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# How to better predict long-term benefits and risks in weed biocontrol: an evolutionary perspective

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Classical biological control (also called importation biological control) of weeds has a remarkable track record for efficiency and safety, but further improvement is still needed, particularly to account for potential evolutionary changes after release. Here, we discuss the increasing yet limited evidence of post-introduction evolution and describe approaches to predict evolutionary change. Recent advances include using experimental evolution studies over several generations that combine -*omics* tools with behavioral bioassays. This novel approach in weed biocontrol is well suited to explore the potential for rapid evolutionary change in real-time and thus can be used to estimate more accurately potential benefits and risks of agents before their importation. We outline this approach with a chrysomelid beetle used to control invasive common ragweed.

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## Introduction

Effectiveness (impact) and safety (host-specificity) are both crucial aspects in developing a successful weed biocontrol program [1] (glossary). When applying the classical management, rigorous studies are required both before and after release of the biological control agent. Pre-release studies are needed to predict and prevent undesirable outcomes, while post-release studies are needed to confirm and mitigate such outcomes. Schwarzländer *et al.* [2] found that almost a quarter of all releases caused heavy impact and that across countries/regions nearly two-thirds of targeted weeds experienced some level of control. Concerning risks, Hinz *et al.* [3•] reported that in recent decades, less than 1% of releases (only two agents released during 1991–2008) caused sustained non-target attack, that is, persistent populations on non-target species regardless of the presence of target weed. Although this is a remarkable track record for efficiency and safety, potential evolutionary changes post-release remain a fundamental area of uncertainty associated with introductions of organisms into new habitats [4].

Scaling up from species interactions at the individual and population level to forecasting species distributions and impact is an especially challenging task, as abiotic tolerances, dispersal rates, and biotic interactions, vary in time and space. While understanding the outcomes of species interactions from an ecological viewpoint is highly relevant for practicing biocontrol, potential evolutionary changes are largely believed to be not assessable pre-release [5]. Here, we explore how to increase the predictive power of effectiveness and host-specificity in weed biocontrol after release by assessing the evolutionary potential pre-release.

## Evolutionary changes in weed biocontrol programs

### The plant invader

Swift and dramatic evolutionary changes in invasive alien plants post-introduction are well documented. The rapid spread of plant invaders has been associated with a multitude of factors, including adaptation to climate and escape from biotic constraints, such as from natural enemies [6–8]. However, in spite of the 1555 intentional releases of 468 biocontrol agents (BCAs) species against 175 target weed species as of 2012 [9], there are yet few experimental studies of evolutionary responses in biocontrol systems where an invasive species becomes re-associated with its key natural enemies now used as a BCA in the new range. Stastny and Sargent [10•] reported that the chrysomelid beetle *Neogalerucella calmariensis* L., introduced into Canada for control of invasive *Lythrum salicaria* L. can rapidly select for increased resistance (increased antiherbivore defenses) and tolerance (faster regrowth). Fukano and Yahara [11] studied introduced common ragweed, *Ambrosia artemisiifolia* L., populations in Japan and found that populations where the exotic chrysomelid beetle *Ophraella communa* LeSage appeared during the past decade presented stronger defensive capabilities (on

**Glossary**

**Artificial selection:** a process in the breeding of animals and in the cultivation of plants by which the breeder chooses to perpetuate only those forms having certain desirable inheritable characteristics

**Biological control of weeds and invasive plants:** the use of an antagonist (mainly arthropods (insects and mites) and plant pathogens (fungi, bacteria, viruses, and nematodes) to bring about suppression of noxious plants, such as agricultural weeds or plant invaders. Three principal methods can be distinguished based on target habitat, origin of the control agent, and the amount of initial inoculum used: (i) The inoculative or classical approach, also called importation biological control, aims to control naturalized weeds by the introduction of exotic control organisms from the weed's native range; (ii) The inundative or bioherbicide method uses periodic releases of an abundant supply of a native or exotic control agent over the entire weed population to be controlled; (iii) the system management or conservation/augmentative approach aims to stimulating the build-up of a disease epidemic or insect outbreak of a native agent on the target weed population [1]

