CHAPTER 27

Success Takes Time: History and Current Status of Biological Control of Purple Loosestrife in the United States

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NON-TECHNICAL SUMMARY

Purple loosestrife (*Lythrum salicaria*, Lythraceae) is a long-lived forb that has negatively affected North American wetlands for decades. Following the introduction of purple loosestrife from Eurasia in the early 1800s, populations gradually spread across North America, eventually leading to the decline of many native birds, plants, and amphibians. Land managers recognized the widespread ecological harm caused by purple loosestrife and called for sustainable control methods, realizing that traditional methods such as chemical treatments had failed to produce desirable outcomes. In response, research to assess biological control options for purple loosestrife began in 1986 in Europe. This biological control program represented one of the first times a plant was targeted for biological control because of its harm to flora and fauna rather than because of its negative impacts to agriculture (Vail et al., 2001). This work led to release of four host-specific insects: two leaf-feeding beetles (*Galerucella calmariensis* and *G. pusilla*; both Coleoptera: Chrysomelidae) and a root-feeding weevil (*Hylobius transversovittatus*; Coleoptera: Curculionidae) in 1992, followed in 1994 by a flower-feeding weevil (*Nanophyes marmoratus*; Coleoptera: Curculionidae). The *Galerucella* leaf-feeding beetles now appear to be widely established and abundant. Data on the abundance and distribution of the root-feeding and flowering-feeding weevils remain sparse. The effect of these insects may vary from site to site, but in many regions across North America—such as the Pacific Northwest, the Great Lakes Region, and the Northeast—biological control of purple loosestrife is now highly effective and economical. For example, long-term data collected from New York document that these insects decrease the density, height, and flower production of purple loosestrife, which in turn allows an increase in native plant diversity—the ultimate goal of management. Many biological control success stories are anecdotal, and purple loosestrife is one of the first examples for which we have strong evidence that control of invasive plants by insects can result in native plant recovery.

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HISTORY OF INVASION AND NATURE OF PROBLEM

Purple loosestrife (*Lythrum salicaria*, Lythraceae) is a widespread, long-lived wetland perennial forb easily recognized by its dense, showy, purple flowers in summer and early fall. It was introduced from Eurasia to the northeastern United States in the early 1800s, both intentionally through the plant trade and likely unintentionally in contaminated ship ballast and on wool fleece. Purple loosestrife quickly spread westward aided by horticulturalists and beekeepers. Populations built up over time, resulting in dense near monocultures. Wetland managers were the first to notice that purple loosestrife was driving widespread degradation of wetlands across much of the United States (Thompson et al., 1987; Skinner et al., 1994; Blossey et al., 2001), which experimental studies later confirmed (see next section for more details). Currently, purple loosestrife occurs in all 48 contiguous states except Florida as well as in nine Canadian provinces. It is listed as a noxious weed in most of the United States and Canadian provinces.

WHY CONTROL THIS INVASIVE SPECIES?

Efforts to control purple loosestrife through flooding, mowing, herbicide application, burning, or disking are unsuccessful. Short-term suppression can sometimes be achieved through herbicide application or flooding, but neither method provides long-term control and both often perpetuate the negative impacts they are trying to mitigate (Malecki and Rawinski, 1985; Haworth-Brockman et al., 1993; Welling and Becker, 1993; Gabor et al., 1995; Gabor et al., 1996; Katovich et al., 1996). For example, repeated herbicide applications are necessary to prevent purple loosestrife reinvasion (Malecki and Rawinski, 1985; Balogh and Bookhout, 1989; Gabor et al., 1995; Gabor et al., 1996), yet these applications also harm native plants that occur in treated areas, leaving a highly disturbed site prone to future invasion. Furthermore, flooding at depths greater than 30 cm (12 in) kills purple loosestrife seedlings (Haworth-Brockman et al., 1993), yet established plants can thrive under flooded conditions. Moreover, maintaining deep water levels prevents germination of many native wetland plant species (Kettenring and Tarsa, 2020).

Both conventional control and doing nothing therefore lead to continued widespread environmental degradation and ecological harm from purple loosestrife. Thus, using biological control to reduce the negative impacts of purple loosestrife, but not eradicate the target plant, seemed a promising alternative to wetland ecologists and land managers.

THE ECOLOGY OF THE PROBLEM

Ecological Effects of Purple Loosestrife

In its native range in Europe, purple loosestrife typically occurs in mixed wetland communities (Shamsi and Whitehead, 1974). Occasionally, disturbances may create near monocultures of purple loosestrife, but they are short lived, likely because specialist insects quickly consume both above- and below-ground plant tissues, in turn driving declines in reproduction (Lehndal et al., 2016). In contrast, in North America before the biological control program, purple loosestrife outcompeted native vegetation (Gaudet and Keddy, 1988; Weiher et al., 1996; Weihe and Neely, 1997) and permanently reduced wetland plant diversity. The ability of purple loosestrife to directly outcompete native plants was likely compounded by indirect competition mediated by shared pollinators; purple loosestrife has reduced the abundance and distribution of winged loosestrife (*Lythrum alatum*)—the most widespread native *Lythrum* species in the United States—through both these mechanisms (direct competition and indirect competition via pollinators) (Blossey et al., 1994a; Brown, 2002). Furthermore, many native animals already struggling due to habitat loss are unable to thrive

in dense and extensive purple loosestrife stands. These species include the American bittern (*Botaurus lentiginosus*), black terns (*Chlidonias niger*), bog turtles (*Glyptemys muhlenbergii*), least bittern (*Ixobrychus exilis*), pied-billed grebes (*Podilymbus podiceps*), sora (*Porzana carolina*), and Virginia rail (*Rallus limicola*) (Thompson et al., 1987; Schneider and Pence, 1992; Lor, 2000).

