an example of the wicked problem in non-native species management (Thompson et al., 1987; Woodford et al., 2016). Introduced in the 1800s from Europe, *L. salicaria*, with its showy magenta flowers, became a favorite of gardeners and beekeepers. However, its spread through North American wetlands worried waterfowl biologists, wetland managers, and conservationists (Thompson et al., 1987). Prior to implementing biocontrol in North America, *L. salicaria* drove long-term reductions in wetland plant diversity, changes in wetland biogeochemistry and hydrology, and further reduced habitat for many native animals of conservation concern, including many species of waterfowl as well as the critically endangered bog turtle (*Glyptemys muhlenbergii*). Thus, after mechanical and chemical treatments failed to curb spread and reduce *L. salicaria* abundance, a biological control program (hereafter "biocontrol") was initiated in 1986, and releases of four flower-, leaf-, and root-feeding insect herbivores began in 1992 (Malecki et al., 1993).

In a companion paper (Blossey et al., 2024), we detail an overwhelming pattern of reduced *L. salicaria* occupancy and stem densities across 33 wetlands in New York State following insect releases (i.e., biological success, as defined in Blossey, 2016). Our findings support the hypothesis that the previous competitive dominance of *L. salicaria* was due to a lack of biotic control by natural enemies rather than a function of other disturbances, changes in hydrology, or eutrophication. Here, we take the next step forward in addressing the safety and efficacy of *L. salicaria* biocontrol by investigating whether suppression of *L. salicaria* has achieved what should be the ultimate goal of any non-native plant management program (Blossey, 2016): a reduction in the negative impacts of the target plant. Specifically, we focus on whether biocontrol of *L. salicaria* has achieved ecological success (i.e., a reduction or reversal of biodiversity declines driven by *L. salicaria*, sensu Blossey, 2016), leading to a transition in plant community composition with increased cover, abundance, and diversity of native species. To this end, we documented plant community change for up to 28 years following insect releases for a subset of the 33 wetlands for which we documented declines in *L. salicaria* (Blossey et al., 2024).

Importantly, the point of our study was not to investigate site-level variation in biocontrol success, but rather to investigate whether there was an overall, emergent pattern of success (or failure) of biocontrol of *L. salicaria* despite natural variation across sites, purple loosestrife density, and other potential drivers of biocontrol success and plant community change. However, to address site-specific variation in plant assemblages, we also provide inference about which plant species are most sensitive to *L. salicaria*, including changes in *L. salicaria* occupancy and stem density at the 1 m^2 level, which may improve understanding of how local variation drives variation in plant community composition in response to biocontrol over time.

Overall, *L. salicaria* is a particularly important system for investigating ecological success, as the biocontrol program itself was contested given fears of potential negative impacts (Hager & McCoy, 1998). Achieving such ecological success provides strong evidence that biocontrol can produce sustainable benefits to plant communities over time, while also showcasing that long-term biodiversity data are key to understanding how to mitigate species loss in today's world of increasingly rapid environmental change.

METHODS

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. Depending on insect releases, we repeated data collection for variable time periods at each site between 1996 and 2009 (see Blossey et al., 2024) and again at all 33 sites in August and September 2019. Thus, we monitored each site for a period of 15–28 years, starting the year insects were first released (Blossey et al., 2024, see Appendix S1: Table S1). Sites varied in hydrology from seasonally moist to floating mats and vegetation composition from old fields to sedge meadows to marshes. Diverse factors from precipitation to beaver activity to intentional drawdown events and manipulations by wetland managers and private landowners contributed to water levels varying considerably through time. Blossey et al. (2024) provide detailed descriptions of sites, insect releases, experimental design, and monitoring protocols. Information about the herbivores, including their life cycle and current distribution in North America, is available in Blossey and Endriss (2023).

In brief, we released leaf-feeding beetles (*Galerucella* spp.) and root-feeding weevils (*Hylobius transversovittatus*) as adults 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). Releases at Montezuma were part of a factorial study (20 sites, at least 2 km apart) where we assessed independent and interactive effects of leaf beetles and root feeders. We randomly assigned five sites each to receive *Galerucella* only, *Hylobius* only, *Galerucella* plus *Hylobius*, or no insects (control). One control site was destroyed shortly after establishment.

At each site, we established 1–15 1-m^2 permanent quadrats spaced 5–50 m apart. Within each quadrat, we visited all sites at recurring yearly intervals (initially annually, and then less frequently over time) in early fall to record metrics of biological success, including the number of stems, stem heights, and traits related to the reproduction of *L. salicaria*. At most of these same intervals (especially in earlier years), in the spring we also measured the presence and abundance of released insects, the presence of other insects, and overall damage to *L. salicaria* (by both insects and deer). These results and a more detailed description of these methods are reported in our companion paper (Blossey et al., 2024).

Here, we focus more on metrics of ecological success—specifically plant community responses to biocontrol implementation. During recurring yearly visits to quadrats in early fall, we therefore also recorded presence and estimated cover (in percentage) for all co-occurring plant species in each quadrat in 16 cover categories (midpoints: 0.01%, 0.5%, 1%, 3%, 5%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%, 95%, and 100%). Importantly, we collected the data over time at each of the 14 sites across three of our sampled geographical regions (Hudson River Valley, Eastern Lake Ontario, and Western New York), but only in 2019 for our additional 19 sites within the Montezuma region. The same individual (VN) recorded all vegetation data at all sites and years.

Statistical analyses

To evaluate changes in plant communities over time, we first calculated quadrat-level summary metrics of total percent cover (negative binomial), richness (Poisson), and Shannon's diversity index (Gaussian) in two ways: for all plant species except for *L. salicaria* and for native plant species only. As initial plots of raw data indicated nonlinear annual fluctuations in these summary metrics, we used the gamm4 function (Wood & Scheipl, 2017) in R v. 4.1.3 (R Core Team, 2022) to accommodate nonlinear relationships between predictor and response variables via smoothing splines by fitting generalized additive mixed models (GAMMs) (Hastie & Tibshirani, 1990). We then fit independent suites of GAMMs to each summary metric (for both all species and for native species only) and selected the best models. Models were fit to only data collected from our 14 sites across our Hudson River Valley, Eastern Lake Ontario, and Western New York regions, as we did not collect detailed data on plant community metrics through time at sites within the Montezuma region. Please see Appendix S1: Table S1 for additional clarification on which sites were used for each set of analyses presented herein.

