Biological Control 151 (2020) 104398

Contents lists available at ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

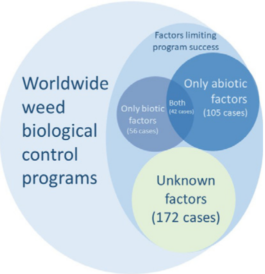
Review

A review of the causes and consequences of geographical variability in weed biological control successes

Nathan E. Harms[a,b,*], James T. Cronin[b], Rodrigo Diaz[c], Rachel L. Winston[d]

[a] *US Army Engineer Research and Development Center, 3909 Halls Ferry Rd., Vicksburg, MS 39180, USA*
[b] *Department of Biological Sciences, 202 Life Sciences Building, Louisiana State University, Baton Rouge, LA 70803, USA*
[c] *Department of Entomology, 404 Life Sciences Building, Louisiana State University, Baton Rouge, LA 70803, USA*
[d] *MIA Consulting, 316 N. Hansen Ave., Shelley, ID 83274, USA*

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Biogeography
Environmental gradients
Geographical distribution
Insect-plant interactions
Invasive plants

ABSTRACT

The impacts of different biotic and abiotic limiting factors on introduced biological control agents and their weed targets may result in geographically variable control, with implications for ongoing management and plans to improve efficacy. Geographic variability in control successes, however, may be underreported. Using the comprehensive catalogue, "Biological control of weeds: A world catalogue of agents and their target weeds", we assessed whether geographic variability in successful control is common, whether variability in programs could be attributed to limiting factors, and which factors were most likely responsible for variable success. In 38% of all reviewed programs, success was deemed spatially variable but nearly half of variable programs had unknown or unreported limiting factors. We discuss the factors that can contribute to geographic variability in agent abundance and associated success of weed biological control, provide case studies and current biological control practices, and finally discuss the potential ecological and evolutionary consequences of this variability. Published data to assess whether geographic patterns of variability were predictable, or to quantify variability along environmental gradients are lacking. Research that addresses the strength of agent-host interactions across environmental gradients, such as temperature or precipitation, or examines spatial variability in a metapopulation or landscape context may provide the best understanding of control failures and contribute to a biogeographic framework within which to evaluate ongoing and future biological control projects.

---

* Corresponding author at: US Army Engineer Research and Development Center, 3909 Halls Ferry Rd., Vicksburg, MS 39180, USA.
E-mail addresses: Nathan.E.Harms@usace.army.mil (N.E. Harms), jcronin@lsu.edu (J.T. Cronin), RDiaz@agcenter.lsu.edu (R. Diaz), rachel@getmia.net (R.L. Winston).

https://doi.org/10.1016/j.biocontrol.2020.104398
Received 27 April 2020; Received in revised form 21 July 2020; Accepted 31 July 2020

1049-9644/ Published by Elsevier Inc.

1. Introduction

Although biological control has a long history of documented successes (Buckingham, 1996; Fowler et al., 2000; McFadyen, 2000; Room et al., 1981; Seastedt, 2015), these successes are often overshadowed by rare but high-profile failures, including instances of non-target impacts (Louda et al., 2003; Pearson and Callaway, 2003) or the lack of agent establishment (Baars, 2003; Bean et al., 2007; Cullen, 1995; Milan et al., 2006). The failure of agents to reduce the abundance of target species in some areas but not others has been linked to phenological, climatic, or genetic mismatches between agent and host, although the frequency of these outcomes has been drastically reduced since modeling and molecular techniques have become more accessible during program development (Van Driesche et al., 2009; Yeates et al., 2012). For weeds with a broad distribution, a biogeographic research emphasis may provide a better understanding of spatial variability in past successes and failures and more realistic expectations for future control across regions (van Klinken et al., 2003). This approach is similar to that employed in modern invasion biology (e.g., Cronin et al., 2015; Pyšek and Richardson, 2006; Wilson et al., 2009) and could be valuable for studying systems in which the invader has been established for a long time before biological control is implemented. Additionally, in many cases there are introductions from multiple source areas (or hybridization; Kwong et al., 2017; Williams et al., 2005), leading to a predicament in decision-making about whether to prioritize one weed genotype over another for biological control, or where to source effective agents (DeLoach et al., 2003; Dray, 2003; Van Driesche et al., 2009).

Variable outcomes in weed biological control programs may be attributed to limited establishment of agents due to poor release procedures (Grevstad, 1999; Lockwood et al., 2005; Shea and Possingham, 2000), variation in host plant quality (Van Hezewijk et al., 2008), Allee effects during establishment of the agent (Courchamp et al., 1999; Hopper and Roush, 1993), incompatibilities between agents and hosts (Boughton and Pemberton, 2011), competition with other established agents (Ehler and Hall, 1982), dispersal limitations and variable spread of agents (Heimpel and Asplen, 2011; Lake et al., 2018), novel associations with predators or disease in parts of the range (Christensen et al., 2011; Goeden and Louda, 1976; Parys and Johnson, 2012), or climate and related physiological limitations of the agents (Augustinus et al., 2020; Milan et al., 2006; Zalucki and Van Klinken, 2006). Given the ecological complexity of reassociating natural enemies and their hosts in a novel range, it is surprising that so much success has been achieved in managing weeds with biological control (Heimpel and Cock, 2018; McFadyen, 2000). Nonetheless, geographic variability in weed control, particularly for widespread species, could be expected due to program or site-specific differences in the factors mentioned above.

The goal of this review is to identify causes and consequences of geographic variability of weed biological control and determine whether it is a commonly reported problem. We reviewed worldwide biological control programs through 2005 using “Table 1. Exotic organisms intentionally introduced” in “Biological control of weeds: A world catalogue of agents and their target weeds”; hereafter referred to as, 'the catalogue' (Winston et al., 2014) to determine which factors likely explain variability in agent impacts. The catalogue is an extensive database of all weed biological control programs implemented around the world and includes information such as weed species, agent species, limiting factors (if known), non-target impacts (Hinz et al., 2019), country where releases were made, and the organization that conducted the releases (Winston et al., 2014). We address the following questions: (i) what proportion of weed biological control programs are geographically variable in control outcomes; and (ii) can spatial patterns of control be attributed to variability in biotic or abiotic factors, and specifically, which factors are likely responsible for generating these patterns? We provide biological control case studies and discuss modern approaches used by biological control researchers to understand the biogeography of their systems. This type of approach can provide a useful framework for understanding past variability in success and give managers more realistic expectations in current and future programs.

2. Review of relevant cases from the world catalogue of agents and their target weeds

To determine whether geographic variability in weed biological control is common, we reviewed the catalogue for all biological control programs in which variable or inconsistent impacts were reported (Winston et al., 2014). The catalogue is a comprehensive accounting of all weed biological control programs between the late 1800s and the present with curated information on program location, year, and the current status of the program (e.g., agent abundance, severity of impact, geographic scale of impact). The catalogue has been used previously to analyze weed biological control agent introductions and their establishment rates (Schwarzländer et al., 2018), and to investigate the frequency of off-target effects from agents (Hinz et al., 2019). The curators of the catalogue compiled information on release programs obtained through extensive literature reviews and expert interviews to estimate the impact severity and geographic extent of control by introduced agents. Although the catalogue has information on native agents used for control (Table 2), agents found but not intentionally introduced (Table 3), and bioherbicides (Table 4), we focused our analysis on a subset of intentional introductions of biological control agents (Table 1). Specifically, we examined programs where general impact was estimated by the curators of the catalogue as “variable”, or the geographic extent of impact by introduced agents was “variable”, “local”, or “regional”. From this shortened list, we excluded newer (releases conducted after 2005) programs to allow time for establishment and assessment of impacts across the potential range. Although the 2005 cutoff is largely arbitrary, we assumed that 15 years would be a sufficient time to allow for determination of program success (McFadyen, 1998). Although we could determine the age of the program based on initial release dates, we could not estimate whether effort towards establishment was continuous or periodic. We also excluded those programs in which the geographic extent of damage was largely or wholly unknown.

For each combination of weed, agent, and release country, we assessed factors associated with limiting the efficacy of the agents. Although the curators of the catalogue had recorded important limiting factors for each agent/target plant interaction, where that information was available, we attempted to verify entries and further subcategorize them. These subcategories included: predation, parasitism, disease, competition with native species, competition with other agents, agent-host incompatibilities, anthropogenic disturbance, phenological asynchrony (all biotic factors), climate, and habitat (abiotic factors). For abiotic factors, we further assigned cases to the following subcategories: precipitation, temperature (climate); soil, wind, flooding, moisture, shade, and nutrients (habitat). We attempted to verify these designations, but in many cases that was not possible because the original information was obtained through extensive interviews with control practitioners. Therefore, we used the catalogue as the authority.

We omitted duplicate entries if an agent was released multiple times (e.g., over several years or potentially as distinct biotypes) in the same country. Multiple introductions of the same agent in the same country are difficult to differentiate in the field, so we merged all instances of a weed-agent combination within a country into a single entry. If multiple important factors were reported for an introduction, those were considered separately. Thus, we calculated the percentage of all programs that were deemed to be limited, at least in part, by each factor. If a program in the catalogue was estimated to be variable with regards to success, but reasons for variability were not previously reported, we reviewed the literature on the program to assess whether the information was currently available. After assigning variable programs as either due to specific biotic or abiotic factors, we examined each program to determine whether data were available to make comparisons about the relative importance of each on control effectiveness. This ultimately was fruitless, as many programs lacked quantitative spatial data on control outcomes, so we discuss the outcome of the survey qualitatively.

To compare whether the reported incidence of biotic or abiotic limiting factors were different, we used a Chi-squared test for independence. For this test, we included all programs with at least one biotic or abiotic limiting factor (i.e. we did not include cases where the limiting factors are unknown). We also conducted a separate Chi-squared test for a subset of countries with a large number of current and historical programs (Australia, South Africa, and the United States of America) to determine whether differences in the incidence of biotic or abiotic factors varied by country. These tests were conducted using SAS, version 9.4 (SAS Institute, Cary, NC).

For the categories and subcategories listed above, we reviewed the literature on the importance of each category for limiting the distribution of organisms. Although our focus is largely on regional-scale variation in success of biological control, we discuss, for example, some factors that may limit efficacy at the local habitat scale, such as soil, shade, and nutrients.