Once purple loosestrife forms dense monocultures, it also triggers alterations in the biogeochemistry and hydrology of invaded wetlands. For example, when purple loosestrife replaces broadleaf cattail (*Typha latifolia*) as the dominant vegetation type, phosphate in pore water pools in the soil declines in the summer (Templer et al., 1998), with a stronger nutrient flush in the fall (Emery and Perry, 1996; Grout et al., 1997). These changes in timing of nutrient release alter wetland function and may increase rates of downstream eutrophication (Emery and Perry, 1996), in turn causing declines in detritivore populations adapted to plant tissues whose decaying biomass typically drops in the spring (Grout et al., 1997). Changes in timing of nutrient release may also have cascading effects on detrital-based food webs, such as by driving further declines in endangered salmon species in the Pacific Northwest (Grout et al., 1997). Furthermore, shifts in litter quality also appear to negatively affect the development of amphibians such as the American toad (*Anaxyrus americanus*) (Brown et al., 2006; Maerz et al., 2010; Martin et al., 2015).

Purple Loosestrife as a Model of Evidenced-Based Management

Wetland managers and state and federal agencies across North America supported the implementation of biological control of purple loosestrife. Yet a small group of academics initially objected to this program, citing a general lack of evidence of negative impacts of purple loosestrife (e.g., Hager and McCoy, 1998). However, just because impacts are not addressed in the peer-reviewed literature does not mean they do not exist. Land managers have deep, daily, connections to specific habitats and their species, and may observe succession and shifting species assemblages that short-term experiments, however sophisticated, are unable to detect. Thus, land managers are an extremely valuable 'early warning system' that may allow us to control invasive species before they inflict irreversible harm. In the case of purple loosestrife, wetland managers were the first to recognize many of the negative ecological impacts that were later experimentally confirmed (as summarized by Blossey et al., 2001; see previous section for more details).

This initial pushback to biological control of purple loosestrife highlights how expected benefits of proposed management actions should always be weighed against their expected costs (both financial and ecological). To be clear, pushback is healthy for the field of biological control and helps maintain and improve rigorous standards that lead to increasingly safe and effective biological control (Hinz et al., 2019, 2020; Szűcs et al., 2019; Paynter et al., 2020; Sun et al., 2020, 2022). Indeed, biological control programs rigorously assess safety and often efficacy of potential biological control agents before their release. However, few weed biocontrol programs quantitatively assess long-term outcomes after insects are released (Crawley, 1989; McClay, 1992; McFadyen, 1998; McEvoy and Coombs, 1999; Morin et al., 2009; Hinz et al., 2020; Schaffner et al., 2020). This information is critical to understanding whether we have achieved sustainable, long-term control of the target weed and successfully mitigated the weed's undesirable effects (Schroeder, 1983; Morin et al., 2009; Schaffner et al., 2020). These types of data also provide evidence of biological control as an effective management tool (Malecki et al., 1993; Morin et al., 2009; Hinz et al., 2020). Invasive species management relies on public trust and goodwill, making data on beneficial outcomes and absence of non-target effects critical to ensuring continued funding for biological control as a management tool.

To help address this knowledge gap, scientists developing biological control of purple loosestrife established a standardized monitoring protocol to evaluate the establishment, abundance, and impact of insects released to control purple loosestrife on both purple loosestrife and its co-occurring plant community. This protocol was first implemented across North America in 1996 and used permanent 1 m^2 (10.8 ft^2) quadrats to assess changes in insect damage, purple loosestrife performance, and plant community composition over time (see Blossey, 2001).

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

The biological control program for purple loosestrife was initiated in 1986 (Malecki et al., 1993), beginning with surveys of purple loosestrife in its native European range to look for potential control agents. Insects were identified as potential agents if they had a widespread distribution in their native range, if initial observations suggested they had strong negative impacts on individual purple loosestrife plants, and they appeared to be highly specific (i.e., fed only on purple loosestrife). Of the more than 100 different insect species observed feeding on purple loosestrife in Europe, only six were considered as candidates for follow-up investigations. The life history, native range distribution, impact on purple loosestrife, and host-specificity of these insects were thoroughly investigated and reported in peer-reviewed publications (Blossey, 1993; Blossey et al., 1994a,b; Blossey, 1995a,b,c; Blossey and Schroeder, 1995). Rigorous cost-benefit evaluations and risk assessments are a critical part of the decision process governing which insects, if any, are approved for release in North America to control target weeds. Thus, it was only after a rigorous suite of experimental laboratory and field studies that five insects were identified as posing minimal threat to North American plant species and were approved for field release: two leaf-feeding beetles (*Galerucella calmariensis* and *G. pusilla*, both Coleoptera: Chrysomelidae), a root-feeding weevil (*Hylobius transversovittatus*; Coleoptera: Curculionidae), a flower-feeding weevil (*Nanophyes marmoratus*; Coleoptera: Curculionidae), and a seed-feeding weevil (*N. brevis*) (Blossey and Schroeder, 1995). The seed-feeding weevil was never introduced because scientists were unable to find nematode-free populations in Europe. The nematode did not appear to harm *N. brevis* yet constituted an unknown, hence unacceptable, potential risk to native North American weevils.