For all models, we included random intercepts for calendar year and for quadrat nested within site to help disentangle, respectively, variation due to biocontrol from variation due to both temporal trends unrelated to time since insect releases as well as to additional natural variation within and across sites not already captured by our model fixed effects. We included site as a random intercept effect, as our main aim was not to explore site-level variation in biocontrol success, but to test predictions of general, emergent patterns of *L. salicaria* decline and, in turn, increases in the cover, richness, and diversity of plant species other than *L. salicaria* over time.

Within each suite of candidate models, we included fixed effects of latitude, longitude, and *L. salicaria* stem density within each quadrat (log transformed) for each full model. We fit candidate models two ways: with a single thin plate regression spline for number of years since biocontrol agents were first released (hereafter "time") across all sites or with a separate spline for time for each sampling region. Incorporating splines in two different ways addressed that plant communities may be more similar within than between regions, due to diverse factors (e.g., differences in management, land use history, and regional species pools). Thus, this approach allowed us, again, to investigate whether emergent patterns due to biocontrol implementation exist across all sites (i.e., the most parsimonious model would include only a single spline) versus whether biocontrol success is strongly mediated by natural site- and regional-level processes (i.e., the most parsimonious model would include a separate spline for each area).

After constructing models, we used stepwise selection with corrected Akaike information criterion ($\mathrm{AIC_c}$) 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 ($\mathrm{VIF} < 5$) (Zuur, 2009). We fully report all candidate models and summaries of the best models in Appendix S1: Tables S2–S5. We also summarize the best models in Table 1.

To evaluate how individual plant species (excluding *L. salicaria*) changed over time, we fit multivariate generalized linear models to percent cover data using the manyglm function in the mvabund package (Wang et al., 2012). The manyglm function does not account for random effects, so we used restricted permutations to account for the lack of independence within unique quadrats over time (Szöcs et al., 2015). As restricted permutations require a balanced design, we only included the first and last recorded sample from each unique quadrat. We fit these models to this reduced dataset using a negative binomial distribution with region, *L. salicaria* stem density (log transformed), time (categorical, first vs. last sampling), time range (number of years between first and last sampling), and an interaction between time and time range as fixed effects. Before fitting models, we

TABLE 1 Summary of "best models" fit to data of ecological success ("best models" followed Burnham & Anderson, 2002 description as the model with the lowest corrected Akaike information criterion [AIC_c] value).

Response	Best model	Adj. R^2	Adj. w_i	Model interpretation	Figures and Tables
All species (except *Lythrum salicaria*)					
% cover	Single spline + stem density + longitude	0.41	0.96	Across all regions, plant cover does not change over time; plant cover increases with decreasing *L. salicaria* stem density ($p = 0.001$) and the further east the site ($p < 0.001$)	Figures 1 and 2a; Appendix S1: Table S2
Richness	Single spline + stem density + longitude	0.30	0.87	Across all regions, plant richness initially decreases, then increases over time ($p < 0.001$); richness increases the further east the site ($p < 0.001$)	Figure 1; Appendix S1: Table S3
Diversity (Shannon Index)	Single spline + stem density + longitude + latitude	0.25	0.55	Across all regions, plant diversity increases over time, but only 20+ years following insect release ($p < 0.01$); diversity increased the further north ($p = 0.03$) and east ($p < 0.001$) the site	Figure 1; Appendix S1: Table S4
Native species only					
Native % cover	Splines by area + stem density + longitude	0.41	0.34	Whether and how native plant cover changes over time depends on the region; native plant cover increases as the number of *L. salicaria* stems decreases ($p < 0.01$) and the further east the site ($p = 0.02$)	Appendix S1: Figure S1, Table S2
Native richness	Single spline + stem density + longitude	0.31	0.49	Across all regions, native plant richness increases over time, but only 20+ years after insect releases ($p < 0.001$); native plant richness increases the further east the site ($p < 0.001$)	Figure 1; Appendix S1: Table S3
Native diversity (Shannon Index)	Splines by area + stem density + longitude	0.24	0.48	Whether and how native plant diversity changes over time depends on the region	Appendix S1: Figure S1, Table S4

Note: All models included random intercept effects for calendar year and for quadrat nested within site.

reduced the dataset to only include plant species with at least four occurrences. To visualize changes in plant communities over time, we used distance-based redundancy analysis (dbRDA) using Bray–Curtis dissimilarities in the vegan package (Oksanen et al., 2019).

Finally, we used the co-occur package (Griffith et al., 2016) to fit a probabilistic model of species co-occurrence (Veech, 2013, 2014) to presence/absence data of plant species within each quadrat across all sites in 2019. Specifically, we used pairwise species comparisons to evaluate whether *L. salicaria* as well as the two most abundant non-native species in 2019 (*Phalaris arundinacea* and *Typha angustifolia*) were more or less likely than expected by random chance alone to occur with each of the other plant species identified within our sites. To this end, for each site we extracted standardized effect sizes for all pairwise interactions and then fitted a linear mixed-effects model to these standardized effect sizes. In our full model, we included species (*L. salicaria*, *P. arundinacea*, or *T. angustifolia*), status of the co-occurring species (native or non-native), time (number of years after initial insect releases), and longitude as fixed effects. We also included site as a random intercept.

Importantly, due to the biocontrol insects' phenology, data on herbivory and insect abundance were collected during a single visit early in the spring, while data on metrics of plant performance and diversity were collected in the fall. Further, impacts of herbivory on plant performance and, in turn, on plant community dynamics are long-term processes that are the result of the accumulation of herbivory across many growing seasons. In contrast, our snapshot measurements of herbivory in the spring were not necessarily reflective of long-term trends, as leaf-feeding *Galerucella* can produce multiple generations each growing season, making total insect abundance and herbivory difficult to capture from a single visit during the year. Furthermore, abundance of root feeders cannot be evaluated without destructive sampling, and responses of plants to this damage will accumulate and only become apparent after years. Thus, we did not include insect abundance or herbivory as predictor variables within any of our models and instead included time after insect release as a more appropriate proxy for herbivory.