**BACIP (Before–After Control-impact) design:** an experimental design used to assess an environmental impact using observations before and after the environmental perturbation, specifically with paired plots one with the impact and the other as a non-impacted control [42]

**Common garden experiment:** A method for inferring genetic differences among groups: If individuals from different groups (e.g. populations) are brought together and reared in a common environment, then phenotypic differences among them are assumed to reflect differences in genotype not environment, provided steps are taken to eliminate effects of the parental environment that carry over to offspring [43]

**'Evolve and Resequence'(E&R) studies:** an approach to assess how populations evolve within one or more controlled environments and are then surveyed with genomic sequencing [44,45]; becoming a popular approach to study the genetic basis of adaptation. The basic principle is the identification of the target of selection in evolving populations by genome-wide sequencing of pools of individuals ( pool-seq, cf. below)

**Experimental evolution:** an "experimental approach in which the phenotypic and/or genomic change is monitored over multiple generations during which experimenters apply a predetermined selective pressure under controlled demographic conditions" [28•].

**Genotype by environment interaction:** differing responses of two or more genotypes to environmental variation. Often measured as a norm of reaction [4]

**Natural experiment:** a method of hypothesis testing in ecological studies that takes advantage of an environmental effect that impacts one area but not another [46]

**Whole-genome sequencing of pools of individuals (pool-seq):** a protocol used for population genomic studies consisting of sequencing libraries of pooled DNA samples that do not require individual tagging of sequences. Pool-seq provides genome-wide polymorphism data at considerably lower costs than sequencing of individuals [28•]

a similar level to native range populations) compared to populations from enemy-free areas in Japan. More recently, Sun and Roderick [12•] using the same system observed reduced competitive ability in introduced Chinese *A. artemisiifolia* populations with — as compared to without — a history of biocontrol by *O. communa*, suggesting a trade-off between competitive ability and herbivore resistance in invasive populations. Together, these findings underpin results from previous studies that defenses of alien populations can be regained rapidly once the native specialist also arrives in the introduced range, which may reduce the long-term efficacy of the BCA.

## The insect biocontrol agent (BCA)

Although numerous studies report changes in the genetic variation and structure of introduced versus native populations of BCAs, the importance of post-release adaptation in the BCA is poorly understood [13•]. However, a review of experiments and theory by Szücs *et al.* [14••] suggests that the changes in a BCA following its introduction are larger than previously considered. Griffith *et al.* [15] demonstrated that the weed BCA, *Eccritotarsus catarinensis* (Carvalho) (Hemiptera: Miridae), underwent post-release adaptation to environments with temperatures beyond those in its native range. Bean *et al.* [16] showed evolution of the seasonal timing of diapause induction in the leaf beetle BCA, *Diorhabda carinulata* (Desbrochers), introduced into North America from China to control exotic *Tamarix* spp. Adaptation over seven years after its introduction allowed it to establish well beyond the geographic limits of the originally introduced genotype resulting in a closer match between the beetle life history and host phenology, and thus to enhance efficacy and widen its ecoclimatic range.

There are only a few reported extensions of host plant use in BCAs, and all such hosts are found within the fundamental host range [3•,13•]. For instance, Fukano *et al.* [17] reported that *Ambrosia trifida* L. is not utilized by the oligophagous *O. communa* in its native North American range, but is extensively utilized in the beetle's introduced range in Japan. Furthermore, introduced *O. communa* beetles showed significantly higher performance on, and preference for, both introduced and native *A. trifida* plants, when compared with native *O. communa*, suggesting an evolutionary change in the beetle leading to this expansion of host use.

Taken together, there is evidence of adaptation through post-introduction evolution in new ranges that could both increase (e.g., by changes in the critical day length for diapause induction and phenology in the insect [16,18]; or in juvenile developmental time [4]) or decrease (e.g., by increased plant defense when exposed to the BCA [10•,11,12•]); the initial efficacy of weed BCAs. However, there is to date sparse evidence of contemporary adaptive evolution in response to hosts [19], and all restricted to the limits of the fundamental host range, with no reported (evolutionary) shifts in host use patterns (sensu Schaffner [20]; cf. review by Hinz *et al.* [3•]).