The four introduced insects are complementary, in that they attack different parts of the plant. The two leaf beetles, *G. calmariensis* and *G. pusilla*, share similar life histories and have similar feeding behavior (Blossey et al., 1994a; Blossey, 1995a). They overwinter as adults (**Fig. 1a**) in the leaf litter, then emerge in the spring to lay eggs (**Fig. 1b**) and feed on above-ground plant tissues in ways that result in distinctive damage. Adults often inflict shothole damage (**Fig. 1c**) that is especially obvious in the spring, while larvae inflict window-pane damage (i.e., stripping the photosynthetic tissue from small sections of leaves, while leaving

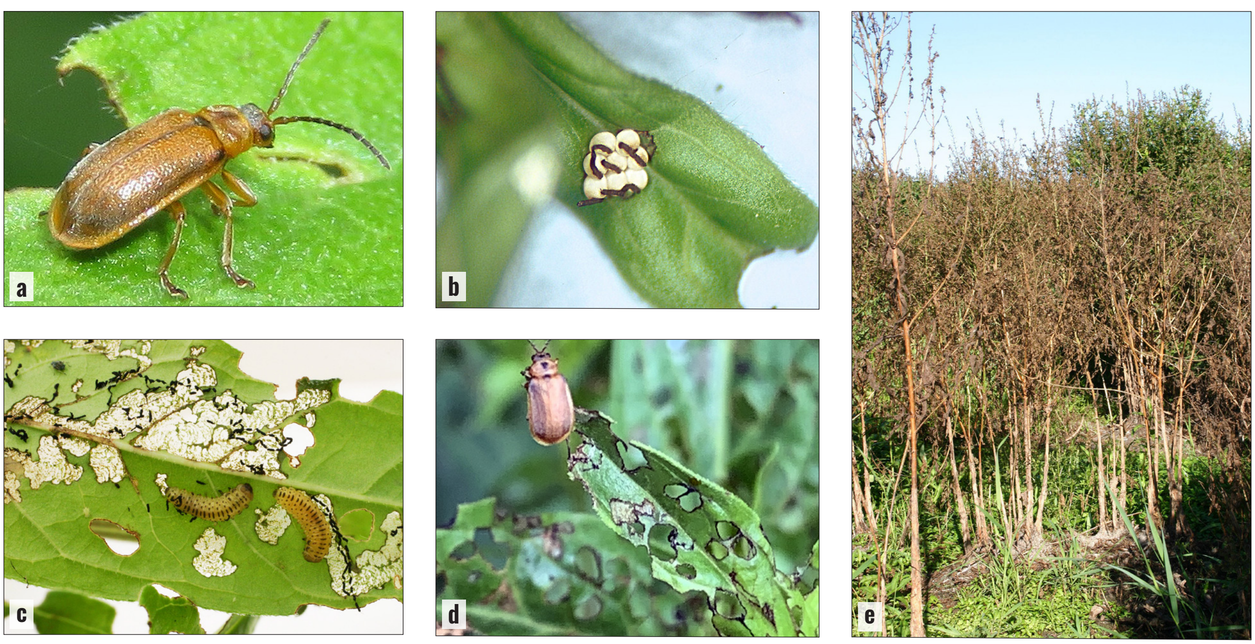

Figure 1. *Galerucella* leaf-feeding beetle: (a) adult; (b) eggs, (c) adult and shothole feeding damage; (d) larvae and window-pane feeding damage; (e) resulting partial defoliation of purple loosestrife stems. (a: Rob Westerduijn; b: Agriculture and Agri-Food Canada; c,e: Eric Coombs, Oregon Department of Agriculture; d: Don Sutherland; a,d: iNaturalist.org CC BY-NC 4.0; b,c,e: Bugwood.org CC BY-NC 3.0 US)

the upper epidermis intact, (**Fig. 1d**). At high population densities, these insects often completely defoliate entire populations of purple loosestrife (**Fig. 1e**). Both species can also produce a single, a partial second, or even two generations per year depending on day length and climate (Blossey 1995a; Grevstad and Coop, 2015; Wepprich and Grevstad, 2021), potentially resulting in multiple defoliation events per year.

The root-feeding weevil *H. transversovittatus* predominately damages the below-ground tissue of purple loosestrife. While adults (**Fig. 2a**) feed on leaves (**Fig. 2b**), the main damage results from larval feeding on root tissues (**Fig. 2c**). Larvae take one to two years to develop and, once mature, create a pupation chamber in the upper portions of the root, emerging as adults from mid-summer to late fall. Adults (10–14 mm in length) are night-active and can live for several years. Females lay eggs in the soil close to a purple loosestrife root or insert eggs in the lower part of the stem. Individuals can be difficult to detect given their nighttime feeding behavior and that larval stages feed below ground. Digging up purple loosestrife roots, however, reveals obvious larval root damage. For detailed descriptions of the life history and ecology of *H. transversovittatus* see Blossey (1993).

Figure 2. *Hylobius transversovittatus*, a root-feeding weevil: (a) adult; (b) adult feeding damage on leaf margin; (c) larva in destroyed rootstock. (a: Jennifer Andreas, Washington State University Extension; b,c: Eric Coombs, Oregon Department of Agriculture, Bugwood.org CC BY-3.0 US)

The univoltine flower-bud weevil *N. marmoratus* (**Fig. 3a**) predominately damages developing ovaries in flowers before they open, which reduces seed output through flower-bud abortion (Blossey and Schroeder, 1995). In spring and early summer, adults first feed on young leaves—creating a shothole pattern—and then on flower buds once they become available. Adults lay eggs in immature buds (**Fig. 3b**), with attack rates that can exceed 70%. A single larva develops within a single bud, creating a distinctive circular hole at the base of the dead bud when individuals emerge as adults (**Fig. 3c**).

The development of mass rearing methods allowed rapid distribution of insects across the continent (Blossey and Hunt, 1999; Blossey et al., 2000). By 1999, more than three million leaf beetles and more than 100,000 root-feeding weevil eggs and adults had been released in >1,500 wetlands in 30 states and several Canadian provinces (Blossey et al., 2001). Following these releases, statewide and regional mass production efforts continued for many years, allowing for rapid adoption of the program across the United States.

Figure 3. *Nanophyes marmoratus,* a flower-feeding weevil: (a) adult; (b) egg within a dissected flower bud; (c) adult emergence hole. (a: Felix Riegel, iNaturalist.org CC BY-NC 4.0; b,c: Gary Piper, Washington State University, Bugwood.org CC BY-3.0 US)

HOW WELL DID IT WORK?