RESULTS

Across all regions, our models predicted an initial decrease in plant species richness and diversity in the first 5–8 years following insect releases, and then a more pronounced increase in plant richness and diversity across longer timescales (Figure 1; Table 1); when we fit models to a reduced dataset including only native plant species, plant species richness still increased, but this increase only became significant 20+ years after insect releases (Table 1; Figure 2). Within one region (Hudson River Valley), plant cover and Shannon Index of native species (additional metrics of ecological success) also significantly increased over time (Table 1; Appendix S1: Figure S1c,g). Plant cover was best explained by *L. salicaria* stem density: plant cover of native species only (as well as cover of all species) increased as *L. salicaria* stem density decreased (all species cover: Figure 3; $p = 0.001$; native species cover: Appendix S1: Figure S2; $p < 0.01$).

Further, the likelihood that *L. salicaria* would co-occur within the same 1 m^2 quadrat with other plant species

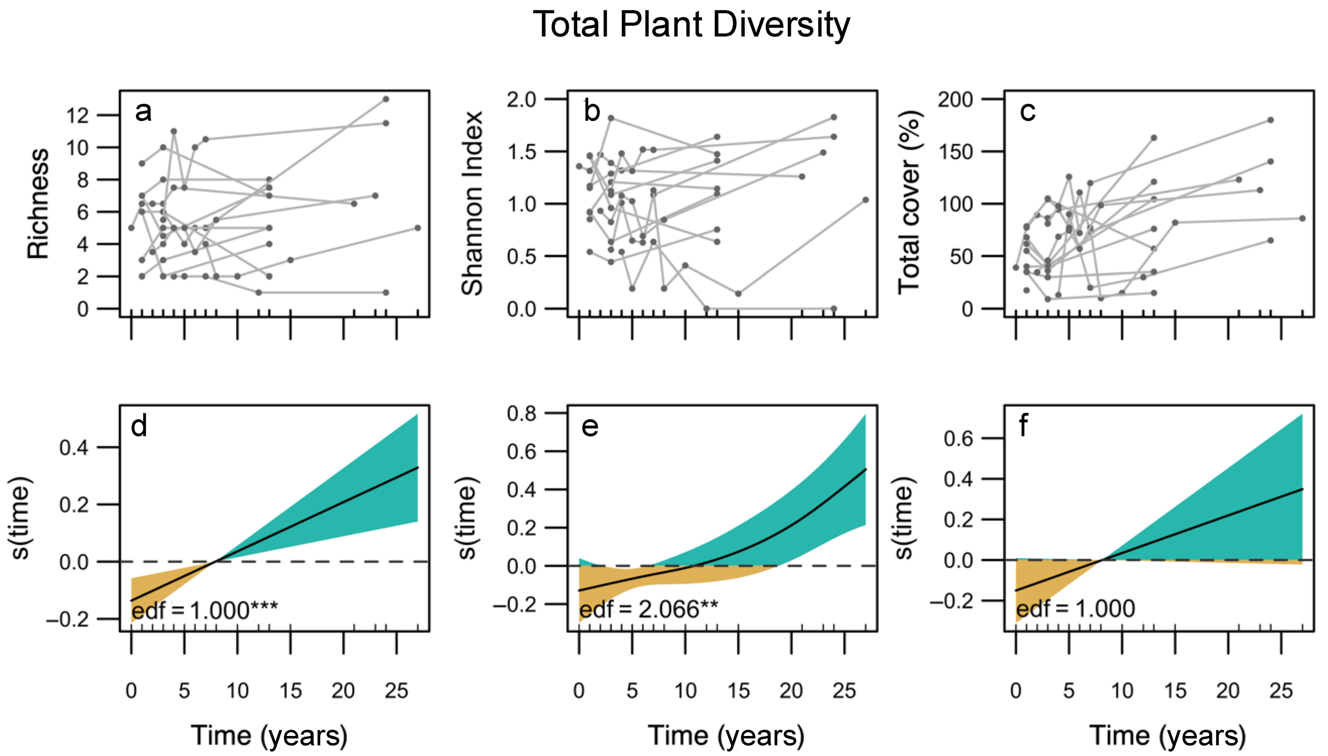

FIGURE 1 Total plant species richness excluding *Lythrum salicaria* (a, d), total diversity (Shannon Index, b, e), and total plant cover (in percentage, excluding *L. salicaria*, c, f) as a function of time (in years) since initial biocontrol agent releases at individual sites (top row) and the corresponding derivative curves (i.e., generalized additive mixed model [GAMM] splines, bottom row). In the bottom row, the y-axis represents the derivative (i.e., slope) of the model estimates of the relationship between time and plant species richness (d), the Shannon Index (e), and total percent cover (f). Black lines represent model estimates, and shading represents 95% credible intervals around this estimate—green for when the slope is positive metrics are predicted to increase with time (i.e., $y > 0$) and orange for when the slope is negative and metrics are predicted to decline with time (i.e., $y < 0$). Estimates are significant if the 95% credible intervals do not overlap with the x-axis (i.e., $y \neq 0$). Further, the estimated df (edf) represents the "wiggliness" 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 (**$p < 0.01$; ***$p < 0.001$). The rug (i.e., tick marks on the inner margin of the x-axis) represent when data were collected. Splines are considered significant if $p < 0.02$, as per Wood (2006).

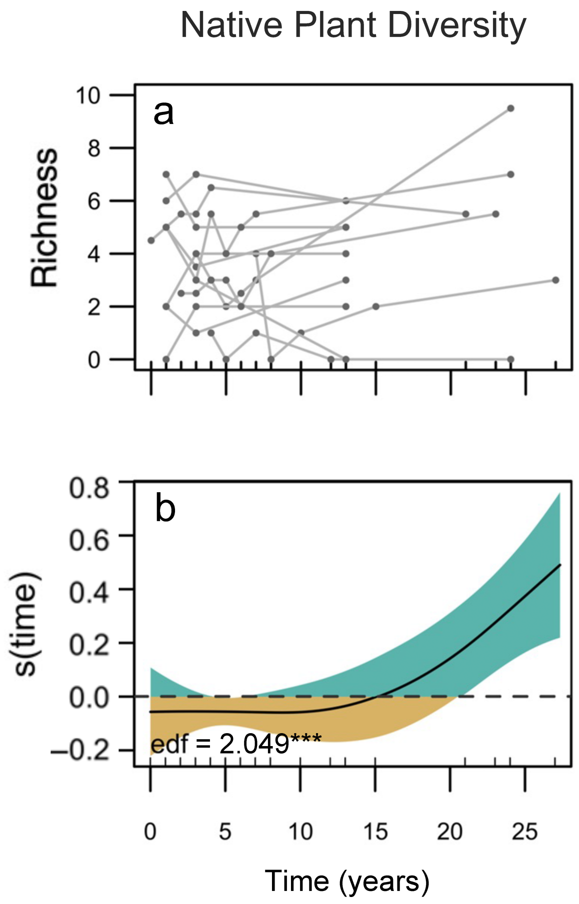

FIGURE 2 Native plant species richness (a, b) as a function of time (in years) since initial biocontrol agent releases at individual sites (top) and the corresponding derivative curve (i.e., generalized additive mixed model [GAMM] splines, bottom row). In the bottom row, the y-axis represents the derivative (i.e., slope) of the model estimates of the relationship between time and native plant richness. Black lines represent model estimates, and shading represents 95% credible intervals around this estimate—please see the caption for Figure 1 for further information about how to interpret these graphs.