Of the 1,014 combinations of agents and target plants reported in Table 1 of the catalogue, 37% (377 combinations) are reportedly geographically variable in their impact and ultimate reduction in target weed populations (Table A.1). Of those, abiotic factors were more common than biotic factors (Chi-square, df $= 1$, $p = 0.001$); 39% were categorized as at least partly limited by abiotic factors, 25.7% partly by biotic factors, and 10.9% limited by both abiotic and biotic factors (Table 1). Additionally, 43% of variable programs reported *only* biotic (15%) or abiotic (28%) factors as important. A large proportion of variable programs (45.6%) did not have adequate information available to determine causes of variability. Most programs with reported variable outcomes came from the countries with the most historically active biological control programs (i.e., the contiguous USA, 78 cases: Australia, 74 cases; South Africa, 41 cases.) Among the three countries with the most programs, 56%, 44%, and 44% of USA, Australian and South African programs, respectively, display geographic variation in control success. There were no differences among the countries in incidence of biotic or abiotic factors (Chi-square, df $= 2$, $p = 0.11$). In the rest of the world (excluding those three countries), 36% of programs have reported variable outcomes. That two of the three most active countries have a greater proportion of variable programs may be due to their large sizes relative to other countries that have historically practiced biological control of weeds, which may promote geographic variation in control due to biogeographic processes acting on agents and hosts across large managed areas.

Table 1
Results from review of the World Catalogue of Agents and Their Target Weeds to determine causes for variable effectiveness of introduced agents. For programs and agents in which variability was postulated, we categorized the limiting factors by biotic and abiotic types. Programs could fall under more than one category (i.e., sum of percent biotic and abiotic factors is greater than 100%). For the analysis, agents released in different countries or that were assessed on multiple target plants were considered separate programs.

Limiting factor		No. of cases	Percent of *variable* programs	Percent of *all* programs
Biotic		97	25.53%	9.57%
Predation		38	10.00%	3.75%
Parasitism		38	10.00%	3.75%
Disease		3	0.79%	0.30%
Competition with native spp.		0	0.00%	0.00%
Competition with other agents		20	5.26%	1.97%
Genetic incompatibility with host		21	5.53%	2.07%
Anthropomorphic disturbance		4	1.05%	0.39%
Phenological asynchrony		6	1.58%	0.59%
Abiotic		147	38.68%	14.50%
Climate		121	31.84%	11.93%
	Precipitation	70	18.42%	6.90%
	Temperature	51	13.42%	5.03%
Habitat		56	14.74%	5.52%
	Soil	3	0.79%	0.30%
	Wind	2	0.53%	0.20%
	Flooding	5	1.32%	0.49%
	Moisture	16	4.21%	1.58%
	Shade	15	3.95%	1.48%
	Nutrients	5	1.32%	0.49%
Effect on host*		17	4.47%	1.68%
Factors not known/ determined		172	45.26%	16.96%

* It is unclear from the literature whether the limiting factor acts directly on the agents or creates an environment where the agents are more effective because the host is impacted by the factor. These cases were not included in the other categories.

3. Influences of abiotic factors in weed biological control

3.1. Climate-precipitation

Climate provides perhaps the most important limitation on species' distributions directly (humidity/precipitation and temperature) or indirectly if host plants, competitors, or predators respond to climate in ways that ultimately impact control agent population dynamics (e.g., photoperiod or temperature-cued plant senescence in some areas but not others, outbreaks of predator or competitor species) (e.g., Augustinus et al., 2020; Crawley et al., 1986; Cullen, 1995; Newman et al., 1998; Zalucki and Van Klinken, 2006). Eighteen percent of programs (70 of 377) that were deemed variable in the catalogue were affected by variation in precipitation.

Precipitation can have limiting effects directly on introduced agents by changing local or regional humidity or physical damage to agents (Dhileepan and McFadyen, 2012; Moran and Hoffmann, 1987; Norris et al., 2002), or indirectly through changes in plant quality or modifications to interactions between species (Deguines et al., 2017). For example, populations of a highly successful biological control agent, the cochineal insect, *Dactylopius opuntiae* (Cockerell), deployed in South Africa against the cactus weed, *Opuntia stricta* (Haw.) Haw., are reduced by heavy rainfall. Rain dislodges the sessile females and nymphs of the cochineal insects from plants at a time when additional moisture encourages vigorous cactus growth (Paterson et al., 2011). Regional control by *D. opuntiae* resulted in a 90% biomass reduction of the host within a decade after introduction, but it is thought that the reduction would have occurred much more rapidly if not for a period of rainfall and flooding shortly after the introduction of *D. opuntiae* (Paterson et al., 2011). In contrast, the rust *Puccinia abrupta* var. *partheniicola* was introduced for control of parthenium weed (*Parthenium hysterophorus* L.) in Australia, but was only established in areas with sufficiently wet winters (Dhileepan and McFadyen, 2012). Precipitation can also lead to apparent variation in biological control success by enhancing plant vigor. For example, Weed et al. (2014) demonstrated that the stem-mining weevil *Mecinus janthiniformis* Toševski & Caldara appeared to vary spatially in its control of Dalmatian toadflax (*Linaria dalmatica* ssp. *dalmatica* (L.) Mill.) but this variability could be largely explained by local precipitation patterns and the positive effect of rainfall on plant growth and reproduction.

3.2. Climate-temperature

Thirteen percent of the weed biological control programs with variable success (51 of 377 cases) were attributed to geographic variation in temperature. Lower thermal limits may restrict agent establishment and survival in a number of control programs where cold winters are common (Cowie et al., 2016). For example, the alligatorweed flea beetle, *Agasicles hygrophila* Selman & Vogt, is restricted by cold winter temperatures to warm coastal areas in the southeastern USA. Areas north of the overwintering range of *A. hygrophila* remain largely uncontrolled (Harms and Shearer, 2017; Vogt et al., 1992). Similarly, the tropical soda apple leaf beetle, *Gratiana boliviana* Spaeth, has a more restricted range than its host in the southeastern USA due to differences in low temperature limits between the two. Thus, control in higher latitude sites of the introduced range is likely to be low (Diaz et al., 2008; Mukherjee et al., 2012).

There are many ways in which biological control practitioners address climate limitations on agents. Commonly, new native-range exploration is undertaken in climates that better match areas in the introduced range where agent abundance is low, with the intention to locate new genotypes (or species) of agents that are better adapted to local conditions (Robertson et al., 2008; Sun et al., 2017; van Klinken et al., 2003). For example, putatively cold-tolerant alligatorweed flea beetles collected in temperate South America were introduced into the USA during the early 1980s in response to the overwintering temperature limitations experienced by established beetle populations (Buckingham and Boucias, 1982; Buckingham et al., 1983). Not typically undertaken, but potentially useful, are surveys in other parts of the introduced range to identify whether sufficient genetic variation exists in the biological control agent to encourage locally adapted populations (e.g., Griffith et al., 2019; Reddy et al., 2019). Reddy et al. (2019) identified an introduced population of the water hyacinth (*Pontederia crassipes* Mart.) weevil *Neochetina eichhorniae* Warner in Australia that performed better at cool temperatures than either introduced populations in California or native populations from Uruguay or Argentina. The Australian introduction of *N. eichhorniae* was made from source populations in the USA, which suggests there may already be better cold-adapted *N. eichhorniae* populations in the USA.

Species' distributions will be influenced by rising average temperatures, the variability of temperature extremes, and increased frequency of extreme weather events associated with global climate change (Easterling et al., 2000; Harms and Cronin, 2020; Parmesan, 2006; Parmesan and Yohe, 2003). Host plant availability is generally not limiting for the distribution of biological control agents, but if increasing global temperatures promote poleward shifts in the distribution patterns (i.e., location and abundance) of both agents and hosts, then unequal expansion rates may lead to increased importance of host-limitations for predicting agent occurrence. Although this has not been addressed explicitly for weed biological control agents and their hosts, there are a number of other systems in which spatial and phenological mismatches between herbivores and plants are likely to occur as a result of climate change (Blois et al., 2013; Tylianakis et al., 2008).

3.3. Habitat

Habitat type and quality (i.e. flooding, shading, moisture, nutrients, soil) may be important for biological control, particularly if it varies regionally. Variability of success in nearly 15% of evaluated programs (56 of 377) was at least partly attributed to habitat variation. For instance, the tansy ragwort (*Jacobea vulgaris* Gaertner) flea beetle, *Longitarsus flavicornis* (Stephens), cannot persist in areas prone to flooding (e.g. floodplain sites) due to high larval mortality (Potter et al., 2007). *Listronotus setosipennis* (Hustache), introduced for control of parthenium weed in Australia, is more abundant on plants in areas with alluvial and black soils than clay and sand. As larval *L. setosipennis* mature, they move from feeding in the stem to roots, ultimately exiting to create a pupal chamber in the soil, which is thought to be the limiting feature of soil type (Dhileepan et al., 2018). Available nutrients may vary regionally and influence control agents' impacts on host plants. Although there are few examples where nutrients are thought to limit the distribution of agents, nutrients have direct effects on agents through altered life history traits and population dynamics (Harms and Cronin, 2019; Room et al., 1989; Uyi et al., 2016; Wheeler and Center, 1997), and indirect effects through modulation of host-plant defenses (Nybakken et al., 2018; Tomley, 1990).

4. Influences of biotic factors in weed biological control

4.1. Biotic resistance (predation, parasitism, disease, competition)

In 26% of variable programs (9.8% of *all* programs), biotic resistance was evident. Strong biotic pressures (predation, competition) in the native range are often absent or much-reduced in the novel range during invasion (i.e. enemy-release) (Keane and Crawley, 2002; Torchin and Mitchell, 2004). Moreover, native predators, parasitoids, or parasites can benefit from, and numerically respond to, the potential food supply that comes with introduction of large numbers of biological control agents (Carlsson et al., 2009). For example, the seed head gall fly (*Urophora affinis* Frauenfeld) introduced for control of spotted knapweed (*Centaurea stoebe* Eichw.) is preyed upon by deer mice (*Peromyscus maniculatus*) in a number of locations during a time when food is otherwise scarce (Pearson et al., 2000), which may explain spatial variation in knapweed biological control in some areas (Story and Nowierski, 1984).