Today (2022), three decades have passed since *Galerucella* spp., *H. transversovittatus*, and *N. marmoratus* were initially released to control purple loosestrife in North America. However, a formal assessment of the North American distribution and impact of the four species across the continent is not available. While in some regions purple loosestrife remains a priority pest subject to management, we typically lack data (at least in the published literature) to evaluate how the abundance of purple loosestrife or its impact on other biota has changed over time, or whether prioritization of the species for herbicide or mechanical management is justified given purple loosestrife's existing impacts or future threats. We therefore also lack data on whether there is a continued need for insect redistribution and whether local eradication attempts via biological control or other treatments are ecologically feasible, desirable, or actually counterproductive as a management goal. Yet in regions where data have been collected, both anecdotal and empirical evidence overwhelmingly support this program's success. In the following section, we combine published evidence on the impact of these insects with knowledge obtained by our interactions with wetland managers and agencies since inception of the program, focusing on three overlapping categories of success: establishment, biological success, and ecological success (**Fig. 4**).

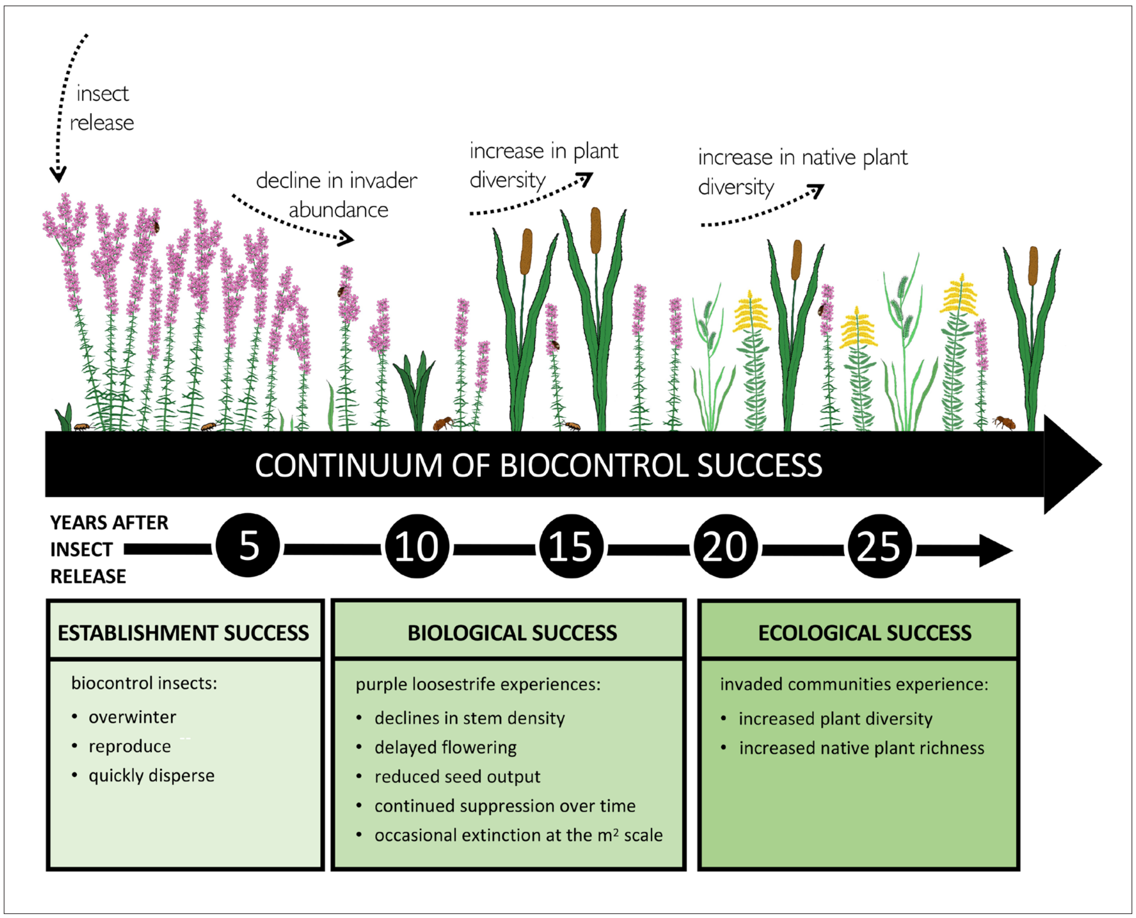

Figure 4. Successful weed biological control represents a slow accumulation of desirable changes across decades and here we summarize evidence that supports the success of biological control of purple loosestrife. Establishment success occurs when species released to control the plant successfully establish, reproduce, and become widespread, resulting in self-sustaining populations. Biological success is achieved through reduced spread or population growth rates of the target plant. Ecological success is achieved when biological control stabilizes or increases the population growth rate of desirable species that are threatened by the target plant. (S. Endriss, Cornell University)

Establishment Success

Establishment success is defined as the ability of released insects to establish self-sustaining populations at release sites. Early evidence suggested that establishment success increases when increased numbers of adults are released (Grevstad, 1999). But early experiments were typically done by releasing a few to a few hundred individuals. The rapid population build-up and mass production capabilities later allowed releases of thousands of individuals per site, and the two *Galerucella* species established self-sustaining populations at many release sites from California to Virginia and north throughout Canada (Hight et al., 1995; Piper, 1996; McAvoy et al., 1997, 2016; Grevstad 1999; Wiebe et al., 2001; Albright et al., 2004; Blossey et al., 2015, Beaulieu et al., 2018).

Anecdotally, *G. calmariensis* appears to be the more common species. When investigated, *Galerucella* establishment was easy to track because adults are readily visible and feeding (larvae and adults) is obvious, often resulting in dramatic defoliation events. However, we know much less about the fate, impact, and persistence of the *Galerucella* species in the Southeast and in areas where purple loosestrife is less abundant.