## Assessing evolutionary potential pre-release: targeted selection experiments

There is a general appreciation of the importance of both pre-release and post-release studies of efficacy and safety in biocontrol [14••,20,21], but little recognition, anticipation, or demonstration in pre-release studies of how biocontrol candidates might evolve upon release in a new environment [22••]. Pre-release studies are necessary to provide key insights into evolutionary processes that

**Table 1**

**Approaches to test evolutionary hypotheses in classical biological control (adapted in part from Hoffmann and Sgrò [47]) (BCA: biological control agent)**

| Approach | Outcome | Limitations | Examples |
|---|---|---|---|
| Pre-release | | | |
| Estimates of standing quantitative genetic variation through full- or half-sib studies of BCAs and also potentially target and/or non-target plants. Genotype x genotype or genotype x environment interactions can be studied at the level of genotypes between the invader plant and the BCA, or at the level of populations, indicating which insect family, strain, or population is most effective against which plant family, strain or population. | Provides estimates of evolutionary potential and genetic parameters | Available for systems where controlled studies are possible | [4] |
| Manipulations of genetic variation through selection of BCA or target or non-target plants | Allows assessment of genetic constraints, genetic variability, and/or importance of hybrid populations; can be used to examine importance of candidate genes | Requires multiple generations; artificial selection in laboratory environment may not reflect processes in the field. | [37,48,49], studies currently underway (see below) |
| Common garden experiments in which individuals from the same populations or sources are reared across different environmental settings. An extension is reciprocal transplants, in which individuals from two or more environments are introduced into each of the other environments. | Allows assessment of adaptation to varying environmental conditions | May not reflect other environmental differences that exist between the types of habitats in nature | [12•,23,38,40,41,50,51] |
| Evolution in simulated environments, such as novel climatic conditions | Allows assessment of adaptation to novel environments, which may be otherwise difficult to assess in natural populations | Conditions may not reflect future conditions in nature | Studies currently underway (see below) |
| Post-release | | | |
| Comparisons between introduced populations and those from presumed origins | Assess actual evolutionary change post-release | Origins are inferred from historical records; source populations may also have evolved since release | [52] |
| BACIP design (glossary), involving Before/After and Control/Impact paired comparisons | Direct evaluation of impact when manipulations are not possible | Does not control genetic origins or relatedness of BCA or plant targets | [53] |
| Natural experiments (glossary) that compare habitats/locations with and without impact | Flexible design to measure impact | Many factors are not controlled including genetic relatedness and multiple environmental characteristics | [12•,54] |

post-release studies cannot address, as well as to make predictions that are critical for efficacy and safety (Table 1). Furthermore, it is possible and profitable to manipulate population characteristics experimentally in the field as part of a release program, such as how released population size influences the likelihood of establishment and subsequent population growth [23]. By contrast, post-release studies allow measurements of actual responses in the field by both BCA and targets, though they suffer in the ability to manipulate individual factors. In addition, emerging molecular genetic approaches offer new possibilities for direct control of pests, though not without environmental and ethical concerns [24], and are considered elsewhere in this volume.

## Experimental evolution

In contrast to studies of adaptive processes in natural populations, controlled selection experiments provide the opportunity to quantify evolutionary changes in real-time over multiple generations. In these studies, genetically diverse experimental populations are subjected to pre-determined selection imposed by the experimenter (experimental evolution *sensu stricto*, Kawecki *et al.* [25]; Lirakis and Magalhaes [22••], glossary).

Furthermore, this approach allows investigators to include thousands of BCA individuals, while studies assessing standing genetic variance in performance or preference traits are usually conducted with much fewer genotypes. Such long-term experimental approaches have attracted recent attention due to the emergence of *-omics* tools that can reveal underlying mechanisms, such as high-throughput sequencing followed by genome scan analyses to detect candidate genes involved in adaptive evolutionary processes (i.e., 'Evolve and Resequence' (E&R) strategies, [26,27,28•]; glossary). For instance, studies using experimental evolution followed by behavioral bioassays (e.g., host acceptance, Messina *et al.* [29]) and performance tests (e.g., population growth rate, offspring viability, Price *et al.* [30]) showed a rapid evolution of the cowpea seed beetle *Callosobruchus maculatus* (F.) to novel host species. Additional E&R studies [31] highlight that host adaptation can occur through a strong selection on multiple loci from standing genetic variation, from which some alleles are even selected against during reversion to the ancestral host [32]. These advances offer much promise for weed biocontrol programs to assess the evolutionary potential benefits and risks of agents before their importation and release.