Acquisition of new predators, parasitoids, or parasites is detrimental to some biological control programs, but evidence for their role in contributing to geographic variation in success or generating distributional boundaries of agents is largely lacking. For instance, a native acquired aquatic parasitoid (*Trichopria columbiana* Ashmead) exerts substantial pressure on the introduced hydrilla (*Hydrilla verticillata* L.f. Royle) biological control agents, *Hydrellia pakistanae* Deonier and *H. balciunasi* Bock in the USA (Coon et al., 2014). Whether *T. columbiana* is partly responsible for restricting the geographic distribution of agents to the southern USA is unclear and has so far not been tested (Coon et al., 2014; Grodowitz et al., 1997). *Trichopria columbiana* is broadly distributed in the northern USA, associated with common native hosts, so may provide some resistance to northward range expansion of agents, though incompatibility between introduced *Hydrellia* spp. and northern hydrilla genotypes is more likely to limit range expansion of the agents (see section *4.2 Genetic variability in host populations and agent-host incompatibilities* below). The egg-parasitoid, *Kalopolynema ema* (Schauff and Grissell), native to the USA, parasitizes eggs of the water hyacinth planthopper (*Megamelus scutellaris* Berg) at field-measured rates up to 26% (Minteer et al., 2016). As with *T. columbiana* and introduced *Hydrellia* spp., evidence is lacking for the influence of *K. ema* on *M. scutellaris* distribution. A number of generalist predators have been implicated in reducing impacts of biological control agents in some areas. For instance, the red imported fire ant (RIFA), *Solenopsis invicta* Buren, can limit control of waterlettuce (*Pistia stratiotes* L.) and common salvinia (*Salvinia minima* Baker) by feeding on introduced biological control agents in some locations (Dray et al., 2001; Parys and Johnson, 2012). In another example of severe ant predation, tamarisk (*Tamarix* spp.) leaf beetles *Diorhabda elongata* Brullé were heavily preyed upon by ants (RIFA and native species) in Texas, limiting establishment to some of the original release sites only (Knutson and Campos, 2019).

Perhaps important but understudied is the influence of interspecific competition with other herbivores on the performance and distribution of introduced biological control agents. Groenteman et al. (2007) found that after introduction of the nodding thistle (*Carduus nutans* L.) seed fly (*Urophora solstitialis* (L.)) in New Zealand, gall numbers were reduced by 46–93% when the earlier-established seed weevil *Rhinocyllus conicus* Frölich was present. However, in a simulation of nodding thistle growth rates under attack by one or both of the introduced agents, it was found that at high densities of both agents, nodding thistle growth rate would be 27% and 18% higher, respectively, than when *U. solstitialis* or *R. conicus* occurred alone. Thus, negative interactions between the agents may be responsible for the spatial variation in nodding thistle control observed in New Zealand (Groenteman et al., 2007). In a rare example of investigation into the compatibility of using insect and pathogen agents to control a weed, Ray and Hill (2016) found that heavy feeding by the introduced mirid, *Eccritotarsus catarinensis* (Carvalho), increased subsequent time for infection by the water hyacinth pathogen, *Acremonium zonatum* (Sawada) W. Gams. Similarly, on melaleuca (*Melaleuca quinquenervia* (Cav.) S.F. Blake) in Florida, fitness of the rust fungus *Puccinia psidii* G. Winter and weevil *Oxyops vitiosa* Pascoe were reduced in areas where both agents were present, with infection lowering larval survival and feeding by *O. vitiosa* reducing available leaves for infection by *P. psidii* (Rayamajhi et al., 2006).

Interactions between agents can be complex, however. For example, Marlin et al. (2013) found both negative and positive interactions between three introduced biological control agents on water hyacinth, which led to variability in plant biomass reduction, depending on the combination of agents. Although geographic considerations were not the focus of Marlin et al. (2013), efforts have been made to understand distributional patterns of water hyacinth insects relative to thermal physiology of the agents, given that some are more cold-hardy than others (Hill and Olckers, 2000; May and Coetzee, 2013). By connecting previous work on water hyacinth agent distributions (and abundance within their distributions) to interactions between agents, it is likely that field measurements would confirm that the strength of agent-agent interactions varies with location and agent abundance. This should be examined in the future and could provide valuable insights into geographic variation in biological control of water hyacinth relative to agent-agent interactions. Furthermore, indirect competition between agents may occur through herbivore-mediated changes in plant chemistry (i.e. induced defenses). Because different natural enemy species (Liu et al., 2018) or agent guilds (i.e., chewing, piercing-sucking, pathogen) (Felton and Korth, 2000; Felton et al., 1994) can induce different responses in their host plants, use of multiple agents in the same feeding guild seems to be more likely to generate a stronger negative competitive interaction than agents in multiple guilds. With such sparse data available on interactions between introduced biological control agents, studies to determine potential interactions between agents could be included in testing for some programs when additional agents are under consideration for release.

4.2. Genetic variability in host populations and agent-host incompatibilities

Incompatibility between agents and hosts or genetic variability in host populations was implicated in nearly 6% of the programs identified in the catalogue. Biological control agent performance may vary geographically because of spatial variation in the genetic makeup of host-plant populations. For example, *Hydrellia pakistanae* was released in the USA for control of the aquatic weed hydrilla (Center et al., 1997), but has been mostly restricted to the southeastern USA where a dioecious genotype of hydrilla occurs (Grodowitz et al., 2010, 2004; True-Meadows et al., 2016). In the northeastern USA, the fly has been unsuccessful in establishing and impacting hydrilla populations of a different, monoecious genotype (Grodowitz et al., 2010). The lack of establishment and impact to monoecious hydrilla has been suggested to result primarily from the annual habit of monoecious hydrilla and the overwintering habitat requirement (plant stems in the water column) of the agent rather than palatability (Dray and Center, 1996) or climate differences, because *H. pakistanae* has been collected as far as N 46° in its native range (Deonier, 1993). If the northern genotype expands southward, the distribution of *H. pakistanae* may shrink further if the two genotypes co-occur but the northern population is more successful because of differential impacts by the agent (i.e. through apparent competition, the negative impact of one species on another mediated by a shared predator or herbivore; Holt and Bonsall, 2017). Similarly, development of biological control for Old World climbing fern (*Lygodium microphyllum* (Cav.) R.Br.) in Florida benefitted from testing agent haplotypes on multiple fern haplotypes from native and introduced ranges (Goolsby et al., 2006a). This led to the discovery of locally adapted agent populations that differed greatly in their performance on Florida plants, depending on the source of agents within the native range. Variation in agent performance may be the result of incorrectly-sourced agents (i.e. from the wrong host haplotypes in the native range), the presence of multiple host haplotypes in the introduced range due to multiple introductions from different source areas, or can result from evolutionary processes acting on plant populations during or after the invasion process (e.g. genetic bottlenecks, hybridization).

Novel host plant genotypes may be formed during the invasion process through hybridization between different source populations or between introduced and native lineages or species (Ellstrand and Schierenbeck, 2000; Lambertini et al., 2012; Moody et al., 2016). Hybrids represent novel genotypes which are absent from the native range of the invasive parent plant and complicate the process of biological control development (Moody et al., 2016). Incompatibilities between agents and hosts were found when testing potential agents for use on native (Brazilian) or the invasive hybrid (Florida, USA) Brazilian peppertree (*Schinus terebinthifolia* Raddi) (Manrique et al., 2008). Among the three potential agents used in those experiments, one performed similarly on native and introduced Brazilian peppertree populations but the other two agents differed greatly between native and introduced weed populations with one performing better on hybrid introduced populations and one performing worse. This study allowed the researchers to select the appropriate agent but was only possible after testing because predicting agent performance on hybrids is difficult (Fritz et al., 1999). For instance, in the USA, both native and introduced watermilfoils (*Myriophyllum* spp.) co-occur and have produced a number of hybrid offspring and backcrosses throughout their range (Borrowman et al., 2014; Moody et al., 2016). In addition to problems with predicting biological and ecological interactions between hybrids, their susceptibility to biological control agents is not always as would be predicted from tests with parental genotypes (Borrowman et al., 2014; Roley and Newman, 2006). In the case of the native North American milfoil weevil, *Euhrychiopsis lecontei* (Dietz), variable performance was found on the multiple new lineages of watermilfoils. Additionally, the high level of genetic diversity in *Phragmites* populations in the USA (Lambertini et al., 2012) and the occurrence of native-invasive hybrids may complicate biological control agent development and lead to differences in impacts between populations when agents are introduced (Cronin et al., 2016). In addition to performance of agents, variable control may result from genotypic differences in performance of the host plant that manifest through increased resource acquisition or growth rate (i.e. hybrid vigor) (Ellstrand and Schierenbeck, 2000; Lee, 2002).

4.3. Phenological asynchrony between agent and host

Although not commonly reported (approximately 2% of the programs), geographic differences in agent and host phenologies (i.e. the timing of important life history events) may limit control in some cases, particularly when the primary impact of the agent is related to seasonality or life stage of the host. For example, the tamarisk leaf beetle, *Diorhabda carinulata* (Desbrochers), was widely introduced into North America from China, but leaf beetle introductions in the southern USA experienced day-length related premature diapause, which reduced their impacts on host trees in southern locations (Bean et al., 2007). Subsequently, evolution of day-length diapause initiation was documented: agents are now better-synchronized with their hosts in southern environments, and as a result efficacy of *D. carinulata* has increased (Bean et al., 2012).

Phenologies of many organisms are expected to change under future climate regimes (Chmura et al., 2019; Scranton and Amarasekare, 2017). If phenologies of interacting species (e.g., biological control agent and host) shift at different rates (Forrest, 2016; Renner and Zohner, 2018), there may be an increase in periods where agent abundance is low relative to susceptible host stages. Additionally, some insects target reproductive structures of host plants which only occur during a short window (e.g. flowers, seeds), and disruption of agent-host synchrony may reduce the impact of the agent to nearly zero in some areas. On the other hand, climate change may lead to increased control of some species in some cases. Experimentally-elevated CO_2 in a field trial led to an advance in the phenology (earlier flowering, faster seed head development) of the prairie invader *Centaurea diffusa* Lam., but damage by the introduced agent *Larinus minutus* Gyllenhal was also higher under experimental conditions (Reeves et al., 2015). Based on this work, the authors suggested that *C. diffusa* and *L. minutus* phenologies would be better matched during climates of the future, at least in the western USA. Although the potential for climate change to disrupt phenological matching of agents and hosts has not received much attention to date, examination of invertebrate biological control has revealed that earlier and warmer springs are likely to reduce efficacy in some systems because of increased phenological mismatch between agent and host (Evans et al., 2013).