The root feeder, *H. transversovittatus*, established across temperate North America (Wiebe et al., 2001; Blossey et al., 2015). Populations of this species are difficult to track due to the nocturnal habits of adults and below-ground feeding of larvae, making how well this species' populations have done or its contribution to biological control of purple loosestrife less clear. The flower feeder, *N. marmoratus*, received less attention in surveys and in redistribution programs. The limited information that does exist suggests it is now common and established at release sites across temperate North America, including sites in Manitoba and Ontario (Blossey et al., 2015; St. Louis et al., 2020).

All four species appear to be strong dispersers. Adult *Galerucella* disperse and colonize even isolated, single purple loosestrife plants, often driven by food shortages at heavily defoliated stands, male aggregation pheromones, and plant-induced volatiles in response to leaf-feeding damage (Bartelt et al., 2008; Hambäck, 2010). Overall, the two leaf-feeding species can on average disperse 50–1,200 m per year (164–3,937 ft/yr) (Grevstad and Herzig, 1997; Ferrarese and Garono, 2010; Swain et al., 2011; McAvoy et al., 2016), with a maximum annual dispersal of 9 km (5.6 mi) recorded in the peer-reviewed literature (Ferrarese and Garono, 2010). These documented dispersal distances are achieved by active flight and passive transport on water (Ferrarese and Garono, 2010; McAvoy et al., 2016) and are likely conservative as annual spread of up to 20 km (12.4 mi) was observed in some areas in Minnesota (L. Skinner, pers. comm.). Flower-feeding weevils have been documented to disperse on average 3.1 km (1.9 mi) per year, 1.5 km (0.9 mi) of which was over water (Ferrarese and Garono, 2010). Information on dispersal of the root-feeding weevil is limited, but damage by *H. transversovittatus* has been found throughout New York state, including at sites where it was not released.

Thus, given enough time, all four species regularly colonize small purple loosestrife populations, including those located in less preferred habitats, and can persist in small populations. For example, Carrie Brown-Lima and Bernd Blossey conducted roadside surveys within a 40-km (25-mi) radius of Ithaca, New York in 2001 (ten years after initial insect releases). They found that dispersal of the two leaf-feeding species and of the flower-feeding weevil was limited by topography and was correlated to prevailing wind directions (C. Brown-Lima, pers. comm.). However, when these same roadside surveys were repeated by Stacy Endriss and Bernd Blossey in 2018 (25 years after insect releases), both the leaf-feeding beetles and the flower-feeding weevil were widespread throughout central New York, and these species had colonized purple loosestrife irrespective of differences in roadside habitat or the population size of their host plant.

Biological Success

Biological success is defined as the ability of biological control to reduce the spread as well as the abundance or population growth of the target plant species (Blossey, 2016). Here, we focus on declines in abundance of purple loosestrife, as reductions in spread are difficult to document without landscape-scale studies, and, to our knowledge, no such study exists in the purple loosestrife system. Again, we note that before their release in

North America, the impact and host specificity of each of the four insect species were thoroughly investigated using indoor potted plant experiments (in both the native and introduced ranges) and outdoor potted plant and field experiments (in the native range) (Blossey, 1993; Blossey et al., 1994a,b; Blossey, 1995a,c; Blossey and Schroeder, 1995). We also emphasize that short-term studies provide valuable insights into the potential mechanisms and impact of biological control (e.g., Katovich et al., 1999, Katovich et al., 2001; Dech and Nosko, 2002; Hunt-Joshi et al., 2004; Hunt-Joshi and Blossey, 2005), but that single-season field visits (Hovick and Carson, 2015; St Louis et al., 2020), short-term studies, and common garden experiments (Stastny et al., 2020) should not be used to predict the long-term impact and region-wide success of biological control; they provide ecological 'snapshots' that generate insights about a specific time or place but cannot capture long-term dynamics. Thus, we focus here on the results of long-term monitoring efforts.

In the case of purple loosestrife, data collected over periods of at least five years across different parts of the continent (Landis et al., 2003; Grevstad, 2006; Boag and Eckert, 2013; Britton et al., 2014; McAvoy et al., 2016) and information from informal reports, poster presentations, and personal communications demonstrate that leaf-feeding *Galerucella* beetles establish, build large populations, and create widespread and repeated defoliation events within a few years of their initial releases. Further, in response to damage by *Galerucella* beetles and other released insect species, purple loosestrife populations often decline over time (**Fig. 5a**), as shown by greatly reduced stem densities (Landis et al., 2003; Britton et al., 2014; McAvoy et al., 2016; but see, Grevstad, 2006) and a much shorter flowering period (B. Blossey, pers. obs.).

For example, eight to ten years following releases of leaf-feeding *Galerucella* beetles in Indiana, the density of purple loosestrife stems and inflorescences had declined at four of four monitored sites (Britton et al., 2014). In addition, in our long-term study (1998–2019) following purple loosestrife-herbivore dynamics for more than two decades across 33 sites in New York (Blossey et al., unpub. data), we observed dramatic insect population fluctuations over time, but purple loosestrife was ultimately no longer present in about half of our 340 permanent meter-square quadrats (1–15 quadrats per site) in 2019. When purple loosestrife did persist, stem densities in permanent quadrats decreased by about 80%, with these declines only becoming statistically significant 7–15 years after insect releases. This finding was similar to that of purple loosestrife populations monitored in Virginia where stem density held steady or increased the first five to seven years following insect releases across three sites, only declining for the two sites that were monitored across longer timescales (McAvoy et al., 2015). Furthermore, in New York, when insects were initially released in 1992, purple loosestrife began flowering in late June with a showy display lasting into September. However, almost 30 years later in 2021, plants begin flowering in late July or even August, severely curtailing seed output. Thus, insect releases appear to have resulted in widespread and sustained biological success in this system.

