Predicting non-target impacts

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Biocontrol of invasive alien weeds has produced great benefits, but concerns over undesirable impacts on non-target plants and/or indirect interactions between biocontrol agents and other biota impede the implementation of biocontrol in some countries. Although great strides have been made, continuing uncertainties predicting the realized host range of candidate agents is probably resulting in some being erroneously rejected due to overestimation of risk. Further refinement of host-range testing protocols is therefore desirable. Indirect interactions are inherently harder to predict, and the risk of both direct and indirect non-target impacts may change over time due to biocontrol agents evolving or expanding their range under climate change. Future research directions to better understand the risk of non-target impacts over time are discussed.

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Introduction

Biological control (biocontrol) is often the most cost-effective way to manage invasive plants [1]. Nevertheless, concerns persist regarding direct damage to non-target plants and potential indirect impacts of weed biocontrol agents [2••]. Weed biocontrol implementation is hampered by perceptions of risk and restrictive regulatory procedures, notably in the USA and Europe [3,4] despite recent evidence that modern host-range testing protocols are highly reliable. Cases of programmes that have

resulted in 'sustained' non-target attack are rare and declining [2••], and for the small fraction (<1%) of deliberately introduced biocontrol agents that caused serious non-target impacts, attack was foreseeable and their release would not be permitted today [5].

A lack of rigorous monitoring could, however, mean non-target attack is under reported, particularly cases of minor impacts [6,7]. In New Zealand, where systematic surveys have been conducted, the proportion of agents known to attack non-target plants (24%) is higher than the worldwide average (13%), probably due to greater sampling effort, although all examples are of minimal or minor damage [7]. Nonetheless, even minor non-target attack is a potential concern if, over time, selection pressures result in agents adapting to exploit non-target plants more effectively.

This review focuses on recent developments in predicting the risk and magnitude of direct and indirect non-target impacts of introducing weed biocontrol agents, as well as newly recognized risks such as the potential for some hemipteran agents to transmit plant diseases. We consider evidence that risks might change over time due to evolutionary processes or climate change. Our review also recognizes the need to weigh up the potential benefits of implementing biocontrol against the potential risks, which puts an increasing emphasis on the development of ecological theory to guide the selection of effective agents [8].

Direct non-target effects

Most examples of non-target attack by weed biocontrol agents are of spill-over damage, which is unlikely to inflict significant population-level impacts on non-target plants [2••]. The realized host range of herbivorous insects can increase at times of population outbreaks [9], which are expected in the period following the release of effective biocontrol agents. Laboratory experiments have been developed specifically to predict spill-over damage on plant species that could not support sustained agent populations [10,11].

Candidate agents, when confined in laboratory conditions, may complete development on plants they would not attack in the field, making interpretation of test results challenging and potentially resulting in the rejection of safe agents [12]. Pre-release assessments of impacts on test and non-target plants over multiple generations of the agent could help risk assessment [13]. For instance, in laboratory tests the psyllid *Arytinnis hakani* persisted, in relatively low numbers, on non-target

Lupinus spp. for multiple generations, but only affected the growth and survival of the target weed *Genista monspessulana* [14]. Nevertheless, open-field host-range testing is considered necessary to confirm *A. hakani* is safe to release in the USA [14].

Researchers have focused on improving the experimental designs of open-field tests to replicate situations that might occur in the new range if the agents were released; for example, interspersing the target weed among test plants and then killing the target plants to force the agents to either disperse to look for more target plants, or accept the non-target plants [15,16]. Interpretation of open-field testing can still be contentious, however. For example, two candidate agents for invasive *Phragmites australis australis* strongly preferred to oviposit on *P. australis australis* and suffered higher mortality rates on native *P. australis americanus*, yet there has been disagreement regarding their potential to inflict deleterious non-target impacts on *P. australis americanus* [17,18]. Moreover, open-field testing in the native range can be prevented by logistical challenges, including restrictions on the movement of plants between countries [16].

It has been demonstrated that the relative performance of candidate weed biocontrol agents on test and target plants during laboratory host-range testing can predict the probability of test plants being attacked in the field [19]. More studies are required to corroborate this approach, but a similar analysis applied to an insect parasitoid data set indicates it may be broadly applicable [20•]. Other approaches aimed at improving host-range testing predictability include developing novel techniques to investigate the importance of olfactory and visual cues to explain host selection behaviour [21•,22]. Similarities in plant volatile profiles can explain the unexpected use of novel host plants for some insect herbivores [23] suggesting that responses to olfactory cues may be of particular importance.