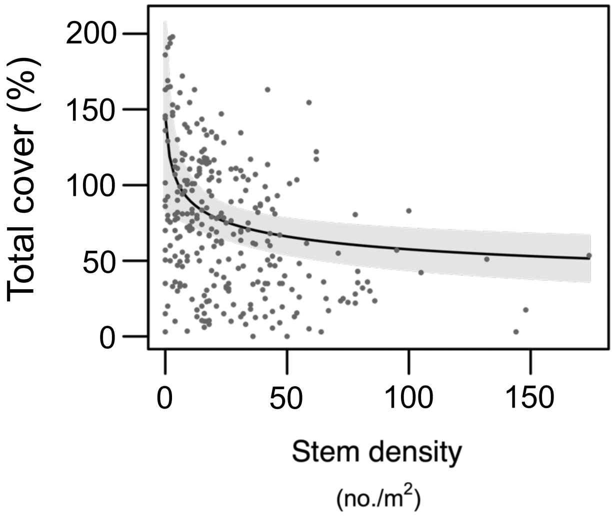

FIGURE 3 *Lythrum salicaria* stem density is negatively correlated with plant cover, as shown by the best generalized additive mixed model (GAMM) model fit to data of plant cover (in percentage). Model estimate (back transformed, black line) and 95% confidence band (gray shading) around change in cover (in percentage) of all plant species (excluding *L. salicaria*) as a function of *L. salicaria* stem density (in number of stems per square meter) ($p < 0.01$). Gray points are raw data. The GAMM included fixed effects of *L. salicaria* stem density (log transformed) and longitude and random intercepts for calendar year and quadrat nested within site.

increased with time since insect release (Figure 4a). A similar pattern was observed for another common non-native species within the plot, *T. angustifolia* (Figure 4c). In contrast, the likelihood that *P. arundinacea*, a third common non-native species, would co-occur with other species within the same 1 m^2 quadrat decreased with time since insect release (Figure 4b). In fact, by 2019 (the last year of sampling), *L. salicaria* had declined to levels that—at least at the 1 m^2 level—typically no longer resulted in competitive exclusion of other species, especially native species (Appendix S1: Table S5, Figure S3).

Finally, changes over time in percent cover of individual plant species (excluding *L. salicaria*) were highly site specific ($p < 0.01$, deviance $= 1668$; Figure 5a), with no emergent patterns within regions. In line with this finding, as sites became less dominated by *L. salicaria*, among-site variation in plant community composition became increasingly pronounced (Figure 5b). Changes over time in percent cover of individual species also depended on how long sites were monitored (time × time range interaction: $p = 0.01$, deviance $= 131$; Figure 5a). Most importantly, the density of *L. salicaria* stems significantly predicted percent cover of individual species ($p = 0.04$, deviance $= 112$; Figure 3)—the top three plant species that drove variation explained by *L. salicaria* stem density were *Cicuta bulbifera* L., *Physalis* sp., and *Cornus racemosa* Lam. (all native species; explained 7.63%, 7.08%, and 6.35% deviance of the density of *L. salicaria* stem density, respectively; Figure 6a). These were different from the species that drove the most variation in the model of percent cover overall—the top three species were *T. angustifolia*, *Penstemon digitalis* Nut., and *Peltandra virginica* (L.) Schott (explaining 4.44%, 3.52%, and 3.45% of the total model deviance, respectively; Figure 6b). The two species that explained the most variation in the model of percent cover overall, *T. angustifolia* and *P. digitalis*, were both non-native. In fact, non-native species on average each explained about 2.47% of the total model deviance, which was ~1.7-fold higher than the percent of the total model deviance explained on average by each native species (1.48%).

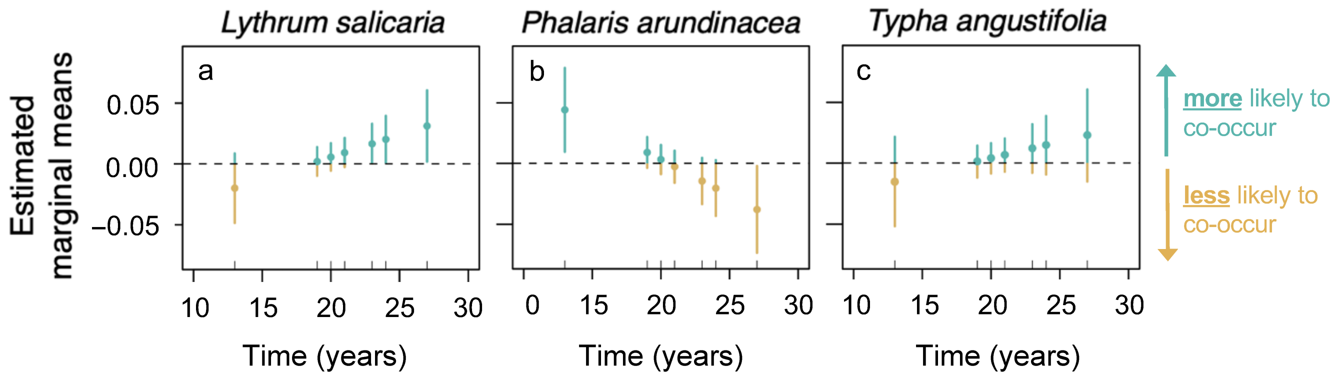

FIGURE 4 Final model for evaluating what drives the likelihood of three abundant non-native species (*Lythrum salicaria*, *Phalaris arundinacea*, or *Typha angustifolia*) that co-occur with other plant species found a significant interaction between species identity and time ($p = 0.003$). Data depict results of a linear mixed-effects model fit to standardized effect sizes extracted from our best probabilistic model of species co-occurrence. Points are estimated marginal means of standardized effect sizes and lines are 95% prediction intervals. Green depicts when the species is predicted to be more likely than random chance alone to co-occur with other plant species (i.e., $y > 0$) and orange depicts when the species is predicted to be less likely than random chance alone to co-occur with other plant species (i.e., $y < 0$). These predicted values are significant if the 95% credible intervals do not overlap with the x-axis (i.e., $y = 0$). Other species were more likely to occur with *L. salicaria* over time (a), while *T. angustifolia* showed a similar, but non-significant trend (c). In contrast, species become less likely to co-occur with *P. arundinacea* with time (b).