Importantly, widespread declines in purple loosestrife abundance, and even local eradication (at the square meter level), does not mean that purple loosestrife has disappeared from the landscape. Thriving individuals with heights comparable to those common 30 years ago can still be found. Purple loosestrife populations remain especially robust in areas subjected to chemical control or regular maintenance activities—such as along roadsides, ditches, or mowed strips—as these heavy disturbances can greatly reduce effectiveness of biocontrol agents (Blossey et al., unpub. data). Local site-specific conditions can also prevent insects from thriving and causing effective control, such as those present at tidal or densely shaded sites. In addition, we have limited understanding of the demographic effects of single generations (only F_1 overwintering), partial generations (F_1 adults and their offspring overwintering), or two generations/year (only F_2 adults overwintering) in leaf-feeding *Galerucella* beetle populations, and how this variation interacts with local climates or predation to determine the local impacts of these beetles on purple loosestrife. Regardless of the mechanism, these sites may eventually achieve biological success given time or may function as permanent purple loosestrife refuges. However, sites where purple loosestrife escapes biological control appear to be the exception to the rule and should not distract from the widespread biological success of this program: land managers no longer need to worry about the threat of purple loosestrife in the vast majority of wetlands across temperate North America. Furthermore, when local purple loosestrife outbreaks do

occur due to seedling recruitment in response to drawdowns or site disturbances, they are quickly followed by population increases of the insects that then suppress these populations. These dynamics now resemble the situation known from purple loosestrife's native range in central Europe.

How each of the four released insect species contributes to this collective success is less understood. Also unclear is whether biological control has less impact on small populations of purple loosestrife, or sites with low stem densities, as insects may be able to successfully establish but may lack sufficient food to reach outbreak population densities. However, across our 33 monitored sites in New York state, we observed declines in stem density even for purple loosestrife populations with initially low stem densities (Blossey et al., unpub. data). Releases at sites with small purple loosestrife populations may also prevent local increases in stem densities or spread to other areas, even if local declines in purple loosestrife vigor and abundance are not observed. We found that more than a decade after releases, even sites with initially low abundance of purple loosestrife remained diverse, with purple loosestrife as a minor component of the plant community.

Importantly, where data have been collected on the outcomes of biological control, site-to-site variation in the impact of biological control is apparent. Yet insect predators, diseases, site conditions, and regional climate overall do not appear to reduce the potential for biological success across North America, as declines in stem density and shortened flowering times are repeatedly observed in the Pacific Northwest, the Midwest, the Northeast, the Mid-Atlantic States, and in Canada (e.g., Landis et al., 2003; Britton et al., 2014; McAvoy et al., 2016). Furthermore, rapid evolution of purple loosestrife in North America following insect releases has not impeded biological success in this system (Stastny et al., 2020).

We emphasize that long-term studies are critical to understanding the outcomes of biological control. As shown in this system, biological success can take many years to materialize given that control agents only reduce host plant performance once they establish and increase to outbreak population sizes. In addition, boom-and-bust cycles are also typical of biological control (Heimpel and Mills, 2017; Hill et al., 2020), with herbivore populations exceeding their food supply, crashing, and then rebuilding after host plant recovery. Anecdotally, these boom-and-bust cycles are dampened over time in response to local food availability (**Fig. 5a**), yet they may also be driven by unpredictable disturbance events.

For example, in the purple loosestrife system, two events almost wiped out thriving *Galerucella* populations in some regions of New York, delaying biological success for many years. The first was extensive mosquito control efforts using aerial insecticide spraying following the arrival of West Nile Virus in 1999. In the Hudson River Valley, this almost eliminated *Galerucella* spp. populations that before these efforts had been continuously increasing. It took many years for *Galerucella* species to recover in this region (B. Blossey and V. Nuzzo, pers. obs.). We suspect that mosquito control efforts using aerial sprays have similarly harmed *Galerucella* spp. populations in the Syracuse area (B. Blossey, pers. obs.), even when sprays were conducted in August after most *Galerucella* activity had subsided. Indeed, selected mosquito control larvicides have been shown to negatively impact *Galerucella* survival and development under controlled laboratory settings (Lowe and Hershberger, 2004).

The second event was an unusually early spring in the early 2000s in the Finger Lakes Region of New York, followed by strong frosts in late May or early June that killed most young purple loosestrife shoots. Although plants recovered quickly, *Galerucella* adults had already been active for a few weeks, and this temporary absence of food killed most of the leaf-feeding beetles that year. Eventually, sites in this region were either recolonized or beetle populations gradually rebuilt from the few surviving individuals. Again, single-season field visits and common garden experiments may completely miss such events because they are unable to capture both changes in site histories and in insect and host plant abundance over time.

Ecological Success

Biological success is important, but the ultimate goal of land management is ecological success—a reduction or elimination of the negative impacts the target plant has on native biota. In this case, ecological success

requires that native species retain and increase their presence in wetlands that were once dominated by purple loosestrife (i.e., increases in the population growth rate of desirable species that are or were threatened by purple loosestrife invasion [Blossey, 2016]).

Data that can be used to evaluate ecological success of weed biological control programs are rare, especially given the decades-long timescales at which these plant biocontrol impacts are realized. Weed biocontrol programs typically do not have the logistics and funding in place to achieve this desired accountability (Blossey, 1999, 2016). Here, however, we provide strong evidence that biological control of purple loosestrife has resulted in ecological success, making it an important case study in support of biological control as an effective management tool. We acknowledge that this evidence is limited to primary producers, and we lack important information on how birds, amphibians, mammals, or insects have responded to declines in purple loosestrife vigor, stem densities, and/or cover.