## Objectives of experimental evolution studies in weed biocontrol using insects

Controlled selection experiments can address the potential of (i) BCAs to select for resistant/tolerant plant genotypes, or (ii) host shifts, defined here as genetically based changes in preference or performance, by exposing plant species that are closely related to the target, ranging from congeneric species already present in the introduced range to crops and native endangered species (cf. Figure 1, Studies 1 and 2). Further, they can help (iii) evaluate the potential for evolutionary adaptations to novel ecoclimatic conditions arising due to a changing climate or range expansion into less suitable habitats and regions in the introduced range that are highly invaded by the target species (cf. Figure 1, Study 3). Significant among-population differences in biocontrol agents in the native range have been well documented, especially for ecological traits linked to climate and host plant use [17,19,33]. In the past, this variation was used to increase genetic diversity by collecting BCAs from distinct populations and subsequently combining to promote adaptation post-release to increase establishment and control [19,34]. Because of the increased risk of non-target effects, modern guidelines for biological weed control no longer allow this practice and further insist that single populations are separately assessed for potential efficacy and safety before their introduction, with a reference collection made of individuals from the population released [35,36]. However, targeted selection on artificial populations resulting from outcrossing among genetically distinct populations from the native range could be used for the above mentioned experiments to assess the potential for the decrease of the biocontrol efficiency over time, as well as to inform about potential risks (or benefits in the case of congeneric plant invaders) of the BCA before the introduction, and to increase the spatial overlap of the suitable habitats for BCA and target weed.