4.4. Anthropogenic disturbances

Management of multiple species is often difficult to coordinate across large areas and jurisdictions. Thus, efforts in one area focused on release and establishment of biological control agents may be negatively impacted by management activities (or lack thereof) of other agencies in the same or adjacent areas (Wheeler et al., 2020). Although the documentation of management conflicts leading to variability in biological control outcomes are rare in the literature (0.5% of variable cases), this potential has been considered. For instance, there has been considerable interest in the compatibility of using herbicides with weed biological control to suppress water hyacinth in Florida, USA (Center et al., 1999; Tipping et al., 2017). Because coordination between weed biological control practitioners and herbicide applicators may not be possible, Center et al. (1999) examined whether the two technologies were passively compatible and determined that they should be used in coordination, in a way that maintains the weed below damage levels but allows persistence of the agents. Similarly, roadside weed management of spotted knapweed (*Centaurea stoebe* sens. lat.) in Arkansas has been examined to determine whether mowing practices could be timed to lessen negative impacts on the seed weevil, *L. minutus* (Ferguson, 2018). Mowing causes massive larval mortality of *L. minutus*, but earlier mowing (before first bud formation) is more compatible with biological control because spring floral resources are required for early-season egg development in *L. minutus* (Ferguson, 2018). In accord with Center et al. (1999), Ferguson (2018) also recommends providing unmanaged refuge areas adjacent to mowed areas to allow long-term local persistence of agent populations. Although, to our knowledge, there have been no examinations of geographic variability in anthropogenic disturbances and their role in biological control efficacy, there is the potential to examine this in the future. Timing of weed management by mowing or herbicides will be largely dependent on geographic location, so comparisons between managed areas, their interactions with other biotic or abiotic factors, and the role in success of biological control are possible.

Due to the high frequency of disturbance and increased nutrient inputs, many target weeds are problematic in areas near agriculture and may be subject to drift of insecticides used for control of invertebrate pests. For example, in South Africa, insecticide drift was implicated in the failure of *Trichapion lativentre* (Béguin Billecocq) to colonize infestations of *Sesbania punicea* (Cav.) Benth. that were close to citrus orchards (Hoffmann and Moran, 1995). Similarly, in a survey of alligatorweed biological control by the alligatorweed flea beetle in the southeastern USA, Cofrancesco (1988) suggested that pesticide use in adjacent agricultural areas could limit the effectiveness of the introduced agents. Although not an agricultural setting, Wheeler et al. (2020) determined that mosquito pesticides commonly used in southern Florida could cause significant mortality of weed biological control agents and should be further investigated for impacts in field populations.

5. Consequences of geographic variability for weed biological control

5.1. Incomplete geographic overlap between agent and host

The primary consequence of variability across an agent's range is the inability to predict outcomes of introductions, at least early in release programs. As control programs mature, practitioners learn the types of habitats that support populations of the agents. Incomplete geographic overlap occurs when different factors act on agent and host to delineate their distributions, or the same factors are differentially limiting to agent and host. This generates a pattern in which the agent is much more localized than the host is. Although biological control is often seen as a solution to the problem of "enemy-release", when agent abundance is limited within the larger host distribution, enemy-free space (see Keane and Crawley, 2002) may be locally or regionally maintained (Lu et al., 2013). Additionally, if enemy-release occurs as a gradient (due to climate or other limiting gradients on agents), then control of target weeds could be expected to follow a similar local or regional pattern. For example, abundance of the tamarisk biological control agent *D. carinulata* now reflects a latitudinal gradient in the western USA because of rapid adaptive responses to photoperiod and critical day length requirements for diapause induction (Bean et al., 2007). How this gradient in agent abundance affects control has not been quantified, but it is thought that agent efficacy could also correlate with the latitudinal gradient.

Evolutionary consequences of complete or partial enemy-release (e.g. increased competitive ability, reduced defenses) are frequently observed in introduced plant populations (Bhattarai et al., 2017; Blossey and Notzold, 1995; Lin et al., 2019; Maron et al., 2004; Zou et al., 2008). Adaptive effects of enemy-release may be observed as increased growth rates or altered defensive chemistry relative to native populations. Tansy ragwort, in multiple introduced ranges (Australia, New Zealand, North America), was found to have evolved increased photosynthetic rate, reduced carbohydrate storage, and increased tolerance to generalist herbivory over native European populations (Lin et al., 2019). When incomplete geographic overlap occurs after introduction of biological control agents, these processes may continue in marginal and extra-marginal populations, leading to further divergence between introduced plant populations or between introduced and source populations. In one of the few reported examples of this type of post-biological control evolution in target weeds, purple loosestrife (*Lythrum salicaria* L.) in North America shows evidence for evolution of increased defense against herbivory in populations that have been historically subject to biological control versus those that have not been exposed to biological control agents (Stastny and Sargent, 2017).

5.2. Current biogeographical practices for developing biological control agents

The process of biological control agent development has greatly matured since early introductions and now uses criteria that promote safety and cost-effectiveness (McFadyen, 1998). In particular, the selection process now includes, in addition to lengthy and phylogenetically-informed host-range testing, climate-matching coupled with molecular matching of target species to ensure potential agents will be suitably adapted to conditions where the host occurs (Goolsby et al., 2006b; Van Driesche et al., 2009). Another promising but potentially labor and data-intensive approach involves environmental niche modeling in combination with agent life-history or vital rate modeling to predict not only distribution but abundances within the introduced range, given that high agent abundance is critical for control

(Augustinus et al., 2020; Zalucki and Van Klinken, 2006). Spatial variability of biological control is rarely studied in a biogeographic framework, but predictions about agent population dynamics, geographic distribution, and potential spatial variability in establishment success could be made based on data that are commonly collected during exploratory surveys or pre-release laboratory developmental studies of potential biological control agents (Zalucki and Van Klinken, 2006). Although these techniques are relatively new, and our analysis focused on programs prior to 2005, we expect that variable outcomes related to abiotic factors will become less frequent as these approaches are more commonly incorporated during biological control agent development.

The foundation of biological control programs is in the exploration of areas within the native range of target plants to identify and prioritize damaging natural enemies (Goolsby et al., 2006b). However, given the constraints on distributions of natural enemies and their hosts, and that abundances and associated impacts may vary along limiting gradients, it could be useful to consider the location of surveys along such gradients. For example, observations of potential agents near their native range boundary may suggest they are unsuitable as control agents in certain portions of the introduced range. However, multiple locally adapted agent genotypes might be sourced in the native range for use in the introduced range, particularly if the introduced range is large and spans variable environments.

6. Opportunities for research using weed biological control systems

Invasion biologists conduct extensive examinations of large-scale invasions and their implications for management (e.g., Cronin et al., 2015; Gaskin et al., 2013; Lu et al., 2018, 2019; Ordonez and Olff, 2013). Examination of species' distributions and the variables constraining them hold particular value for biological control programs because the geographical limits of an agent (and agent abundance within those limits) determines where and what magnitude of control may be expected to occur (Augustinus et al., 2020). A fruitful area of research might be to use various distributional hypotheses such as the Abundant Center Distribution (ACD) (Sagarin and Gaines, 2002) to examine patterns of agent and target weed abundance across a large area and to generate a list of testable hypotheses, many of which could be suitable for application in biological control systems. In particular, the following hypotheses (adapted from Table 1 *in* Sagarin and Gaines, 2002, and others) may be of value for advancing our understanding of range margin ecology and weed biological control:

i. Sites near the range margin of biological control agents will see gradual abundance increases as climate change shifts species' ranges (Fréjaville et al., 2020; Lenoir and Svenning, 2015).
ii. Marginal populations of biological control agents are genetically distinct and will promote local adaptation of control agents to marginal environments (Chevin and Lande, 2011; Kawecki, 2008).
iii. Gene flow into marginal populations will have negative impacts on biological control success. Gene flow from interior (central) to marginal (edge) populations will limit biological control agent adaptation to marginal environments through genetic swamping (Kawecki, 2008).
iv. Gene flow from interior into marginal weed biological control agent populations will be beneficial to counteract negative effects of inbreeding depression (Kawecki, 2008).
v. Marginal population dynamics will be more variable than interior population dynamics (Gaston, 2003). Because the climate will be more extreme at the distributional margin (relative to agents' limits), and thus abiotic factors will be more important to biological control success, variability in abiotic factors will promote unstable agent-host interactions in marginal populations.
vi. Extinctions in weed biological control agent populations are more likely at margins (Gaston, 2003; Wilson et al., 2002) and therefore biological control will be less successful in marginal environments.
vii. Outbreak dynamics will be, on average, more likely in interior populations (Hrinkevich and Lewis, 2011; Marini et al., 2012). However, as the geographic area representing the range center shifts or expands, biological control agent outbreaks will be more common and occur in new places, leading to increased temporary control in marginal areas.
viii. Competition will be more or less important at range margins (Godsoe et al., 2017; Louthan et al., 2015). If multiple biological control agents are introduced or generalist herbivores are common, stress on agents corresponding to marginal environments coupled with competitive interactions will lessen biological control effects and even contribute to defining the location of the range margin (because competition is more important). In contrast, because competition is density-dependent, in marginal populations it may be reduced because populations of agents are expected to be small (and competition less important). In both cases, outcomes will depend on whether the environment is also marginal for the other competing species.
ix. A stochastic event at a range margin will have a greater impact than in the range interior (Beddington et al., 1976; Gaston, 2003). Because a marginal environment is already at the extreme of the agent's niche limit, random pulses of stress or disturbance will have a greater relative effect on agent demography in marginal than in interior populations.