In general, the pattern observed in longer-term studies is a slow but persistent increase in total and native species diversity and abundance as insect feeding drives declines in purple loosestrife stem density and cover (**Fig. 5**) (Landis et al., 2003; Albright et al., 2004; Britton et al., 2014). This process is gradual, as it requires a significant loss of dominance by purple loosestrife and—once purple loosestrife declines—a sustained recruitment of native species that can take decades. The rate and degree of such events varies across the landscape and over time. For example, species richness of non-target plant species was higher six years after insect releases at four of five sites monitored by Landis et al. (2003) in Michigan; in contrast, at four sites in Indiana, native plant species had not increased after 10 years despite heavy impacts of the leaf beetles as well as increases in overall plant richness across three of the four sites (Britton et al., 2014). Furthermore, at our 33 long-term monitoring sites in New York state, plant diversity and richness increased over time, but became significant only more than a decade after initial insect releases (Blossey et al., unpub. data). Importantly, we were able to find support that increases in the abundance of non-target plant species (including native plant species) were correlated with declines in purple loosestrife stem density. This is especially convincing because without this mechanistic link, it can be hard to distinguish the impact of biological control from other processes that may similarly drive shifts in plant communities over time.

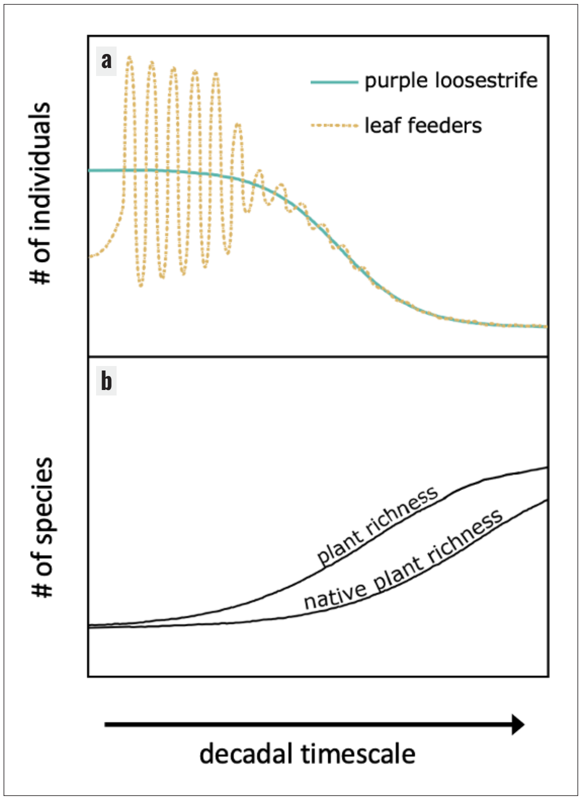

Figure 5. Conceptual diagram depicting the general pattern of purple loosestrife biocontrol through the lens of (a) insect dynamics and changes in purple loosestrife stem densities and (b) the response of total and native plant species richness over time. Note that insect abundances are at least an order of scale higher than purple loosestrife stem densities but are scaled to more easily visualize the relationship between insect dynamics and declines in target plant abundance over time. (S. Endriss, Cornell University)

These findings highlight that just as insects need time to establish, build up their populations and achieve biological success, the species that co-occur with purple loosestrife also need time to recover and respond to declines in purple loosestrife abundance (**Fig. 5b**). The gradual decline in purple loosestrife vigor due to biological control allows native species to slowly rebuild their populations and occupy vacated space. This contrasts with the rapid but short-term decline of purple loosestrife following herbicide campaigns, where annuals or other invasive species are favored, and entire sites are reset to the beginning of successional

development following treatment. Successful biological control therefore not only takes time, but biological control is likely so successful because it takes time.

However, we caution that increases in plant diversity are not always desirable, especially if incoming species represent new invaders or other species that may not deliver the desired benefits to wetland function or native fauna that were the goal of the biological control program. For example, species that can establish dominance and near monocultures, such as *Phalaris arundinacea* (reed canary grass), introduced *Phragmites australis australis* (Phragmites), or even extensive stands of *Typha* spp. (cattail), may have detrimental effects similar to purple loosestrife. Examples of this undesirable replacement were reported by Hovick and Carson (2015) and were also found for some sites in our long-term study in New York (Blossey et al., unpub. data).

Finally, the safety of non-target species is a crucially important consideration in host specificity screening of potential biological control agents. Early critiques of implementing biological control of purple loosestrife included concerns that the introduced insects would feed upon and harm native populations of *L. alatum* (winged loosestrife) and *Decodon verticillatus* (swamp loosestrife or waterwillow) (e.g., Hager and McCoy, 1998). Pre-release evaluations documented that the root-feeding and leaf-feeding biocontrol insects were able to complete their larval development on these plants under laboratory conditions, as well as inflict small to moderate amounts of feeding damage on these species (Kok et al., 1992; Blossey et al., 1994b). Post-release field studies, however, demonstrated that minor feeding and 'spillover' events are unlikely to result in population-level declines of these species (Corrigan et al., 1998; Blossey et al., 2001). In our long-term monitoring efforts in New York, *D. verticillatus* was present at the start of insect releases at some sites, and two decades later the species was thriving in the presence of biocontrol, accounting for at least 20% of plant cover at these sites. While *L. alatum* was not present in our monitoring quadrats, the species has been 'rediscovered' in the larger Montezuma wetlands in areas where it was thought to have been replaced by purple loosestrife (B. Blossey, pers. obs.; F. Morlock, pers. comm.).

BENEFITS OF BIOLOGICAL CONTROL OF PURPLE LOOSESTRIFE

As detailed above, the benefits of biological control of purple loosestrife are widespread across temperate North America. However, not all benefits are reflected in the peer-reviewed literature. For example, herbicide use has been greatly reduced or in some areas eliminated entirely because managers no longer need to worry about purple loosestrife outbreaks. Furthermore, fears of sustained non-target effects on native plants that are closely related to purple loosestrife and of severe losses for the beekeeping industry have not materialized. Finally, wetland managers and individuals without specialized knowledge of insects have become aware of the uses and benefits of biological control, a side benefit of the rapid development of techniques for the mass production and distribution of purple loosestrife biocontrol agents across the United States and Canada. Even today, management campaigns and insect distribution networks are maintained by states such as in Wisconsin (Scherer, 2020).