DISCUSSION

After nearly three decades of monitoring, we provide evidence that biocontrol not only successfully reduces *L. salicaria* abundance (i.e., biological success; see Blossey et al., 2024), but also reduces its negative impacts on surrounding biota (i.e., ecological success; Figure 7). Specifically, we found that total plant diversity and native plant richness consistently increased following insect releases to control *L. salicaria* across 14 diverse wetlands (Table 1; Figures 1 and 2). Our findings represent an important case study in support of biocontrol as an effective management strategy, especially as published and peer-reviewed evidence of ecological success of non-native plant management programs is incredibly rare, including for weed biocontrol programs (Blossey, 2016; Kettenring & Adams, 2011).

Our findings are correlative, yet compelling. We did establish "no insect" controls within our Montezuma sampling region, but these sites were colonized by leaf-feeding *Galerucella* dispersing from neighboring release sites within a few years after releases at sites >2 km away. Additionally, other alternatives for establishing "baseline" data for how sites with vs. without biocontrol insects change over long time periods are fraught with problems (Agrawal & Maron, 2022). In brief, excluding insects through caging or insecticide applications in sections of our experimental sites, or other wetlands that could function as "control," would have been prohibitively cost expensive to implement across our 33 sites. Insects released to control *L. salicaria* also included a root feeder whose larvae are unobservable without excavation and require using insecticides that would kill belowground feeders to establish an insect exclusion treatment. These approaches are non-selective and would have driven broader changes in community dynamics—such as in pollination, predation, food web structure, and overall herbivory on non-target species—that we would have been unable to disentangle from the impacts of excluding biocontrol insects (Hunt-Joshi et al., 2004, 2005; Hunt-Joshi & Blossey, 2005). Additionally, the biocontrol insects have now spread through all regions in New York and many other states (Blossey & Endriss, 2023). Thus, finding "control" sites without our released insects would have required selecting sites where *L. salicaria* is at the edge of its North American range, if such sites even exist. These sites would differ significantly in climate, regional species pools, and many other factors, thus they do not represent appropriate controls. Establishing "baseline" data was therefore an impossibility in this system and, realistically, an unavoidable reality of any system in which biocontrol is successful—a necessary component of biocontrol success is that agents rapidly establish and disperse with minimal human intervention after their initial releases.

However, as detailed in Blossey et al. (2024), across our monitored sites within the Montezuma region: (1) herbivory was initially higher for sites where leaf-feeding *Galerucella* and/or root-feeding *H. transversovittatus* had been released compared to neighboring control sites, (2) herbivory levels doubled within 1–4 years following insect releases, (3) increases in herbivory levels across the first few years

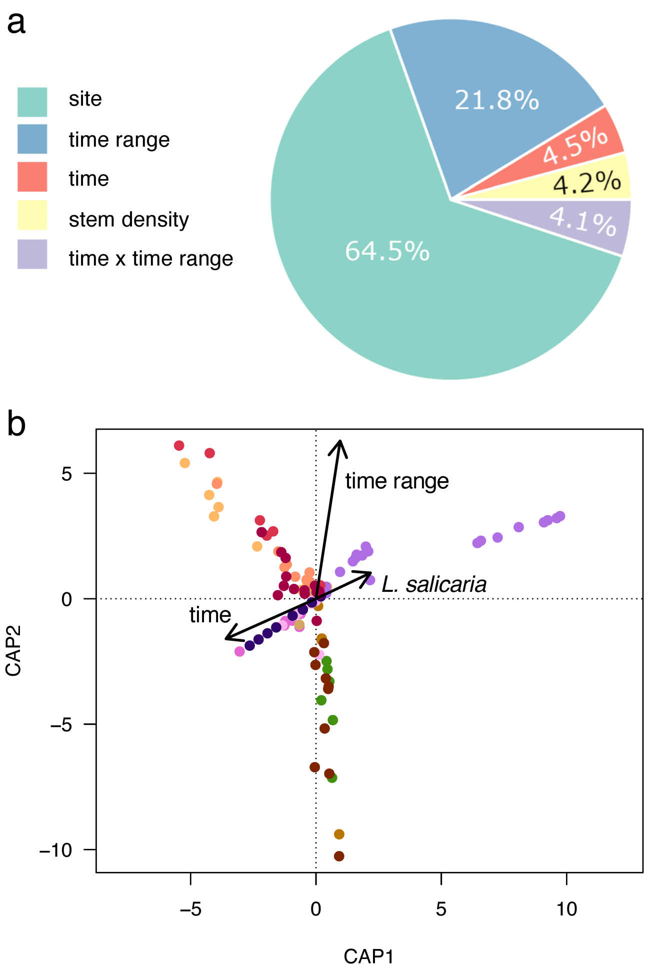

FIGURE 5 (a) Cumulative (in percentage) deviance for each predictor variable in multivariate models used to evaluate how individual plant species (excluding *Lythrum salicaria*) changed over time. As restricted permutations require a balanced design, we only included the first and last recorded sample from each unique quadrat for our analyses using the manyglm package. We fit these models to this reduced dataset using a negative binomial distribution with site, *L. salicaria* stem density (log transformed), time (categorical, first vs. last sampling), time range (number of years between first and last sampling), and the interaction between time and time range as fixed effects. (b) Using the same subset data used to fit multivariate models, we conducted a distance-based redundancy analysis (dbRDA) of Bray–Curtis dissimilarities for the 14 sites for which we recorded percent cover of each unique plant species over time. Points are color coded by site and represent individual 1 m^2 quadrats. The closer values are in ordination space, the more similar the plant communities. Arrows represent the associations between plant community composition and *L. salicaria* stem density (*L. salicaria*), time, and time range. Thus, how plant communities change over time is highly site specific, with *L. salicaria* typically decreasing in abundance over time.