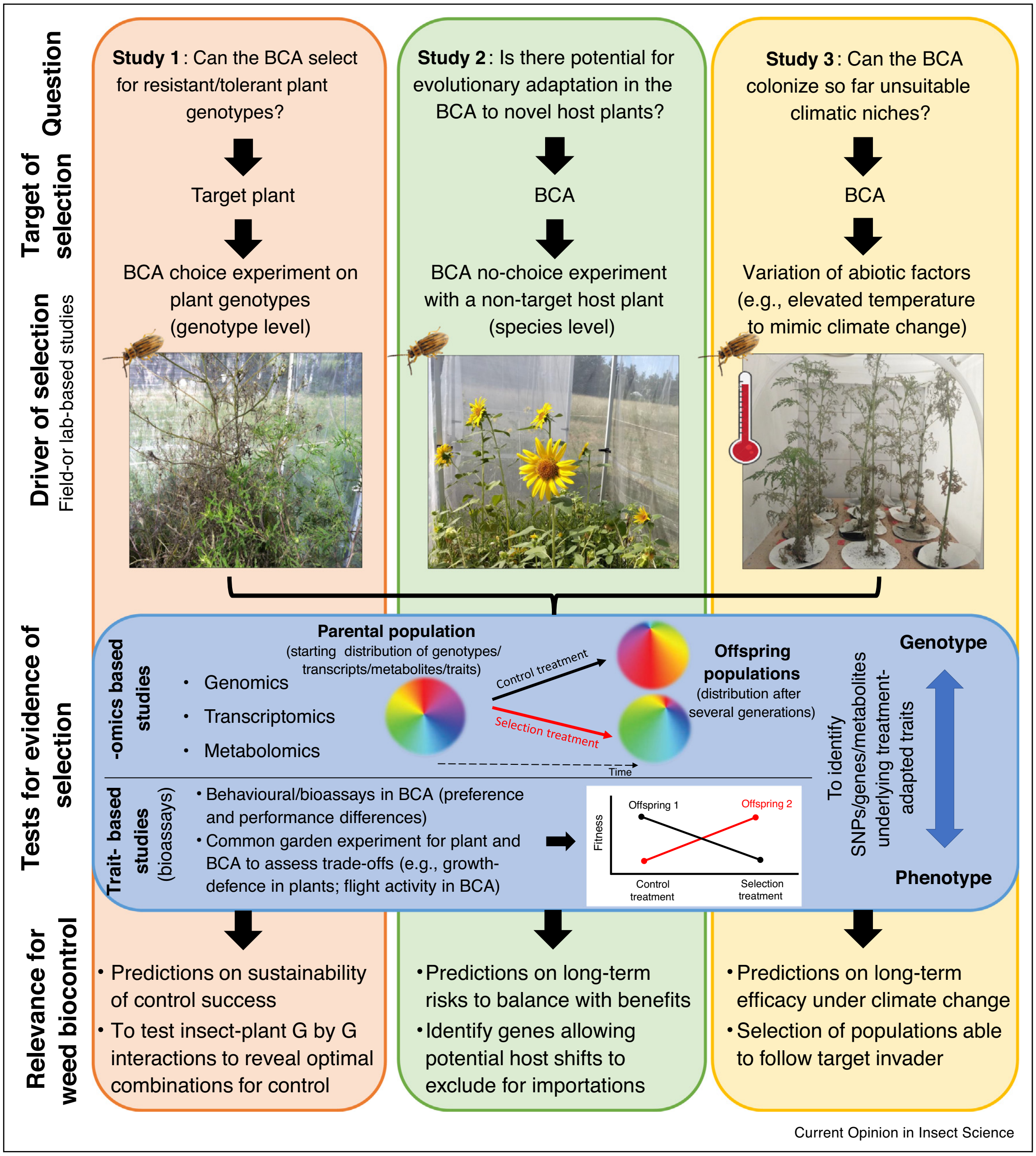
## Ongoing studies as examples

As an example of how studies in experimental evolution could be designed and integrated in pre-release studies of biocontrol projects, we briefly describe a coordinated European research program on the 'Sustainable management of *Ambrosia artemisiifolia* in Europe' (COST-SMARTER, Müller-Schärer *et al.* [37]). The North American oligophagous chrysomelid beetle *O. communa*, already successfully used as a BCA in Asia [38], was first recorded in Europe in 2013 [37]. This created an urgent need for national authorities to decide whether the accidental establishment of *O. communa* in Europe should be considered as a fortunate coincidence in the campaign against the highly invasive *A. artemisiifolia* or whether it should be considered as a threat to closely related wild or crop species [39]. A series of ecological studies evaluating the effectiveness and safety of this beetle were initiated along with experimental evolution experiments to assess the beetle's potential to select for resistant/tolerant *A. artemisiifolia* populations, as well as for evolutionary adaptation of *O. communa* to closely related sunflower (cf. Figure 1, Studies 1 and 2, respectively).

Two field studies were initiated in Northern Italy in 2016: (1) Large caged plots were established with genetically similar *A. artemisiifolia* plants from a wide range of European populations and *O. communa* was released in half of them (beetle as the driver of selection). (2) Replicated experimental cages containing either sunflower, *Helianthus annuus* L. (a closely related crop and potential alternative host species) or *A. artemisiifolia* were installed and *O. communa* that had been widely collected across the present distribution in Italy was released in all cages (host plants as drivers of selection). Population genomic and phenotyping analyses are presently ongoing for both studies. Sequential next-generation sequencing (pool-seq, glossary) and genome scan analyses were applied to detect selected alleles/genomic regions over time in both *A. artemisiifolia* (first study) and *O. communa* (second study). Furthermore, traits were measured and a common garden approach was used to test for trade-offs between growth and defense in the plants exposed or not to the beetles (Figure 1, Study 1). These were complemented by behavioral bioassays to evaluate potential population differentiation in host choice and larval performance over time of the beetles from the *A. artemisiifolia* versus sunflower cages (Figure 1, Study 2).

To our knowledge, this is the first attempt to assess rigorously and simultaneously the evolvability of a

**Figure 1**



Three key examples of the proposed framework to assess the evolutionary potential of a biological control agent (BCA) and its targeted plant invader pre-release using an experimental evolution approach.

BCA and its target weed. Many additional experimental evolution studies could be envisaged, such as selection of the various *A. artemisiifolia* genotypes and assemblages on *O. communa*, and interactions of the above described selection treatments with different environmental conditions (climate change or adaptions to colder areas presently heavily invaded by *A. artemisiifolia*, but not predicted as suitable habitats for the beetle, cf. Figure 1, Study 3). Another goal might be to examine phenotype by environment and genotype by environment interactions (glossary) by using different origins of *O. communa*. From such studies, data on evolutionary changes in the plant invader, in the BCA, and of their interaction could then be included in models of geographic distribution, population dynamics, and rate of expansion, to improve biocontrol efficiency and safety.