Few studies have demonstrated the demographic consequences of non-target attack [24•]. Inclusion of demographic models in host-specificity testing to predict the population-level implications of non-target feeding could fundamentally reform the assessment of risk [24•].

Indirect non-target effects
Indirect impacts to food webs and ecosystems include competition, apparent competition (indirect competition between two or more species that share a natural enemy), and potential 'ecological traps' if native parasitoids attack agents but cannot complete development within them [25–27]. They are difficult to predict and quantify, but the lack of studies to understand indirect impacts of agents is a common criticism of weed biocontrol [25,26].

Agents that possess ecological analogues (native arthropods taxonomically related to the agent that have a similar feeding niche) are predictably susceptible to attack by parasitoids that attack their analogues, potentially reducing their efficacy and increasing the risk of indirect non-target impacts in food webs [28]. Candidate agents that possess ecological analogues have been given a low priority for introduction [29].

A similar approach may help predict the risk of indirect non-target impact mediated by predators. For example, in New Zealand two agents (*Tetranychus lintearius* and *Aceria genistae*) have close taxonomic relatives that occupy similar niches on native plants confamilial with their target weeds. These agents are attacked by native specialist predators that are congeneric with the main predators that attack them in their respective native ranges [7]. Furthermore, the contrasting abundances of these agents in New Zealand mirrored their abundance in the native range, indicating that the impacts of predation are predictable [7].

Most predators that attack arthropod weed biocontrol agents are, however, generalists [7]. Assuming all biocontrol agent species are subject to some degree of predation by generalist predators, then indirect interactions will be inevitable. The key to minimizing such indirect effects is assumed to rely on selecting effective biocontrol agents that reduce their own abundance by suppressing the target weed. Nevertheless, concerns were raised that rapid suppression of *Tamarix* L. spp. by *Diorhabda* spp. might harm native biodiversity [30]. However, all management tools that rapidly remove *Tamarix* cause indirect short-term effects. Indeed, biocontrol reduces *Tamarix* infestations more slowly than other control options, such as burning and mechanical control, and incorporating restoration activities to increase native tree cover should mitigate any effects of a reduction in *Tamarix* cover [30].

Although competition and apparent competition may lead to declines of native species, they are unlikely to result in extinctions [26]. Moreover, plant invasions have much greater ecological impacts than invasive herbivorous insects [27], implying that agents that suppress the target weed should have overall positive effects on biodiversity.

Newly recognized risks
Several insects in the superfamily Psylloidea can transmit plant pathogenic bacteria such as *Candidatus* Liberibacter [31] including a biocontrol agent, the broom psyllid *Arytainilla spartiophila*, which vectors '*Ca*. L. europaeus' [32]; a disease that had not been described when *A. spartiophila* was introduced into New Zealand. '*Ca*. L. europaeus' may enhance biocontrol impacts [32], but there is a risk it could be transmitted to non-target plants.

The risk that *Calophya* spp. (candidate agents for Brazilian peppertree *Schinus terebinthifolia*) may harbour plant pathogens was investigated by characterizing their microbiomes [31]. Plant pathogens were absent, but putative insect parasites *Wolbachia* spp. were detected [31], demonstrating that molecular techniques may also improve the detection of entomopathogens in biocontrol agent cultures and potentially prevent the release of agent populations that are debilitated by entomopathogens.

Molecular tools have also been used to investigate the risks posed by fungal associates of a gall midge, *Asphondylia prosopidis*, a potential biological control agent of invasive mesquite (*Prosopis* spp.) in South Africa [33].

Another newly recognized risk concerns the potential for poisoning of livestock grazing on plants infested with toxic sawfly (Hymenoptera: Pergidae) larvae that are being considered as potential biocontrol agents [34]. The toxic peptides present in sawfly larvae are absent from their host plants and are thought to be synthesized by insect endosymbionts [35]. In contrast, biocontrol agents that sequester toxins from host plants that are unpalatable to livestock, such as the cinnabar moth *Tyria jacobaeae* [36], have not been associated with incidental livestock poisoning, perhaps because livestock avoid their toxic host plants so that accidental ingestion rarely occurs.

Can risks change over time?
Evolution
Biocontrol agents exhibit extreme phylogenetic conservatism, and micro-evolutionary changes are very unlikely to result in changes to the fundamental host range [24•]. Where non-target attack is already occurring, however, selection pressures may result in increased levels of non-target attack over time. Only one example of increased larval survival on a non-target host has been reported [37•,38], but this may reflect a lack of monitoring [17] and laboratory studies investigating changes in performance on non-target hosts [19].