following releases paralleled increased *Galerucella* abundance over time, and (4) *L. salicaria* was more likely to be damaged if we detected *Galerucella* eggs within the quadrat. Overall, we, therefore, found that increased herbivory of *L. salicaria* coincided with biocontrol establishment, and that levels of herbivory quickly rose to levels consistent with those previously documented to drive declines in *L. salicaria* growth and performance over time in large field cage, potted plant, and greenhouse experiments (Blossey & Schat, 1997; Hunt-Joshi & Blossey, 2005; Hunt-Joshi et al., 2004; Nötzold et al., 1998; Schat & Blossey, 2005). Thus, although establishing manipulative experiments may seem to be an appealing "gold standard" for collecting baseline data for how sites with versus without insects changed over time, we find our correlative evidence that biocontrol drives declines in *L. salicaria* both persuasive and to be the best available option given our current toolbox and the realities of assessing impacts of herbivory on plant community dynamics in general, and of weed biocontrol in particular.

Here, we take the next step forward to show that declines in *L. salicaria* in turn have important consequences for plant community dynamics. For example, both percent cover of all plant species excluding *L. salicaria* and of native plant species only increased as *L. salicaria* stem density decreased (Table 1: $p = 0.001$ and $p < 0.01$, respectively; Figure 3 and Appendix S1: Figure S2, respectively). Further, our best models not only predicted significant increases in plant species richness and diversity over time since insect releases, but also always included *L. salicaria* stem density as a predictor variable within the model. Thus, while this study—like all studies—was not designed to encompass all possible factors influencing *L. salicaria*, we find the explanation that biocontrol drives declines in *L. salicaria*, and in turn increases in plant diversity over time, is the most likely and parsimonious interpretation of our data.

Our findings also emphasize that successful biocontrol takes time. For example, increases in total plant species richness only became significant after 8+ years, and increases in native plant richness took 18+ years after initial insect releases to become apparent (Table 1, Figures 1 and 2). This is similar in duration to findings of a meta-analysis that showed changes in non-target plant communities only became significant 7 years following implementation of weed biocontrol (Clewley et al., 2012). Yet, there are precious few long-term studies, as underscored by the fact that the duration of our work exceeds those reported in Clewley et al. (2012) by more than a decade.

Changes in native plant diversity over time were quite variable across regions, but annual changes for Shannon Index and percent cover varied in some regions, but not all (Appendix S1: Figure S1, Tables S2 and S4), and increases either did not become significant by the end of our monitoring period or became significant only after pronounced lag periods of eight to 20+ years following

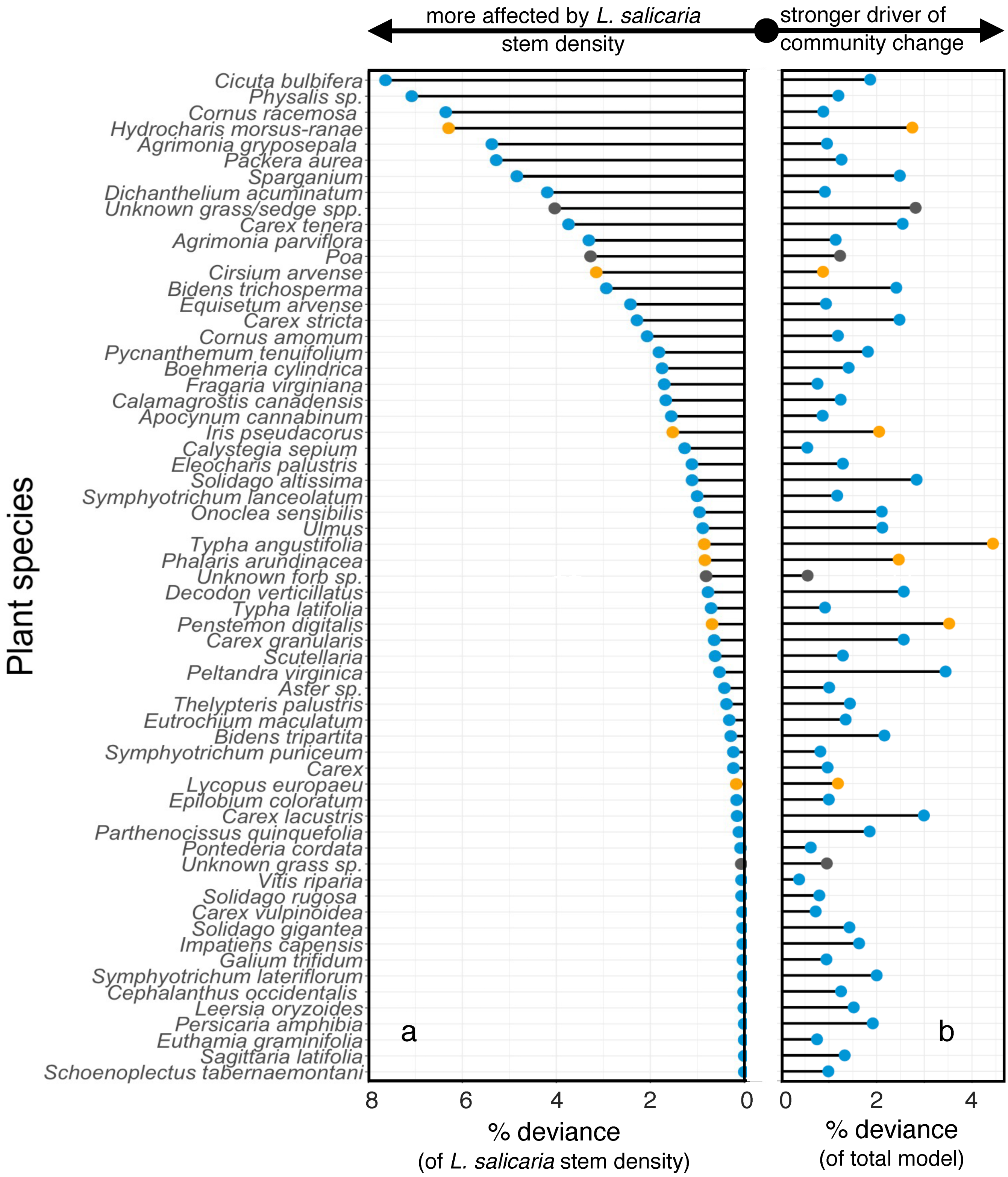

FIGURE 6 Deviance (in percentage) explained by *Lythrum salicaria* stem density (log transformed) for each univariate model that evaluated changes in the abundance of each species over time (a). Model deviance (in percentage) of each univariate model as compared to the cumulative deviance across all univariate models (b). The colors of the lollipop plots depict status of plant species as native (blue), non-native (orange), or unknown (dark gray).

