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Biocontrol of invasive weeds under climate change: progress, challenges and management implications

Yan Sun[1], Jianqing Ding[2], Evan Siemann[3] and Stephen R Keller[4]

Climate change is predicted to increase the frequency and impact of plant invasions, creating a need for new control strategies as part of mitigation planning. The complex interactions between invasive plants and biocontrol agents have created distinct policy and management challenges, including the effectiveness and risk assessment of biocontrol under different climate change scenarios. In this brief review, we synthesize recent studies describing the potential ecological and evolutionary outcomes for biocontrol agents/candidates for plant invaders under climate change. We also discuss potential methodologies that can be used as a framework for predicting ecological and evolutionary responses of plant-natural enemy interactions under climate change, and for refining our understanding of the efficacy and risk of using biocontrol on invasive plants.

Addresses
[1] Department of Biology/Ecology & Evolution, University of Fribourg, 1700 Fribourg, Switzerland

[2] School of Life Sciences, Henan University, Kaifeng, Henan 475004, China
[3] Biosciences Department, Rice University, Houston, TX USA
[4] Department of Plant Biology, University of Vermont, USA

Corresponding author: Sun, Yan (yan.sun@unifr.ch)

Introduction

Climate change and plant invasions significantly impact biodiversity, human welfare, and the economy, making it critical to predict the interactive effects of climate change on invasive plants and their management. Anthropogenic climate changes driven by greenhouse gas emissions include alterations in temperature, precipitation, CO_2, insolation and the frequency of extreme climatic events (i.e., flood, fires, intense storms, heat waves). These changes can influence multiple stages of the plant invasion process, from initial introduction through establishment, spread and impact [1,2]; consequently, interactions between climate change and plant invasion may have a profound influence on species interactions, ecosystem services and people's livelihoods [3].

Classical biocontrol ('biocontrol' hereafter) has proven to be an effective and cost-efficient approach to mitigating plant invasions [4], but consideration of how climate change may alter the dynamics between plant hosts and biocontrol agents is relatively unexplored. Biocontrol involves the deliberate release of specialist natural enemies from the plant invader's native range to reduce its abundance in the introduced range below an ecological or economic threshold [4]. The complexity of interactions involving invasive plants and the biotic and abiotic components of the invaded habitats under different climatic scenarios has created distinct policy and management challenges including the effectiveness of biocontrol. Climate change is expected to impact invasive weeds and biocontrol agents (e.g., through effects on metabolism, phenology, physiology) and their interactions as well as the effects on non-target attack of native plant species.

In parallel to the growing concern of climate change and plant invasions, there has been a large increase in studies on climate change and biocontrol over the past 10 years (Appendix Fig. S1). However, our understanding of the response of these plant-herbivore interactions to the full complement of climate-driven changes remains rudimentary. Multiple reports suggest that climate change may promote plant invasions and increase their impact [5], while other studies report both positive and negative effects of climate change on the performance of biocontrol agents, with various consequences for their efficacy (Table 1; Figure 1).

The goal of this paper is to review the available evidence of climate change effects on weed biocontrol outcomes, provide an overview of the biocontrol methodologies used with key examples, discuss potential ecological and evolutionary outcomes for the interaction of plant invaders and their biocontrol candidates/agents under climate change, and raise awareness of how climate change may alter biocontrol efficacy and risk to increase our ability to predict these outcomes through pre-release assessment.

Climate change and weed biocontrol: a complex interplay

Ecological effects

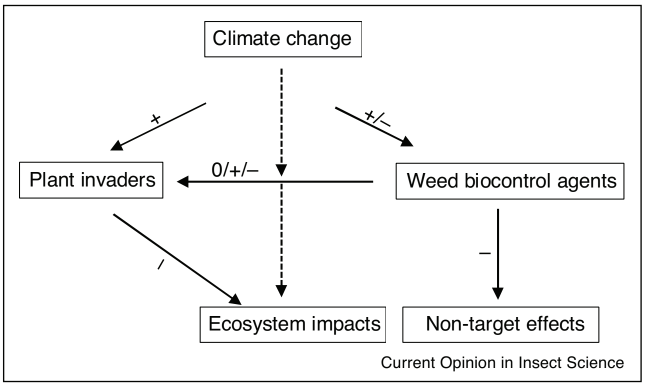
Climate change has the potential to alter interactions of invasive weeds and biocontrol agents by phenotypic