## Predicting outcomes of species interactions in novel environments: the way forward in weed biocontrol

As environmental impacts caused by climate change, pollution, and habitat destruction are predicted to increase in the near future, understanding, and predicting eco-evolutionary outcomes of species interactions under novel environmental conditions, such as encountered in the case of weed biocontrol programs, becomes more challenging, but also more pressing. Presently, field evaluations of such eco-evolutionary outcomes are nearly non-existent and approaches to assess the potential for rapid evolution pre-release are not yet part of weed biocontrol programs.

Biocontrol introductions offer an exciting opportunity to understand more general eco-evolutionary dynamics of species interactions in novel environments, given the ample knowledge increasingly available on source populations and their genetic make-up, and the number and size of introductions. Furthermore, intentional releases allow specific manipulations for introductions and redistributions and thus for testing-specific hypotheses for improving biocontrol efficacy and potential changes of host range. Knowledge gained from such post-release studies will help to design more targeted pre-release studies, such as described above.

We specifically advocate studies of experimental evolution be conducted pre-release to advance biocontrol towards a more predictive, efficient, and sustainable management strategy under changing climatic conditions. Genomic tools, such as those described above, are steadily being improved both technically/analytically and in terms of cost-effectiveness. Applying genetic and genomic knowledge to improve biocontrol agents has recently been referred to as 'next generation biocontrol' [21]. We acknowledge that experimental evolution studies remain labor and cost-intensive and may delay biocontrol programs. Hence, studies, as outlined above, should for now be primarily applied in BCA-test plant systems that are suitable for experimental evolution experiments (e.g., multivoltine BCAs, simple rearing protocols for BCA and test plants).

Considering the possibility of rapid evolution of control organisms upon release into a new environment can lead to new ways of thinking. For example, the longstanding ecological question of using single versus multiple enemy species can be reformulated as an evolutionary question: Should one release a single, best performing, genotype in each local environment or should one introduce a collection of genotypes from a single population with a large standing genetic variation and let natural selection sort out which genotype or combination of genotypes works best? This assumes, with some grounding from the examples above that suitable heritable traits influencing abundance, distribution, and impact can be identified before release.

In addition, such pre-release evolutionary experiments may ultimately shed light on the yet unanswered, enigmatic question of why despite the often large genetic variation available in both the plant invader (e.g., in defense mechanisms) and the BCA (e.g., in host preference and performance), resistance/tolerance against the BCA or host shifts by the BCA are rarely observed [40,41].

## Conflict of interest

None.

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This is the most recent and complete review of all known cases (as of 2008) of direct nontarget attack (NTA) by intentionally released weed BCAs. The majority of NTA was spillover and the proportion of agents causing sustained NTA declined over time to less than 1% of releases (i.e., two agents released from 1991–2008). This trend is likely to continue with scientific advancements. The authors strongly advocate for systematic post release monitoring to assess the value of pre-release host range testing.

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Populations of purple loosestrife, *Lythrum salicaria*, with a history of biocontrol evolved both higher resistance and greater tolerance to a BCA compared to unexposed populations. The study illustrates that an invasive species can evolve in response to a BCA rapidly, a phenomenon that has been largely overlooked. Studies that monitor the co-evolutionary dynamics between the plant invader and its BCAs are virtually nonexistent but highly recommended to improve long-term biocontrol efficiency and safety.

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Populations of ragweed from native (USA) and introduced (China) together with herbivores introduced for biological control were compared under controlled conditions using neutral microsatellite genetic loci ($F_{ST}$) as well as quantitative traits ($Q_{ST}$). Performance traits were significantly greater in invasive compared to native populations and differed from expectations through genetic drift alone, demonstrating evolutionary adaptive response of an invasive plant to novel environments. Furthermore, invasive populations with a history of biological control showed reduced competitive ability, an observation that suggests a trade-off between competitive ability and herbivore resistance.

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