Tests of these hypotheses could help to understand the ways in which biological control agent abundance varies across geographic ranges and the potential for range expansion in the future. For instance, genetically distinct edge/marginal populations (hypothesis #ii) (Pironon et al., 2017) may have greater adaptive potential to future climate change and other extreme events (Lesica and Allendorf, 1995). However, whether marginal populations remain genetically isolated may depend on the agent, with strong-dispersing agents promoting gene flow from interior to marginal populations and limiting opportunities for local adaptation to marginal environments (hypothesis #iii). On the other hand, in genetically depauperate marginal populations (such as those undergoing multiple genetic bottlenecks during agent development and introduction), gene flow from other areas may enhance adaptive potential and reduce negative effects of inbreeding depression (hypothesis #iv) (Sexton et al., 2011). Because the basis of these hypotheses is that abundance may depend to one degree or another on environmental gradients and connectedness of agent and plant populations, a combined metapopulation and population growth-modelling approach may be useful to predict agent and host occurrence and abundance along these gradients (Gotelli and Kelley, 1993) in marginal areas (Öckinger, 2006).

7. Conclusions

Weed biological control systems can be used to address basic ecological and evolutionary hypotheses surrounding plant invasions and trophic interactions. Additionally, implementation of weed biological control often occurs once the target plant has spread and reached damaging levels in the introduced range. When targeted weed populations occur across a large geographic area, variability in control success might be expected due to differential limitations on the weed and the introduced agents. Since the effectiveness of weed biological control relies on successful establishment, population build-up, and subsequent impact on the target weed, factors that contribute to geographic variation in these items are important to understand.

Here we presented a review of biotic and abiotic factors implicated in variability of weed biological control efficacy. We found that although climatic variability was the most commonly reported cause of variability in program success, many studies (45%) had insufficient information to determine underlying causes. Although limiting gradients (e.g., winter severity) are certainly a factor in many instances, there are few studies that explicitly address their effects on agents and subsequent control of the target weed (Augustinus et al., 2020). We recommend a biogeographical approach to weed biological control. Plant invasions are heterogeneous, so future management must be flexible to deal with that heterogeneity. Weed biological control is inherently a biogeographical field of study (Wilson et al., 2009). Thus, incorporation of concepts and hypotheses from studies on geographical variability may contribute to the broader ecological and evolutionary literature, increase the understanding of why agents perform better in some areas but not others, encourage more accurate modeling of species distributions and abundance in introduced areas, and assist decision making during biological control development and implementation.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRediT authorship contribution statement

Nathan E. Harms: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Funding acquisition. **James T. Cronin:** Conceptualization, Resources, Writing - review & editing, Supervision. **Rodrigo Diaz:** Conceptualization, Writing - review & editing. **Rachel L. Winston:** Data curation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the following for providing data, ideas, comments, or valuable discussion regarding geographic ranges and impacts of biocontrol agents: Bernd Blossey, Al Cofrancesco, Michael Grodowitz, Phillip Tipping, Paul Pratt, Julie Coetzee, Martin Hill, and Matthew Purcell. Thanks to Rieks Van Klinken, Julie Nachtrieb, and Ian Knight for comments and suggestions on an earlier version of this manuscript, and two anonymous reviewers whose suggestions greatly improved this version. This work was conducted in partial fulfillment of a Doctoral degree (NEH) from Louisiana State University. Partial support was provided by the US Army Engineer Research and Development Center Aquatic Plant Control Research Program.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2020.104398.

References

Augustinus, B., Sun, Y., Beuchat, C., Schaffner, U., Müller-Schärer, H., 2020. Predicting impact of a biocontrol agent: integrating distribution modeling with climate-dependent vital rates. Ecol. Appl. 30 (1). https://doi.org/10.1002/eap.v30.110.1002/eap.2003.

Baars, J.-R., 2003. Geographic range, impact, and parasitism of lepidopteran species associated with the invasive weed *Lantana camara* in South Africa. Biol. Control 28 (3), 293–301. https://doi.org/10.1016/S1049-9644(03)00070-7.

Bean, D.W., Dalin, P., Dudley, T.L., 2012. Evolution of critical day length for diapause induction enables range expansion of Diorhabda carinulata , a biological control agent against tamarisk (Tamarix spp.) : Evolution and range expansion of a biocontrol agent. Evol. Appl. 5 (5), 511–523. https://doi.org/10.1111/j.1752-4571.2012.00262.x.

Bean, D.W., Dudley, T.L., Keller, J.C., 2007. Seasonal timing of diapause induction limits the effective range of *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae) as a biological control agent for tamarisk (*Tamarix* spp.). Environ. Entomol. 36, 15–25. https://doi.org/10.1603/0046-225X(2007)36[15:STODIL]2.0.CO;2.

Beddington, J.R., Free, C.A., Lawton, J.H., 1976. Concepts of stability and resilience in predator-prey models. J. Animal Ecol. 45 (3), 791. https://doi.org/10.2307/3581.

Bhattarai, G.P., Meyerson, L.A., Anderson, J., Cummings, D., Allen, W.J., Cronin, J.T., 2017. Biogeography of a plant invasion: genetic variation and plasticity in latitudinal clines for traits related to herbivory. Ecol. Monogr. 87 (1), 57–75. https://doi.org/10.1002/ecm.1233.

Blois, J.L., Zarnetske, P.L., Fitzpatrick, M.C., Finnegan, S., 2013. Climate change and the past, present, and future of biotic interactions. Science 341 (6145), 499–504. https://doi.org/10.1126/science.1237184.

Blossey, B., Notzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J. Ecol. 83 (5), 887. https://doi.org/10.2307/2261425.

Borrowman, K.R., Sager, E.P.S., Thum, R.A., 2014. Distribution of biotypes and hybrids of *Myriophyllum spicatum* and associated *Euhrychiopsis lecontei* in lakes of Central Ontario, Canada. Lake Reservoir Manage. 30 (1), 94–104. https://doi.org/10.1080/10402381.2013.876469.

Boughton, A.J., Pemberton, R.W., 2011. Limited Field Establishment of a Weed Biocontrol Agent, *Floracarus perrepae* (Acariformes: Eriophyidae), Against Old World Climbing Fern in Florida - A Possible Role of Mite Resistant Plant Genotypes. Env. Entom. 40 (6), 1448–1457. https://doi.org/10.1603/EN11030.

Buckingham, G.R., 1996. Biological control of alligatorweed, *Alternanthera philoxeroides*, the world's first aquatic weed success story. Castanea 232–243.

Buckingham, G.R., Boucias, D., 1982. Release of potentially cold tolerant alligatorweed flea beetles (Agasicles hygrophila Selman and Vogt) into the United States from Argentina. In: Army, D.o.t., (Ed.). Waterways Experiment Station, Corps of Engineers, Environmental Laboratory, Vicksburg, MS.

Buckingham, G.R., Doucias, D., Theriot, R., 1983. Reintroduction of the alligatorweed flea beetle (*Agasicles hygrophila* Selman and Vogt) into the United States from Argentina. J. Aquatic Plant Manag. 21, 101–102.

Carlsson, N.OL., Sarnelle, O., Strayer, D.L., 2009. Native predators and exotic prey –an acquired taste? Front. Ecol. Environ. 7 (10), 525–532.

Center, T.D., Dray, J., Allen, F., Jubinsky, G.P., Grodowitz, M.J., 1999. Biological control of water hyacinth under conditions of maintenance management: can herbicides and insects be integrated? Environ. Manage. 23, 241–256. https://doi.org/10.1007/s002679900183.

Center, T.D., Grodowitz, M.J., Cofrancesco, A.F., Jubinsky, G., Snoddy, E., Freedman, J.E., 1997. Establishment ofHydrellia pakistanae (Diptera: Ephydridae) for the Biological Control of the Submersed Aquatic PlantHydrilla verticillata (Hydrocharitaceae) in the Southeastern United States. Biol. Control 8 (1), 65–73. https://doi.org/10.1006/bcon.1996.0491.

Chevin, L.-M., Lande, R., 2011. Adaptation to marginal habitats by evolution of increased phenotypic plasticity. J. Evolutionary Biol. 24, 1462–1476, doi: 10.1111/j.1420-9101.2011.02279.x.

Chmura, H.E., Kharouba, H.M., Ashander, J., Ehlman, S.M., Rivest, E.B., Yang, L.H., 2019. The mechanisms of phenology: the patterns and processes of phenological shifts. Ecol. Monogr. 89 (1), e01337. https://doi.org/10.1002/ecm.1337.

Christensen, R.M., Pratt, P.D., Costello, S.L., Rayamajhi, M.B., Center, T.D., 2011. Acquired Natural Enemies of the Weed Biological Control Agent *Oxyops vitiosa* (Colepotera: Curculionidae). Florida Entomologist 94 (1), 1–8. https://doi.org/10.1653/024.094.0101.

Cofrancesco, A.F., 1988. Alligatorweed survey of ten southern states. In: Army, D.o.t., (Ed.). Waterways Experiment Station, Corps of Engineers, Environmental Laboratory, Vicksburg, MS.

Coon, B.R., Harms, N.E., Cuda, J.P., Grodowitz, M.J., 2014. Laboratory biology and field population dynamics of *Trichopria columbiana* (Hymenoptera: Diapriidae), an acquired parasitoid of two hydrilla biological control agents. Biocontrol Sci. Tech. 24 (11), 1243–1264. https://doi.org/10.1080/09583157.2014.933311.

Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. 14 (10), 405–410. https://doi.org/10.1016/S0169-5347(99)01683-3.

Cowie, B.W., Venturi, G., Witkowski, E.T.F., Byrne, M.J., 2016. Does climate constrain the spread of Anthonomus s antacruzi, a biological control agent of Solanum mauritianum, in South Africa? Biol. Control 101, 1–7. https://doi.org/10.1016/j.biocontrol.2016.06.005.

Crawley, M.J., Kornberg, H.L., Lawton, J.H., Usher, M.B., Southwood, S.R., O, R.J., apos, Connor, Gibbs, A., Kornberg, H.L., Williamson, M.H., 1986. The population biology of invaders. Philosophical Trans. Royal Soc. London. B, Biological Sci. 314, 711–731, doi: 10.1098/rstb.1986.0082.