Table 1

Examples of studies on weed biocontrol under climate change

Issues	Methods	Climate change aspects			host invasive plant	Biocontrol agent	Findings	Ref.
		Temp.	CO_2	precipitation				
Ecological effects	Chambers/lab	×			*Parthenium hysterophorus*	*Zygogramma bicolorata*	Occurrence of heat waves may influence the performance and survival of *Z. bicolorata*	[64••]
	Common garden		×	×	*Alternanthera philoxeroides*	*Agasicles hygrophila*	Minor effects of elevated CO_2 on the efficacy of the biocontrol agent	[65•]
	Field experiment		×		*Centaurea diffusa*	*Larinus minutus*	Elevated CO_2 increased plant fitness, but also agent density	[66••]
Evolutionary aspects	Common garden	×			*Jacobaea vulgaris*	*Longitarsus jacobaeae*	post-introduction climate adaptation by life-history changes	[36]
Efficacy prediction	Species distribution model	×	×	×	*Ambrosia artemisiifolia*	six potential agents	The spatial mismatch of *A. artemisiifolia* and its potential agents is further amplified by climate change	[38••]
	Population dynamics model			×	*Prosopis* spp.	*Evippe* spp.	The effect being dampened by herbivory suppressing seed production irrespective of preceding rainfall	[67••]
non-target attack	Field survey and field experiment	×			*Alternanthera sessilis*	*Agasicles hygrophila*	Climate warming increases biocontrol agent impact on a non-target species	[22••]

Figure 1



Impact of climate change on plant invasions, weed biocontrol and their interactions (dash lines) as evidenced from literature. Signs of 0/+/– represent no-, positive and negative effects.

changes in traits (physiology, biochemistry, life history, phenology) or by changing the abiotic and/or biotic environments in which interactions occur, both aboveground and belowground. This in turn can alter the frequency, timing, intensity, and duration of interactions between plant invaders and biocontrol agents and so the impact of agents on plant invaders may be enhanced or reduced. For instance, elevated CO_2 may change the amount of herbivore damage by altering plant primary metabolism (e.g., increased tissue C:N, which typically increases herbivore consumption [6,7]). CO_2-driven changes in secondary metabolism that underlie plant chemical defenses [8,9•,10] or volatiles [11] may also influence herbivore damage (e.g., phenolics typically increase under elevated CO_2 and can reduce herbivore attack [12], but other chemicals have variable responses [12]). Elevated CO_2 also often increases plant growth rates [9•,13] which may contribute to increased plant tolerance to herbivore damage [7,14]. Increased temperature, and potentially longer growing seasons, can change the interactions of biocontrol agents and weeds by increasing the number of generations per year of the agents [15] and potentially increase its impacts on the weed host [6,16,17]. Because plants differ in their susceptibility to damage at different life stages (e.g., vegetative growth versus seed production) changes in timing of emergence of insects and weeds with climate change could modify the consequences of insect feeding [18]. Changes in geographic distributions, especially as the climate continues to warm and extreme events become more common, can impact interactions between biocontrol agents and weeds as differential migration rates of insects, host plants, higher trophic levels and other species create novel biotic interactions and new above- and belowground communities [19,20,21•,22••,23]. The net effect of climate change on weed biocontrol will depend on the relative strengths of these various responses to multiple factors of climate change [6].

Evolutionary aspects

Recent studies have highlighted that rapid evolutionary change can occur in both invaders and their biocontrol agents in response to a shift in environmental conditions [24,25]. Many cases of rapid adaptive evolution have been reported for invasive plants, including shifts in resource allocation from defense to growth [26], local adaptation to new habitats [27] and climates such as by the evolution of phenotypic clines along climatic gradients [28], the evolution of greater dispersal ability [29] and increases in the rate of population growth and expansion [30,31••]. Evolutionary adaptation is also expected for biocontrol agents when they encounter novel environments or changes in climatic conditions, especially for species with short generation times [31••,32,33•].