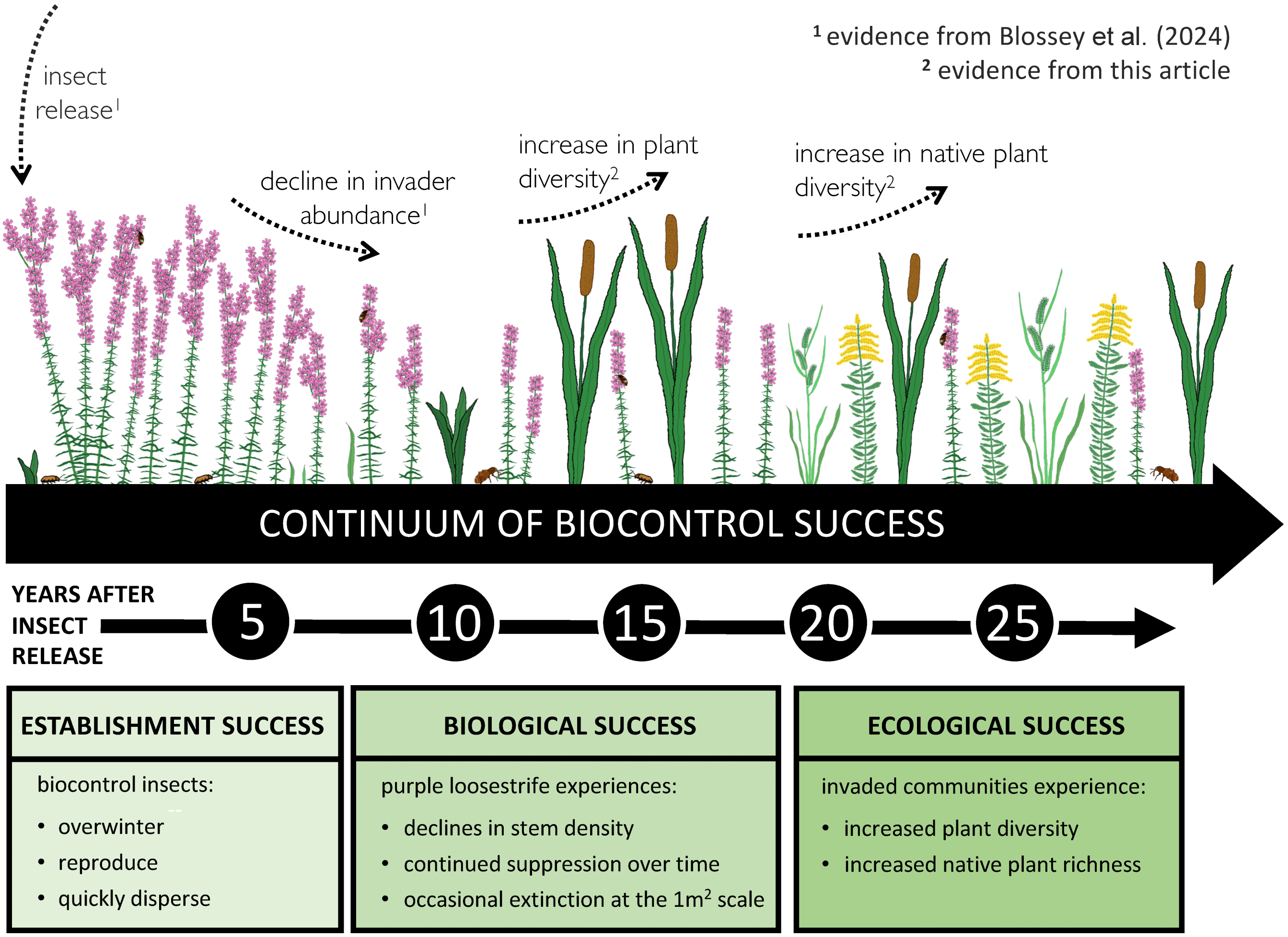

FIGURE 7 Summary of evidence of successful biocontrol of purple loosestrife in central New York over time. Modified from Endriss et al. (2022). Establishment success is defined as evidence that biocontrol agents successfully establish, overwinter, and disperse with minimal human intervention following their initial releases (i.e., the treatment is sustainable). Biological success refers to significant declines in the abundance, population growth rate, and/or spread of the target invader in response to biocontrol (Blossey, 2016). Ecological success refers to a significant reduction in (or even reversal of) the negative ecological impacts of the invader in response to biocontrol (Blossey, 2016). Illustration credits: Stacy B. Endriss.

insect releases. Thus, our nearly 30-year monitoring period still may not be long enough to capture the full extent of long-term native plant recovery that biocontrol enabled. Britton et al. (2014) report increases in overall plant richness for three of their four monitored sites, but not in native plant richness, after 10 years of herbivory by *Galerucella* in Indiana. Similar results are reported in Michigan (Landis et al., 2003). Longer recovery periods for native plant species than for all plant species may reflect increased seed availability by colonizer species, higher abundance and seed output by non-native species, or may simply be an artifact of fewer species in a subset of the data when only native species are included, making it harder to detect significant changes over time.

The slow but persistent change in plant community demonstrates the extended time required for biocontrol programs to be ecologically successful. We would argue that while this slow progression (compared to mowing or chemical treatments) requires patience by land managers, biocontrol programs are successful because they take time (Endriss et al., 2022). Insects need time to build up their populations, deplete plant reserves in rootstocks, reduce overall seed output, stem height and competitive ability of *L. salicaria* individuals to translate into significant declines in stem density. This slow decline allows plants that are initially in low abundance, or even locally absent, to respond to "windows of opportunity," enabling them to respond demographically by increasing growth, seed output, and dispersal. In contrast, herbicide and mowing, for example, can suppress target non-native plants immediately, or within a few days, but these methods are non-selective. Thus, these methods "reset" plant community succession and unintentional harm to native species is often reported when data are collected (Kettenring & Adams, 2011; Pearson et al., 2016; Rinella et al., 2009). The gradual decline in *L. salicaria* and gradual recovery of diversity may help explain why we observed such consistent ecological success in response to biocontrol insects, irrespective of differences in site hydrology, land use history, water level management, starting plant community composition, and a myriad of other potential factors.