Cronin, James T., Bhattarai, Ganesh P., Allen, Warwick J., Meyerson, Laura A., 2015. Biogeography of a plant invasion: plant–herbivore interactions. Ecology 96 (4), 1115–1127. https://doi.org/10.1890/14-1091.1.

Cronin, James T., Kiviat, Erik, Meyerson, Laura A., Bhattarai, Ganesh P., Allen, Warwick J., 2016. Biological control of invasive *Phragmites australis* will be detrimental to native *P. australis*. Biol Invasions 18 (9), 2749–2752. https://doi.org/10.1007/s10530-016-1138-x.

Cullen, J., 1995. Predicting effectiveness: fact and fantasy. In: Proceedings of the VIII International Symposium on Biological Control of Weeds, pp. 103–109.

Deguines, Nicolas, Brashares, Justin S., Prugh, Laura R., Rodriguez-Cabal, Mariano, 2017. Precipitation alters interactions in a grassland ecological community. J. Anim. Ecol.

86 (2), 262–272. https://doi.org/10.1111/1365-2656.12614.

DeLoach, C.Jack, Lewis, Phil A, Herr, John C, Carruthers, Raymond I, Tracy, James L, Johnson, Joye, 2003. Host specificity of the leaf beetle, *Diorhabda elongata deserticola* (Coleoptera: Chrysomelidae) from Asia, a biological control agent for saltcedars (*Tamarix*: Tamaricaceae) in the Western United States. Biol. Control 27 (2), 117–147. https://doi.org/10.1016/S1049-9644(03)00003-3.

Deonier, D., 1993. A critical taxonomic analysis of the *Hydrellia pakistanae* species group (Diptera: Ephydridae). Insecta Mundi 7, 133–158.

Dhileepan, Kunjithapatham, Callander, Jason, Shi, Boyang, Osunkoya, Olusegun O., 2018. Biological control of parthenium (Parthenium hysterophorus): the Australian experience. Biocontrol. Sci. Tech. 28 (10), 970–988. https://doi.org/10.1080/09583157.2018.1525486.

Dhileepan, K., McFadyen, R.C., 2012. Parthenium hysterophorus L.–parthenium. Biological control of weeds in Australia, 448–462.

Diaz, Rodrigo, Overholt, William A., Samayoa, Ana, Sosa, Freddy, Cordeau, Diane, Medal, Julio, 2008. Temperature-dependent development, cold tolerance, and potential distribution of Gratiana boliviana (Coleoptera: Chrysomelidae), a biological control agent of tropical soda apple, Solanum viarum (Solanaceae). Biocontrol. Sci. Tech. 18 (2), 193–207. https://doi.org/10.1080/09583150701861543.

Dray Jr., F.Allen, Center, Ted D., 1996. Reproduction and Development of the Biocontrol AgentHydrellia pakistanae(Diptera: Ephydridae) on Monoecious Hydrilla. Biol. Control 7 (3), 275–280. https://doi.org/10.1006/bcon.1996.0094.

Dray Jr., F. Allen, Center, Ted D., Wheeler, Greg S., 2001. Lessons from Unsuccessful Attempts to Establish *Spodoptera pectinicornis* (Lepidoptera: Noctuidae), a Biological Control Agent of Waterlettuce. Biocontrol. Sci. Tech. 11 (3), 301–316. https://doi.org/10.1080/09583150120055718.

Dray Jr, F.A., 2003. Ecological genetics of *Melaleuca quinquenervia* (Myrtaceae): Population variation in Florida and its influence on performance of the biological control agent *Oxyops vitiosa* (Coleoptera: Curculionidae). Biology. Florida International University, Miama, Florida, pp. 176.

Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R., Mearns, L.O., 2000. Climate extremes: observations, modeling, and impacts. Science 289, 2068–2074. https://doi.org/10.1126/science.289.5487.2068.

Ehler, L.E., Hall, R.W., 1982. Evidence for competitive exclusion of introduced natural enemies in biological control. Environmental Entomology 11, 1–4, doi: 10.1093/ee/11.1.1.

Ellstrand, N.C., Schierenbeck, K.A., 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proc. National Acad. Sci. 97, 7043–7050, doi: 10.1073/pnas.97.13.7043.

Evans, E.W., Carlile, N.R., Innes, M.B., Pitigala, N., 2013. Warm springs reduce parasitism of the cereal leaf beetle through phenological mismatch. J. Appl. Entomol. 137, 383–391, doi: 10.1111/jen.12028.

Felton, G.W., Korth, K.L., 2000. Trade-offs between pathogen and herbivore resistance. Curr. Opinion Plant Biol. 3, 309–314, doi: 10.1016/S1369-5266(00)00086-8.

Felton, G.W., Summers, C.B., Mueller, A.J., 1994. Oxidative responses in soybean foliage to herbivory by bean leaf beetle and three-cornered alfalfa hopper. J. Chem. Ecol. 20, 639–650, doi: 10.1007/bf02059604.

Ferguson, M., 2018. Impact of roadside maintenance practices on Larinus minutus (Gyllenhal), a biological control agent of spotted knapweed Entomology. University of Arkansas, p. 96.

Forrest, Jessica RK, 2016. Complex responses of insect phenology to climate change. Curr. Opin. Insect Sci. 17, 49–54. https://doi.org/10.1016/j.cois.2016.07.002.

Fowler, S.V., Syrett, P., Hill, R.L., 2000. Success and safety in the biological control of environmental weeds in New Zealand. Austral Ecology 25, 553–562, doi: 10.1046/j.1442-9993.2000.01075.x.

Fréjaville, Thibaut, Vizcaíno-Palomar, Natalia, Fady, Bruno, Kremer, Antoine, Benito Garzón, Marta, 2020. Range margin populations show high climate adaptation lags in European trees. Glob. Change Biol. 26 (2), 484–495. https://doi.org/10.1111/gcb.14881.

Fritz, Robert S., Moulia, Catherine, Newcombe, George, 1999. Resistance of hybrid plants and animals to herbivores, pathogens, and parasites. Annu. Rev. Ecol. Syst. 30 (1), 565–591. https://doi.org/10.1146/annurev.ecolsys.30.1.565.

Gaskin, J.F., Schwarzländer, M., Kinter, C.L., Smith, J.F., Novak, S.J., 2013. Propagule pressure, genetic structure, and geographic origins of Chondrilla juncea (Asteraceae): An apomictic invader on three continents. Am. J. Botany 100, 1871–1882, doi: 10.3732/ajb.1200621.

Gaston, K.J., 2003. The structure and dynamics of geographic ranges. Oxford University Press, New York, USA.

Godsoe, William, Holland, Nathaniel J., Cosner, Chris, Kendall, Bruce E., Brett, Angela, Jankowski, Jill, Holt, Robert D., 2017. Interspecific interactions and range limits: contrasts among interaction types. Theor Ecol 10 (2), 167–179. https://doi.org/10.1007/s12080-016-0319-7.

Goeden, R D, Louda, S M, 1976. Biotic interference with insects imported for weed control. Annu. Rev. Entomol. 21 (1), 325–342. https://doi.org/10.1146/annurev.en.21.010176.001545.

Goolsby, J.A., De Barro, P.J., Makinson, J.R., Pemberton, R.W., Hartley, D.M., Frolich, D. R., 2006a. Matching the origin of an invasive weed for selection of a herbivore haplotype for a biological control programme. Molecular Ecol. 15, 287–297, doi: 10.1111/j.1365-294X.2005.02788.x.

Goolsby, John A., van Klinken, Rieks D., Palmer, William A., 2006b. Maximising the contribution of native-range studies towards the identification and prioritisation of weed biocontrol agents. Aust. J. Entomol. 45 (4), 276–286. https://doi.org/10.1111/j.1440-6055.2006.00551.x.

Gotelli, Nicholas J., Kelley, Walter G., 1993. A general model of metapopulation dynamics. Oikos 68 (1), 36. https://doi.org/10.2307/3545306.

Grevstad, F.S., 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. Biol. Invasions 1, 313–323. https://doi.org/10.1023/a:1010037912369.

Griffith, T.C., Paterson, I.D., Owen, C.A., Coetzee, J.A., 2019. Thermal plasticity and microevolution enhance establishment success and persistence of a water hyacinth biological control agent. Entomol. Exp. Appl. 167, 616–625. https://doi.org/10.1111/eea.12814.

Grodowitz, M., Nachtrieb, J., Harms, N., Freedman, J., 2010. Suitability of using introduced Hydrellia spp. for management of monoecious Hydrilla verticillata (Lf) Royle. U.S. Army Engineer Research and Development Center, Vicksburg, MS, USA, p. 14.

Grodowitz, Michael J., Center, Ted D., Cofrancesco, Alfred F., Freedman, Jan E., 1997. Release and Establishment ofHydrellia balciunasi(Diptera: Ephydridae) for the Biological Control of the Submersed Aquatic PlantHydrilla verticillata (Hydrocharitaceae) in the United States. Biol. Control 9 (1), 15–23. https://doi.org/10.1006/bcon.1997.0513.

Grodowitz, M.J., Smart, M., Doyle, R.D., Owens, C.S., Bare, R., Snell, C., Freedman, J., Jones, H., 2004. Hydrellia pakistanae and H. balciunasi, insect biological control agents of hydrilla: boon or bust? , XI International Symposium on Biological Control of Weeds, p. 529.

Groenteman, R., Kelly, D., Fowler, S.V., Bourdôt, G.W., 2007. Interactions between nodding thistle seed predators. New Zealand Plant Protection 60, 152–157, doi: 10.30843/nzpp.2007.60.4674.

Harms, Nathan E., Cronin, James T., 2019. Variability in weed biological control: effects of foliar nitrogen on larval development and dispersal of the alligatorweed flea beetle, *Agasicles hygrophila*. Biological Control 135, 16–22. https://doi.org/10.1016/j.biocontrol.2019.05.002.

Harms, Nathan, Cronin, James, 2020. Biological control agent attack timing and population variability, but not density, best explain target weed density across an environmental gradient. Sci Rep 10 (1). https://doi.org/10.1038/s41598-020-68108-w.

Harms, N.E., Shearer, J.F., 2017. Early-season dynamics of alligatorweed biological control by *Agasicles hygrophila* in Louisiana and Mississippi. J. Aquatic Plant Manag. 55, 89–95.