We argue that evolutionary studies should be better integrated into the different stages of a weed biocontrol program (Figure 2). For example, by using reciprocal transplants or common garden experiments coupled with population modeling, researchers could match up climatically adapted biocontrol candidates with their target release environments, or evaluate their potential evolvability under changing selection pressures (Figure 2). High genetic variance in life history and abiotic stress tolerance traits may allow researchers to screen for strains or populations that could adapt to future climatic conditions [34]. For instance, Reddy *et al.* [35••] compared four biotypes of the weevil, *Neochetina Eichhorniae* Warner (Coleoptera: Curculionidae), a biocontrol agent of water hyacinth, *Eichhornia crassipes* (Mart.) Solms. They found variation in tolerance to cold among populations and suggested that the introduction of *N. Eichhorniae* from Australia into northern California would result in climate matching between source and release environments and increase the distribution and densities of weevils, and by this improve biocontrol efficacy. Szűcs *et al.* [36] found post-introduction climatic adaptation through life-history changes in aestival diapause and shifts in phenology in *Longitarsus Jacobaeae* Waterhouse (Coleoptera:Chrysomelidae), a biocontrol agent of *Jacobaea vulgaris* Gaert.

In the following, we explore how specific studies of ecological and evolutionary processes during a weed biocontrol program can incorporate implications of climate change scenarios, and help inform the selection of effective and safe agents.

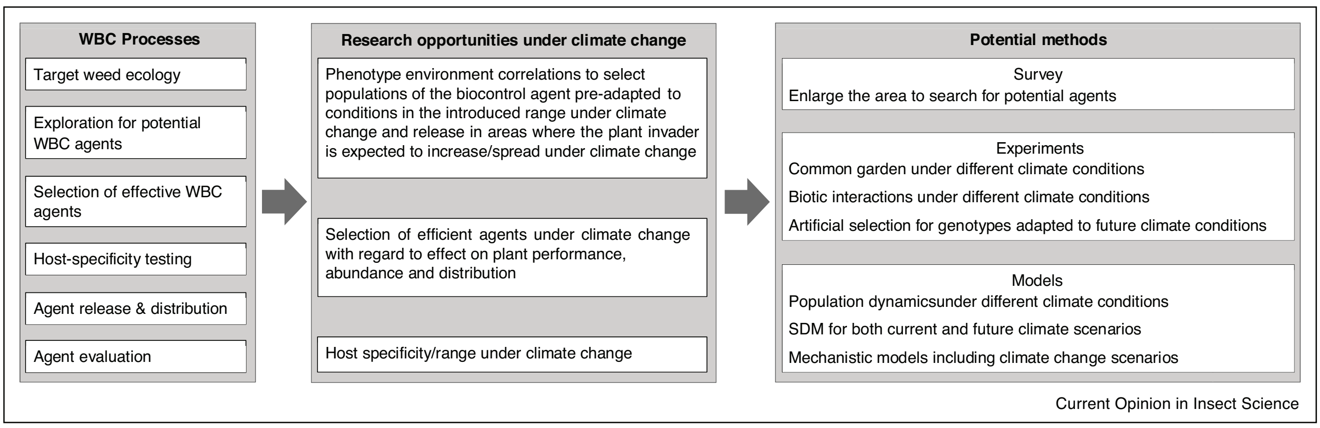
Weed biocontrol efficiency under climate change

Ecological context

Responses of plant and natural enemy populations to climate change through short-term (within-generation) shifts in their geographical distribution or timing of growth and species interactions can be predicted through field surveys along latitudinal transects, experimental measurements under controlled conditions, and through predictive modeling. For example, using field surveys along latitudinal transects and simulated warming experiments, Lu *et al.* [22••] showed that climate warming may allow the beetle *Agasicles hygrophila* Selman and Vogt (Coleoptera:Chrysomelidae), a biocontrol agent of the invasive weed *Alternanthera philoxeroides* (Mart.) Griseb, to expand its range and benefit biocontrol in regions that are currently too cold for the insect. However, because *A. philoxeroides* will also expand its range further north in response to warming, and the plant tolerates cold better than *A. hygrophila*, the overall effect of biocontrol may be weak in some higher latitude regions if the insect cannot establish robust populations due to the cold climate.