Other evolutionary changes post-introduction may affect risk; for example, to thermal tolerances [37•]. Rapid evolution enabled *Diorhabda carinulata* to expand southwards into regions where colonization had been inhibited by inappropriate diapause induction cues, which had evolved under photoperiodic regimes at the northern latitudes of two Eurasian collection sites [30]. Practitioners should therefore be wary about assuming a potential non-target plant is safe if it occurs outside the predicted distributional limits of a candidate agent.

Climate change
Climate change is expected to result in widespread effects on insect–plant interactions [39,40], potentially altering the risk of non-target damage; for example, by increasing risk of spill-over damage to non-target plants due to increased abundance of agent populations under warming temperatures [41]; expansion of the distribution of a biocontrol agent into areas where at-risk non-target species occur [41,42]; altering the vulnerability to attack of non-target plants due to changes in the phenology or life history of biocontrol agents, their targets, and non-target plants [39,43]; or changes in plant nutritional quality [39].

Predicting the consequences of climate change on non-target damage is difficult because plants and insects can respond to elevated CO_2, increasing temperatures, and extreme weather events in very different ways [44]. Nevertheless, there is a case for re-evaluating risk assessment where current mismatches in phenology and geographical range protect non-target species from potential attack, especially if mechanistic niche models predict that their potential distributions and seasonal phenology might overlap under future climate scenarios [45].

Discussion and conclusions
Since the 1990s research on biological control has increasingly focused on the associated risks [46] (Figure 1), despite modern host-range testing protocols have a good and improving track record of preventing the release of agents that inflict serious direct non-target damage [2••,5]. Nevertheless, greater monitoring is needed, both to improve the detection of non-target attack and to investigate whether there are examples of evolutionary change in the ability of agents to attack non-target plants [6,7]. Furthermore, the 'relative performance' approach of correlating agent performance on test and target plants with

Figure 1

Current Opinion in Insect Science
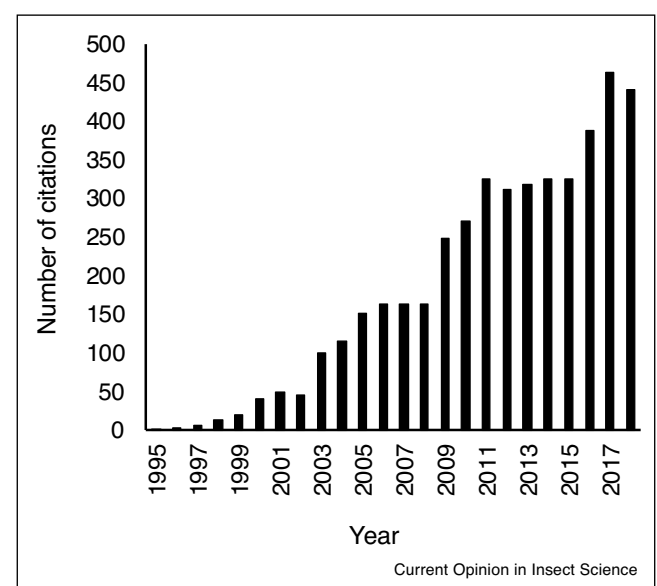
Sum of citations per year (up to 2018) for publications identified by a Web of Science search using the Topic search terms: Biological control AND weed AND non-target.

field host use requires rigorous testing using reliable field survey data.

The potential for indirect effects of weed biocontrol agents to have negative impacts continues to raise concerns [25,26], yet few field studies have investigated the magnitude and spatial aspects of such effects, and this is an area where further study could be of great value.

Molecular tools have identified hitherto unknown risks of biocontrol, and techniques for mitigating them [31,32], and they are becoming an increasingly important tool for biocontrol practitioners. A standardized practice of screening for potentially harmful micro-organisms associated with new biocontrol agents would be a useful addition to risk assessment protocols.

Many jurisdictions consider the risks of introducing weed biocontrol agents but do not weigh the risks against the potential benefits, and there are examples of successful and safe weed biocontrol agents released in the past that would not be introduced under modern risk assessment protocols [12]. Ideally, the impact of the target weed should also be considered, so that the risk of 'doing nothing' and the potential benefits of weed biocontrol are included in the assessment [47].

Declarations of interest
None.

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References and recommended reading
Papers of particular interest, published within the period of review, have been highlighted as

- of special interest
- •• of outstanding interest

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