Heimpel, George E., Asplen, Mark K., 2011. A 'Goldilocks' hypothesis for dispersal of biological control agents. Biocontrol 56 (4), 441–450. https://doi.org/10.1007/s10526-011-9381-7.

Heimpel, G.E., Cock, M.J.W., 2018. Shifting paradigms in the history of classical biological control. BioControl 63, 27–37, doi: 10.1007/s10526-017-9841-9.

Hill, M., Olckers, T., 2000. Biological control initiatives against water hyacinth in South Africa: constraining factors, success and new courses of action. In: Julien, M.H., Hill, M.P., Center, T.D., Ding, J., (Eds.), ACIAR proceedings 102. ACIAR, pp. 33–38.

Hinz, Hariet L., Winston, Rachel L., Schwarzländer, Mark, 2019. How safe is weed biological control? A global review of direct nontarget attack. Q. Rev. Biol. 94 (1), 1–27. https://doi.org/10.1086/702340.

Hoffmann, J.H., Moran, V.C., 1995. Localized failure of a weed biological control agent attributed to insecticide drift. Agric. Ecosyst. Environ. 52, 197–203. https://doi.org/10.1016/0167-8809(94)00532-J.

Holt, Robert D., Bonsall, Michael B., 2017. Apparent Competition. Annu. Rev. Ecol. Evol. Syst. 48 (1), 447–471. https://doi.org/10.1146/annurev-ecolsys-110316-022628.

Hopper, Keith R., Roush, Richard T., 1993. Mate finding, dispersal, number released, and the success of biological control introductions. Ecol. Entomol. 18 (4), 321–331.

Hrinkevich, K., Lewis, K.J., 2011. Northern range limit mountain pine beetle outbreak dynamics in mixed sub-boreal pine forests of British Columbia. Ecosphere 2, art116, doi: 10.1890/es11-00150.1.

Kawecki, Tadeusz J., 2008. Adaptation to Marginal Habitats. Annu. Rev. Ecol. Evol. Syst. 39 (1), 321–342.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17, 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0.

Knutson, A.E., Campos, M., 2019. Ants as predators of *Diorhabda elongata* (Chrysomelidae), a biological control agent of saltcedar (*Tamarix* spp.), in Texas. Southwestern Entomologist 44, 1–9. https://doi.org/10.3958/059.044.0101.

Kwong, Raelene M., Broadhurst, Linda M., Keener, Brian R., Coetzee, Julie A., Knerr, Nunzio, Martin, Grant D., 2017. Genetic analysis of native and introduced populations of the aquatic weed *Sagittaria platyphylla* – implications for biological control in Australia and South Africa. Biol. Control 112, 10–19.

Lake, Ellen C., Smith, Melissa C., Rayamajhi, Min B., Pratt, Paul D., Dray Jr, F. Allen, 2018. Minimum threshold for establishment and dispersal of *Lilioceris cheni* (Coleoptera: Chrysomelidae): a biological control agent of *Dioscorea bulbifera*. Biocontrol Sci. Tech. 28 (6), 603–613.

Lambertini, C., Mendelssohn, I.A., Gustafsson, M.H., Olesen, B., Tenna, R., Sorrell, B.K., Brix, H., 2012. Tracing the origin of Gulf Coast Phragmites (Poaceae): a story of long-distance dispersal and hybridization. Am. J. Botany 99, 538–551, doi: 10.3732/ajb.1100396.

Lee, Carol Eunmi, 2002. Evolutionary genetics of invasive species. Trends Ecol. Evol. 17 (8), 386–391.

Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts - a global multidimensional synthesis and new research directions. Ecography 38 (1), 15–28.

Lesica, Peter, Allendorf, Fred W., 1995. When are peripheral populations valuable for conservation? Conserv. Biol. 9 (4), 753–760.

Lin, T., Klinkhamer, P.G.L., Pons, T.L., Mulder, P.P.J., Vrieling, K., 2019. Evolution of increased photosynthetic capacity and its underlying traits in invasive Jacobaea vulgaris. Front. Plant Sci. 10, 1–14, doi: 10.3389/fpls.2019.01016.

Liu, Mu, Zhou, Fang, Pan, Xiaoyun, Zhang, Zhijie, Traw, Milton B., Li, Bo, 2018. Specificity of herbivore-induced responses in an invasive species, *Alternanthera philoxeroides* (alligator weed). Ecol. Evol. 8 (1), 59–70.

Lockwood, Julie L., Cassey, Phillip, Blackburn, Tim, 2005. The role of propagule pressure in explaining species invasions. Trends Ecol. Evol. 20 (5), 223–228.

Louda, S.M., Pemberton, R., Johnson, M., Follett, P., 2003. Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annu. Rev. Entomol. 48, 365–396. https://doi.org/10.1146/annurev.ento.48.060402.102800.

Louthan, Allison M., Doak, Daniel F., Angert, Amy L., 2015. Where and when do species interactions set range limits? Trends Ecol. Evol. 30 (12), 780–792.

Lu, Xinmin, He, Minyan, Ding, Jianqing, Siemann, Evan, 2018. Latitudinal variation in soil biota: testing the biotic interaction hypothesis with an invasive plant and a native congener. ISME J. 12 (12), 2811–2822.

Lu, X., He, M., Tang, S., Wu, Y., Shao, X., Wei, H., Siemann, E., Ding, J., 2019. Herbivory may promote a non-native plant invasion at low but not high latitudes. Ann. Botany 124, 819–827, doi: 10.1093/aob/mcz121.

Lu, Xinmin, Siemann, Evan, Shao, Xu, Wei, Hui, Ding, Jianqing, 2013. Climate warming affects biological invasions by shifting interactions of plants and herbivores. Glob. Change Biol. 19 (8), 2339–2347.

Manrique, Veronica, Cuda, J.P., Overholt, W.A., Williams, D.A., Wheeler, G.S., 2008. Effect of host-plant genotypes on the performance of three candidate biological control agents of *Schinus terebinthifolius* in Florida. Biol. Control 47 (2), 167–171.

Marini, Lorenzo, Ayres, Matthew P., Battisti, Andrea, Faccoli, Massimo, 2012. Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Clim. Change 115 (2), 327–341.

Marlin, Danica, Hill, Martin P., Byrne, Marcus J., 2013. Interactions within pairs of biological control agents on water hyacinth, *Eichhornia crassipes*. Biol. Control 67 (3), 483–490.

Maron, John L., Vilà, Montserrat, Arnason, John, 2004. Loss of enemy resistance among introduced populations of St. John's wort (*hypericum perforatum*). Ecology 85 (12), 3243–3253.

May, Bronwen, Coetzee, Julie, 2013. Comparisons of the thermal physiology of water hyacinth biological control agents: predicting establishment and distribution pre- and post-release. Entomol. Exp. Appl. 147 (3), 241–250.

McFadyen, R.C., 2000. Successes in biological control of weeds. In: Proceedings of the X International Symposium on Biological Control of Weeds. Montana State University Bozeman, MT, pp. 3–14.

McFadyen, Rachel E. Cruttwell, 1998. Biological control of weeds. Annu. Rev. Entomol. 43 (1), 369–393.

Milan, J., Harmon, B., Prather, T., Schwarzländer, M., 2006. Winter mortality of Aceria chondrillae, a biological control agent released to control rush skeletonweed (Chondrilla juncea) in the western United States. J. Appl. Entomol. 130, 473–479, doi: 10.1111/j.1439-0418.2006.01090.x.

Minteer, C., Tipping, P.W., Knowles, B.K., Valmonte, R.J., Foley, J.R., Gettys, L., 2016. Utilization of an introduced weed biological control agent, Megamelus scutellaris (Hemiptera: Delphacidae), by a native parasitoid. Florida Entomologist 99, 576–577, doi: 10.1653/024.099.0343.

Moody, Michael L., Palomino, Nayell, Weyl, Philip S.R., Coetzee, Julie A., Newman, Raymond M., Harms, Nathan E., Liu, Xing, Thum, Ryan A., 2016. Unraveling the biogeographic origins of the Eurasian watermilfoil (Myriophyllum spicatum) invasion in North America. Am. J. Bot. 103 (4), 709–718.

Moran, V.C., Hoffmann, J.H., 1987. The effects of simulated and natural rainfall on cochineal insects (Homoptera: Dactylopiidae): colony distribution and survival on cactus cladodes. Ecological Entomol. 12, 61–68, doi: 10.1111/j.1365-2311.1987.tb00985.x.

Mukherjee, A., Diaz, R., Thom, M., Overholt, W.A., Cuda, J.P., 2012. Niche-based prediction of establishment of biocontrol agents: an example with *Gratiana boliviana* and tropical soda apple. Biocontrol. Sci. Tech. 22 (4), 447–461.

Newman, R., Thompson, D., Richman, D., 1998. Conservation strategies for the biological control of weeds. In: Barbosa, P., (Ed.), Conservation Biological Control. Academic Press, New York, pp. 371–396.

Norris, R.J., Memmott, J., Lovell, D.J., 2002. The effect of rainfall on the survivorship and establishment of a biocontrol agent. J. Appl. Ecol. 39, 226–234, doi: 10.1046/j.1365-2664.2002.00712.x.

Nybakken, L., Lie, M.H., Julkunen-Tiitto, R., Asplund, J., Ohlson, M., 2018. Fertilization changes chemical defense in needles of mature Norway spruce (Picea abies). Front. Plant Sci. 9, doi: 10.3389/fpls.2018.00770.

Öckinger, Erik, 2006. Possible metapopulation structure of the threatened ButterflyPyrgus armoricanus in Sweden. J Insect Conserv 10 (1), 43–51.

Ordonez, Alejandro, Olff, Han, 2013. Do alien plant species profit more from high resource supply than natives? A trait-based analysis: Alien-native leaf trait differences. Glob. Ecol. Biogeogr. 22 (6), 648–658.

Parmesan, Camille, 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37 (1), 637–669.

Parmesan, Camille, Yohe, Gary, 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421 (6918), 37–42.

Parys, Katherine A., Johnson, Seth J., 2012. Impact of the Red Imported Fire Ant, *Solenopsis invicta* (Hymenoptera: Formicidae), on Biological Control of *Salvinia minima* (Hydropteridales: Salviniaceae) by *Cyrtobagous salviniae* (Coleoptera: Curculionidae). Florida Entomologist 95 (1), 136–142.