Species distribution models (SDMs) [37] are often used to predict the efficacy of potential biocontrol agents in current and future conditions by measuring the overlap of predicted habitat suitability with that of their target host plant. For example, based on habitat suitability in SDMs, the invasive plant *Ambrosia artemisiifolia* L. is predicted to experience decreased geographic overlap with six biocontrol candidates under climate change in its introduced European range [38••]. SDMs can also use climate suitability to predict demographic rates and the ability of biocontrol agents to quickly attain high

Figure 2



Schematic overview of processes in a weed biocontrol (WBC) project, research opportunities that include climate change scenarios and their potential methods (SDM: species distribution models).

population densities, which are critical for significant impacts on the target plant invader [39] and management success [40]. Moreover, combining SDM and mechanistic (process-based) models by integrating physiological models of insect development into SDMs based on habitat suitability may enable more robust predictions of both range shifts [41] and population abundances [42,43]. Using such a combined approach, Augustinus *et al.* [44] identified the climatic factors limiting the population build-up of *Ophraella communa* Lesage (Coleoptera: Chrysomelidae), a biocontrol candidate of invasive *A. artemisiifolia*, and predicted its potential population density across its suitable European range and the relative importance of those climatic factors on population growth. Population dynamics models are also commonly used to explore and predict changes in population densities over time, such as Integral Projection Models (IPMs) [45] and DYMEX (Hearne Scientific Software) [46]. Kriticos *et al.* [47] used a process-based population dynamics model to predict that invasive *Buddleja davidii* Franch. would succumb rapidly to herbivore damage by its biocontrol weevil *Cleopus japonicus* Wingelmüller (Coleoptera: Curculionidae) under warming conditions. Further studies would benefit from integrating theoretical modeling, physiological/behavioral experiments and experimental population studies under climate change conditions (i.e., latitudinal space-for time and climatron/FACE (free-air CO_2 enrichment) type experimental settings [13]) into a biocontrol program (Figure 2).

Evolutionary context

Examples of evolutionary responses to climate change are accumulating, suggesting some organisms are capable of rapid evolution on a time scale concomitant with ongoing changes in climate [28,32]. While the tools of ecological genetics are able to test for and identify genetic differences attributable to local environments, predicting future responses is more difficult. The breeder's equation postulates that the response (R) of a population to selection on a quantitative trait will be proportional to the product of the trait heritability (h^2, the ratio of additive genetic variance, V_A, to total phenotypic variance, V_P) and the strength of selection (S), whereby $R = h^2S$ [48]. Thus, predicting evolutionary responses of weed biocontrol efficacy under climate change requires information about the current amount of standing genetic variance present for traits involved in the agent-host interaction in both the native and introduced ranges that may become mismatched under climate change. Accurate predictions may require knowledge of how this variation is spatially distributed among geographic regions of current (and possibly future) overlap. In addition, genetic correlations among traits create tradeoffs that result in indirect selection that may constrain the response of traits to direct selection during climate change [49,50]. Given these biological complexities, a promising approach is to use experimental evolution or artificial selection experiments that measure the change in trait means over multiple generations in response to selection under controlled conditions [51]. Such experiments may allow the direct measurement of each population's evolvability in response to selection on a focal trait, such as host plant life history or allocation to growth and defense, as well as revealing changes in correlated traits that may have evolved as a result of indirect selection [52].

While it would be logistically challenging to carry out experimental evolution for both host plants and biocontrol agents, one feasible solution might be to evolve agents reared on host plant tissues developed under controlled growing conditions mimicking climate change (e.g., earlier spring warmup, drought stress). Tracking the across-generation response of traits measured in the biocontrol agent to this change in selective environment would allow a realized measure of evolutionary potential that integrates over existing trait correlations. This approach could be coupled with the strategy of 'evolve and re-sequence' [53], in which the genomic targets of selection and evolutionary response can be revealed by performing genome-wide DNA or RNA (transcriptomic) sequencing of population pools to test for gene-specific changes in allele frequencies from the start to the end of the experiment. This would require large experimental populations of the biocontrol agent (in the several thousands or more); thus, logistics and permitting may necessitate that such studies be restricted to the native range before the introduction of biocontrol, or perhaps in the introduced range in cases where biocontrol has already been accidentally introduced. Such an approach could be particularly useful for identifying large effect genetic variants that might serve as useful biomarkers for genes in biocontrol agents that are likely to be responsive to selection under changing climates. Traits such as host plant chemical defenses or insect metabolic genes that detoxify these compounds would be ideally suited towards this goal; however other more quantitative forms of plant defense and many other life history traits are likely to be highly polygenic [54], and thus better suited to a quantitative genetic framework.