Interestingly, other plant species were increasingly likely to co-occur with *L. salicaria* within our 1 m^2 quadrats with time since initial insect releases (Figure 4), which suggests that biocontrol successfully mitigated negative impacts of *L. salicaria* over time, most likely due to a reduction in competitive ability of *L. salicaria* individuals. These findings are critical, as relationships between abundance of non-native species and magnitude of negative impacts are notoriously difficult to understand and predict (Sofaer et al., 2018; Thiele et al., 2010). Thus, the mechanistic link between declines in non-native species abundance and ecological success too often remain a "black box." Addressing this "black box" is an important step forward in non-native species management, as decisions to manage non-native species are often motivated by the desire to protect native species and, in turn, assumptions that reducing non-native species abundance reduces its negative impacts on native biota.

To be clear, environmental variation and differences in regional processes undeniably influence plant community dynamics, both independent of and as mediated by biocontrol. For example, we already know that local conditions, such as tidal or densely shaded sites, can prevent insects from thriving, lessening their ability to control *L. salicaria* (as reviewed by Endriss et al., 2022). Here, site-level variation helped us disentangle the impact of biocontrol from other potential drivers of community change. For example, each of our metrics of plant community change was always better explained when *L. salicaria* was included as an explanatory variable (Table 1, all final models include *L. salicaria* stem density), helping support the mechanistic link between declines in *L. salicaria* and corresponding increases in plant richness and diversity over time. Those same models also all included longitude and/or latitude as an explanatory variable (Table 1), which can be good proxy variables for climate, regional species pools, and other environmental variables that may mean that sites that are closer together are more similar than those that are further apart. This is in line with our finding that changes in plant composition over time are also highly site specific (Figure 5). However, this variation does make our finding of general increases in plant diversity following biocontrol especially powerful: even in the presence of significant, meaningful site-level variation, we still found an emergent pattern of success (i.e., increased plant diversity) across all sites, irrespective of differences in purple loosestrife density, environment, and other potentially unmeasured drivers of biocontrol success and plant community change.

Site-level variation also provides more nuanced insights into the impact of biocontrol over time. Increases in plant diversity are not always desirable, such as when new arrivals are themselves non-native species that become dominant and outcompete co-occurring biota. For example, in addition to *L. salicaria*, two species considered non-native and invasive (*Phalaris arundinacea* [reed canary grass] and *Typha angustifolia* [narrow leaved cattail]) were also commonly found within our sites. While we found that other plant species became more likely to co-occur with *L. salicaria* with time since initial insect releases, other plant species (excluding *L. salicaria*) became less likely to co-occur with *P. arundinacea* with time since initial insect releases (Figure 4a vs. Figure 4b). These results are in line with findings by Hovick and Carson (2015), who found that the presence of *P. arundinacea* was inversely related to the abundance of *L. salicaria*. Additionally, two of the three species that explained variation in plant community change over time were non-native (Figure 6b). These findings emphasize that continued monitoring and site-specific management is critical to sustaining healthy and diverse plant communities over time. In line with this recommendation, we provide inference regarding the sensitivity of different plant species to *L. salicaria* stem density (Figure 6a), which may provide valuable insights into which species may be especially helpful to further investigate or to monitor when investigating impacts of *L. salicaria*. However, we did not monitor the long-term impacts of *L. salicaria* on other biota (including amphibians, turtles, or birds) thought to be threatened by *L. salicaria*, which themselves are also strongly influenced by site conditions, plant community composition, and other site-specific processes.

Finally, one of the main critiques of biological control is the possibility that purposefully introduced insects will feed upon and cause long-term harm to populations of native plants (Havens et al., 2019; Louda et al., 1997, 2003; Simberloff & Stiling, 1996), despite rigorous modern safety protocols that support a strong safety record (Hinz et al., 2014, 2019). We note that host-specificity studies found some minor attack and even limited larval development on two native species (*Lythrum alatum* [winged loosestrife] and *Decodon verticillatus* [swamp loosestrife or waterwillow]) when leaf- and root-feeders were given no choice among food plants (Blossey et al., 1994a, 1994b). While we did not design our monitoring program to specifically assess the fate of these two species, *D. verticillatus* was present at some of our release sites and was still thriving at these sites in 2019, at some sites accounting for 20% of total plant cover. Interestingly, *L. alatum*, a species thought to have been outcompeted by *L. salicaria*, was recently "rediscovered" in the Montezuma wetlands with plants free of insect attack while neighboring *L. salicaria* were heavily attacked (D. Werier, and T. Rawinski, personal communications to BB, September 2019). Our data for *L. salicaria* support previous post-release field studies that suggest that even if agents "nibble" on non-target species, these "spillover" events are unlikely to drive population-level declines of native species (Blossey, Casagrande, et al., 2001; Corrigan et al., 1998). Thus, our findings add to a growing body of literature supporting plant biocontrol's strong safety record (Catton et al., 2016; Paynter et al., 2015; Suckling & Sforza, 2014).

Our study provides evidence that the release of host-specific herbivores decreased *L. salicaria* presence and abundance, most likely due to the reduced competitive ability of individuals and reversed negative impacts of *L. salicaria*. However, these processes played out over decadal timescales. Thus, success requires patience, not a rush to action. Overall, our long-term monitoring supporting *L. salicaria* as a major driver of plant community change (Figure 7) confirms previous claims by wetland managers (Blossey, Skinner, et al., 2001; Thompson et al., 1987) that were contested by some academics (Hager & McCoy, 1998; Lavoie, 2010). We also help address long-standing critiques that in weed biocontrol—and in non-native plant management more broadly—we desperately need data to confirm whether assumptions regarding invader impacts and benefits of management match reality (Blossey, 1999; Davis et al., 2011; Downey, 2011; Duenas et al., 2018). In response to this need, here we provide an important conservation success story: native species can recover as non-native species gradually decline in response to biocontrol.

AUTHOR CONTRIBUTIONS

Bernd Blossey and Victoria Nuzzo conceptualized and designed the experiment and collected the data. Stacy B. Endriss analyzed the data and wrote the statistical analyses and results sections. All authors were actively engaged in writing other sections and in revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Endriss et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.z8w9ghxmk.

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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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