Paterson, I.D., Hoffmann, J.H., Klein, H., Mathenge, C.W., Neser, S., Zimmermann, H.G., 2011. Biological Control of Cactaceae in South Africa. African Entomology 19 (2), 230–246.

Pearson, Dean E., Callaway, Ragan M., 2003. Indirect effects of host-specific biological control agents. Trends Ecol. Evol. 18 (9), 456–461.

Pearson, D.E., McKelvey, K.S., Ruggiero, L.F., 2000. Non-target effects of an introduced biological control agent on deer mouse ecology. Oecologia 122, 121–128, doi: 10.1007/PL00008828.

Pironon, Samuel, Papuga, Guillaume, Villellas, Jesús, Angert, Amy L., García, María B., Thompson, John D., 2017. Geographic variation in genetic and demographic performance: new insights from an old biogeographical paradigm: the centre-periphery hypothesis. Biol. Rev. 92 (4), 1877–1909.

Potter, K.J.B., Ireson, J.E., Allen, G.R., 2007. Survival of larvae of the ragwort flea beetle, Longitarsus flavicornis (Coleoptera: Chrysomelidae), in water-logged soil. Biocontrol Sci. Tech. 17, 765–770, doi: 10.1080/09583150701409020.

Pyšek, Petr, Richardson, David M., 2006. The biogeography of naturalization in alien plants. J. Biogeography 33 (12), 2040–2050.

Ray, Puja, Hill, Martin P., 2016. More is not necessarily better: the interaction between insect population density and culture age of fungus on the control of invasive weed water hyacinth. Hydrobiologia 766 (1), 189–200.

Rayamajhi, M.B., Van, T.K., Pratt, P.D., Center, T.D., 2006. Interactive association between *Puccinia psidii* and *Oxyops vitiosa*, two introduced natural enemies of *Melaleuca quinquenervia* in Florida. Biol. Control 37 (1), 56–67.

Reddy, Angelica M., Pratt, Paul D., Hopper, Julie V., Cibils-Stewart, Ximena, Walsh, Guillermo Cabrera, Mc Kay, Fernando, 2019. Variation in cool temperature performance between populations of *Neochetina eichhorniae* (Coleoptera: Curculionidae) and implications for the biological control of water hyacinth, *Eichhornia crassipes*, in a temperate climate. Biol. Control 128, 85–93.

Reeves, Justin L., Blumenthal, Dana M., Kray, Julie A., Derner, Justin D., 2015. Increased seed consumption by biological control weevil tempers positive CO2 effect on invasive plant (*Centaurea diffusa*) fitness. Biol. Control 84, 36–43.

Renner, Susanne S., Zohner, Constantin M., 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu. Rev. Ecol. Evol. Syst. 49 (1), 165–182.

Robertson, Mark P., Kriticos, Darren J., Zachariades, Costas, 2008. Climate matching techniques to narrow the search for biological control agents. Biol. Control 46 (3), 442–452.

Roley, Sarah S., Newman, Raymond M., 2006. Developmental Performance of the Milfoil Weevil, *Euhrychiopsis lecontei* (Coleoptera: Curculionidae), on Northern Watermilfoil, Eurasian Watermilfoil, and Hybrid (Northern × Eurasian) Watermilfoil. Environ Entomol 35 (1), 121–126.

Room, P., Julien, M., Forno, I., 1989. Vigorous plants suffer most from herbivores: latitude, nitrogen and biological control of the weed Salvinia molesta. Oikos, 92–100, doi: 10.2307/3565901.

Room, P.M., Harley, K.L.S., Forno, I.W., Sands, D.P.A., 1981. Successful biological control of the floating weed salvinia. Nature 294, 78–80, doi: 10.1038/294078a0.

Sagarin, Raphael D., Gaines, Steven D., 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? Ecol. Lett. 5 (1), 137–147.

Schwarzländer, M., Hinz, H.L., Winston, R.L., Day, M.D., 2018. Biological control of weeds: an analysis of introductions, rates of establishment and estimates of success, worldwide. BioControl 63, 319–331, doi: 10.1007/s10526-018-9890-8.

Scranton, Katherine, Amarasekare, Priyanga, 2017. Predicting phenological shifts in a changing climate. Proc. Natl. Acad. Sci. USA 114 (50), 13212–13217.

Seastedt, Timothy R., 2015. Biological control of invasive plant species: a reassessment for the Anthropocene. New Phytol. 205 (2), 490–502.

Sexton, J.P., Strauss, S.Y., Rice, K.J., 2011. Gene flow increases fitness at the warm edge of a species' range. Proc. National Acad. Sci. 108, 11704–11709, doi: 10.1073/pnas.1100404108.

Shea, K., Possingham, H.P., 2000. Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. J. Appl. Ecol. 37, 77–86.

Stastny, M., Sargent, R.D., 2017. Evidence for rapid evolutionary change in an invasive plant in response to biological control. J. Evolutionary Biol. 30, 1042–1052, doi: 10.1111/jeb.13078.

Story, J.M., Nowierski, R.M., 1984. Increase and dispersal of Urophora affinis (Diptera: Tephritidae) on spotted knapweed in western Montana. Environmental Entomology 13, 1151–1156, doi: 10.1093/ee/13.4.1151.

Sun, Y., Brönnimann, O., Roderick, G.K., Poltavsky, A., Lommen, S.T.E., Müller-Schärer, H., 2017. Climatic suitability ranking of biological control candidates: a biogeographic approach for ragweed management in Europe. Ecosphere 8, e01731, doi: 10.1002/ecs2.1731.

Tipping, Philip W., Gettys, Lyn A., Minteer, Carey R., Foley, Jeremiah R., Sardes, Samantha N., 2017. Herbivory by biological control agents improves herbicidal control of waterhyacinth (Eichhornia crassipes). Invasive Plant Sci. Manag. 10 (3), 271–276.

Tomley, A., 1990. Megacyllene mellyi-a biological control agent for groundsel bush, Baccharis halimifolia, in Queensland. In: Proceedings of the 9th Australian Weeds Conference, pp. 513–515.

Torchin, M.E., Mitchell, C.E., 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2, 183–190. https://doi.org/10.1890/1540-9295(2004)002[0183:PPAIBP]2.0.CO;2.

True-Meadows, S., Haug, E.J., Richardson, R.J., 2016. Monoecious hydrilla—a review of the literature. J. Aquatic Plant Manag. 54, 1–11.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363, doi: 10.1111/j.1461-0248.2008.01250.x.

Uyi, Osariyekemwen O., Zachariades, Costas, Hill, Martin P., 2016. Nitrogen fertilisation improves growth of *Chromolaena odorata* (Asteraceae) and the performance of the biological control agent, *Pareuchaetes insulata* (Erebidae). Biocontrol Sci. Tech. 26 (3), 373–385.

Van Driesche, R., Hoddle, M., Center, T., 2009. Control of pests and weeds by natural enemies: an introduction to biological control. John Wiley & Sons.

Van Hezewijk, Brian H., De Clerck-Floate, Rosemarie A., Moyer, James R., 2008. Effect of nitrogen on the preference and performance of a biological control agent for an invasive plant. Biol. Control 46 (3), 332–340.

van Klinken, Rieks D, Fichera, Gio, Cordo, Hugo, 2003. Targeting biological control across diverse landscapes: the release, establishment, and early success of two insects on mesquite (*Prosopis* spp.) insects in Australian rangelands. Biol. Control 26 (1), 8–20.

Vogt, G.B., Quimby, P.C., Kay, S., 1992. Effects of weather on the biological control of alligatorweed in the lower Mississippi Valley region, 1973–83. United States Department of Agriculture, Agricultural Research Service, pp. 143.

Weed, Aaron S., Schwarzländer, Mark, Paynter, Quentin, 2014. Density dependence, precipitation and biological control agent herbivory influence landscape-scale dynamics of the invasive Eurasian plant *Linaria dalmatica*. J. Appl. Ecol. 51 (3), 825–834.

Wheeler, G.S., Center, T.D., 1997. Growth and development of the biological control agentbagous hydrillaeas influenced by hydrilla (Hydrilla verticillata) stem quality. Biol. Control 8 (1), 52–57.

Wheeler, Gregory S., Lake, Ellen C., Rayamajhi, Min B., Smith, Melissa C., 2020. Acute toxicity of mosquito pesticides on weed biological control agents in south Florida, USA. Biocontrol Sci. Tech. 30 (8), 855–861.

Williams, D.A., Overholt, W.A., Cuda, J.P., Hughes, C.R., 2005. Chloroplast and microsatellite DNA diversities reveal the introduction history of Brazilian peppertree (Schinus terebinthifolius) in Florida. Molecular Ecol. 14, 3643–3656, doi: 10.1111/j.1365-294X.2005.02666.x.

Wilson, J.R.U., Dormontt, E.E., Prentis, P.J., Lowe, A.J., Richardson, D.M., 2009. Biogeographic concepts define invasion biology. Trends Ecol. Evolution 24, 586, doi: 10.1016/j.tree.2009.07.004.

Wilson, R.J., Ellis, S., Baker, J.S., Lineham, M.E., Whitehead, R.W., Thomas, C.D., 2002. Large-scale patterns of distribution and persistence at the range margins of a butterfly. Ecology 83, 3357–3368, doi: 10.2307/3072085.

Winston, R., Schwarzlander, M., Hinz, H., Day, M., Cock, M.J., Julien, M., 2014. Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds. Forest Health Technology Enterprise Team, USDA Forest Service, Morgantown (West Virginia).

Yeates, Alice G., Schooler, Shon S., Garono, Ralph J., Buckley, Yvonne M., 2012. Biological control as an invasion process: disturbance and propagule pressure affect the invasion success of *Lythrum salicaria* biological control agents. Biol. Invasions. 14 (2), 255–271.

Zalucki, Myron P, van Klinken, Rieks D, 2006. Predicting population dynamics of weed biological control agents: science or gazing into crystal balls? Aust. J. Entomol. 45 (4), 331.

Zou, Jianwen, Rogers, William E., Siemann, Evan, 2008. Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum*. Biol. Invasions. 10 (3), 291–302.