Recently, the integration of genomic polymorphism data with SDMs have enabled modeling intra-specific variation in species-climate relationships, including the potential to identify which areas within a species' geographic range may become most affected by a change in climate [55,56]. If local selection by climate has shaped the genomic diversity of the plant host, then genomics-enabled SDMs could help predict portions of the host range that could be most vulnerable to short-term fitness impacts from climate change. Genomics-enabled SDMs of biocontrol agents may also be useful in predicting the best match between source and release climates. Another possibility involves the use of geographic variation in host trait expression (for example, in palatability or defense) as predictors of genomic variability underlying local adaptation of the agent to its host in the native range [57]. This type of an approach could help reveal potential co-evolutionary hotspots between host plants and their biocontrol agents that could be used to target agent sources in the native range and release locations in the introduced range.

An important caveat of all SDM methods (genomics-enabled or otherwise) is that these models are inherently correlative, and thus model predictions require careful validation testing before making changes in conservation priorities or management [58,59]. Further, SDM predictions of shifts in suitable ranges or genomic vulnerability of particular populations under climate change are likely to be most useful for short-term projections (relative to the generation time and dispersal distances of the organisms), particularly for biocontrol agents with short generation times that may be capable of rapid evolution relative to that of the host plant.

Climate change and non-target attack of biocontrol agents

A few studies reported non-target attack of intentionally released or actively redistributed weed biocontrol agents [60•] that resulted in direct negative effects on native plant species [61,62], or negative indirect effects [63]. In a recent review, Hinz *et al.* [60•] showed that incidences of unpredicted non-target attack decreased over time and this trend is thought to continue with scientific advancement. Their results suggest that appropriate selection of test species could have avoided more than 90% of unpredicted non-target attack. Incorporating climate change factors may further improve such predictions in the future. This is because climate-induced shifts in the synchrony of plant–insect interactions could affect insect distribution and abundance on invasive and native plants that may alter non-target effects in biocontrol. For instance, Lu *et al.* [22••] showed that elevated temperature can shift the phenology of the non-target native plant, *Alternanthera sessilis* Linn. from annual to perennial and increase overwintering, damage and impact of the biocontrol agent *A. hygrophila* on seedling recruitment. However, warming alters the interactions between invasive *A. philoxeroides* and native *A. sessilis* and shifts the plant community from invader-dominated to native-dominated, but only in the presence of *A. hygrophila* as a result of the disproportionate increases in herbivory on the invader [21•]. This suggests that biocontrol may enhance the competitive ability of native plants under climate change. Thus, climate change could substantially alter the interactions of invasive plants, native species and biocontrol agents and the 'net' non-target effects should be carefully assessed by field monitoring, common garden experiments, population dynamics models and SDMs.

Climate change affects the likelihood of new invasions (e.g., disturbance of communities) directly by changing invasive plant distribution, growth and reproduction, and indirectly through modifying plant-insect interactions. Understanding responses of invasive plants and their natural enemies to climate change is critical for future biocontrol of invasive plants. The effects of climate change on weed biocontrol management are complex (positive, negative or neutral), creating a particular challenge for predicting its efficacy and risk. Although many current pre-release tests are robust in predicting biocontrol efficacy and non-target effects, incorporating climate change factors may allow researchers to predict how they will affect the phenology, distribution and abundance of biocontrol agents and invasive and native plants together with their interactions and biocontrol outcomes. However, such studies (Figure 2) would greatly benefit from partnerships of biocontrol practitioners with evolutionary biologists and modelers in academia.

Conflict of interest statement

Nothing declared.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.cois.2020.02.003.

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