Importantly, biological control programs that are successful tend to be forgotten, in large part because of their success; the invasive species and biocontrol insects now behave like thousands of native plant species and their natural enemies, without the drama of outbreaks or the perceived need to intervene when large monocultures develop. This, in turn, results in reduced attention by land managers, the media, and scientists. We see this in the purple loosestrife program in that the nationwide attention the species had 20–30 years ago now has been diverted to other problems. A few scientific papers continue to be published on this system, but at a greatly diminished rate compared to a few decades ago and, at least within the United States, with increasing focus on non-management issues. Despite this reduced attention, these successful biocontrol programs maintain their success—they continue to 'chug along', characterized by only small-scale annual fluctuations in plant and insect abundance (**Fig. 5a**).

This long-term success underscores the need for greater support to collect data on the outcomes of biological control. The United States spends millions of dollars each year on traditional control methods, often with little evidence of long-term success. Effective biological control, including the work done for purple loosestrife, represents a sustainable and overall low-cost management alternative. Yet significant start-up costs, uncertainty whether biocontrol will ultimately be successful, and concerns about safety of non-target species have greatly reduced biocontrol implementation (Moran and Hoffmann, 2015). This is further compounded by a general lack of data on the outcomes of many biological control programs, particularly across the timescales needed to accurately observe biological and ecological success. Biological control of purple loosestrife is, therefore, one of the first examples of successful recovery of native plant species following control by insects and provides strong support that the benefits of biological weed control are worth the investment.

WORK STILL TO BE DONE

Today, 30 years after initial insect releases in 1992, is there still work that needs to be done or can we move on to other management priorities? In both the United States and Canada, local and regional redistribution efforts of the leaf-feeding *Galerucella* species continue. But are they necessary? Purple loosestrife is most apparent when flowering in late summer (August/September), which is when we receive inquiries regarding purple loosestrife biological control and requests for insects to be released the following spring. Yet the need to release biocontrol agents should be assessed in early spring when *Galerucella* adults, eggs, larvae, and feeding damage are most visible—not in the fall when leaf beetles are overwintering and purple loosestrife has recovered from spring and summer insect feeding damage. In some regions of the United States, especially those with isolated populations of purple loosestrife, leaf-feeding *Galerucella* beetles may be absent. However, for the vast majority of cases in the northeastern United States, interest in biological control voiced in the fall is not followed up with actual requests in the spring, as leaf-feeding *Galerucella* beetles are found to already be widely established in the areas of concern.

Requests for additional insects may also be related to unrealistic expectations as to the speed or level of control these insects may achieve. Indeed, despite widespread recognition that biological control of purple loosestrife has been successful and is sustainable, we continue to see recommendations and attempts at eradication, continued herbicide applications (Knezevic et al., 2018), or attempts to integrate chemical with biological control (Henne et al., 2005). However, biological control requires patience, time, and non-interference. Based on our experience in the northeastern United States, and New York specifically, we strongly discourage use of additional management of purple loosestrife (including digging, mowing, and chemical treatments) to allow biological control to be maximally effective. For example, even if herbicide applications do not reduce the efficacy of insects feeding on purple loosestrife plants (Henne et al., 2005), these applications likely have strong, negative non-target effects on the native species we are trying to protect. This is true for purple loosestrife and for other weed biocontrol systems as well (Peterson et al., 2020). Furthermore, as described above, traditional forms of active management facilitate long-term persistence of purple loosestrife and do not achieve sustained suppression. Traditional management also likely has significant negative impacts on non-target species, but these impacts are rarely reported. For example, a review of published evidence found that chemical treatment resulted in more harm than leaving the introduced species untreated (Kettenring and Adams, 2011). In the purple loosestrife system, herbicide treatments should be discouraged.

Most importantly, at low purple loosestrife stem densities, the negative impacts that drove the development of biological control will have disappeared or have never materialized. We should not expect, or even desire, eradication because remnant plant and insect populations ensure that herbivores are present and can respond should disturbances create ideal conditions for increased germination and seedling

recruitment of purple loosestrife. Once insects are well established, booms in purple loosestrife abundance will therefore be short-lived. To this end, if *Galerucella* beetles are already established at a site, no further releases should be made. Adding insects (except for the root-feeding weevil) will not aid in purple loosestrife declines, as levels of suppression are instead determined by local site conditions. As we detailed above, some sites with heavy shade, or tidal sites with repeated daily flooding, may function as purple loosestrife refuges or may only transition from plant communities dominated by purple loosestrife to something different after many decades of slow purple loosestrife declines. However, as purple loosestrife populations expand geographically into areas where they have not previously occurred, insect releases can still be justified. This situation may be particularly relevant in the western parts of the United States and Canada, where purple loosestrife continues to spread to previously unoccupied areas via waterways.

Thus, while a national or continental assessment of ecological and economic outcomes or a cost-benefit analysis of the biocontrol program targeting purple loosestrife would be desirable, the lack of appropriate datasets and methodological problems associated with economic valuations of species makes such an evaluation unlikely to be achieved and, if achieved, unlikely to be reliable. We know of vast datasets in the files of management agencies, but whether they will ever be published in an easily digestible format remains questionable. Many of the land managers and scientists who were instrumental in funding and supporting initial insect releases across North America are retired or no longer accessible. As a result, their expertise on historic baselines in North American wetlands, even before purple loosestrife gained and then lost dominance, has often been permanently lost.

Despite these sources of potentially unrecoverable data, evidence of the long-term outcomes of biological control in this system remains strong. The absence of extensive and detailed evaluations of weed biocontrol implementation outcomes in other systems is a major handicap preventing weed biocontrol from becoming a more acceptable and better financed management alternative, and the collection of similar data across other programs would help ensure that weed biological control continues to be funded and successful moving forward.

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