

Making weed biological control predictable, safer and more effective: perspectives from New Zealand

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Abstract A persistent problem in weed biocontrol is how to reliably predict whether a plant that supports development in laboratory host-specificity testing will be utilized in field conditions, and this is undoubtedly preventing releases of safe and effective agents. Moreover, the potential for unanticipated undesirable indirect effects of weed biocontrol on ecological networks has raised concerns by policy-makers and the general public. The key to minimizing risks of non-target impacts is prioritizing candidate agents that are both host-specific and effective, such that the number of agents required to bring the weed under control is minimized. As a consequence both the weed and its biocontrol agents become minor components of the local biota. Here we review recent attempts in New Zealand to improve the predictive ability of host-range testing, to avoid potentially safe and effective agents being rejected. Research in New Zealand aimed at

predicting whether an agent is likely to experience enemy-release (i.e. reduced parasitism and predation) could assist agent prioritization, potentially making biocontrol both environmentally safer and more effective.

Keywords Host-range · Specificity · Weed biocontrol · Direct and indirect non-target impacts

Introduction

The environmental safety of weed biocontrol has been debated for several decades (e.g. Louda et al. 1997; Strong 1997; Suckling and Sforza 2014). A problem that troubles biocontrol practitioners to this day is reliably predicting whether a plant that supports development in laboratory host-specificity testing is likely to be utilized in field conditions (Louda et al. 2003). A risk-averse approach to regulating the introduction of new organisms would be to reject all candidate biocontrol agents that can complete development on any valued non-target plants. Inflexibly applying this approach, however, is likely to result in environmentally safe and potentially successful agents being rejected, because the ‘field’ or ‘ecological’ host-range of an agent is usually only a subset of its fundamental host-range. This is because, when given no-choice in a laboratory test, candidate agents may feed on plants that they would never attack in field

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conditions (van Klinken 2000). Authorities have become more risk-averse and gaining approval for the introduction of a biocontrol agent into at least some jurisdictions has been subject to delays, or is becoming increasingly difficult (Becker et al. 2013; Hill et al. 2013; Hinz et al. 2014; Klein et al. 2011; Sheppard et al. 2003). It has also been noted that a number of safe and effective biocontrol agents that were released in the past would not be approved for release under current regulatory regimes (Groenteman et al. 2011; Hinz et al. 2014). Examples such as the denial of a release permit for *Ceratapion basicorne* (Illiger) (Coleoptera: Brentidae) in the USA, despite open field specificity tests which demonstrated that *C. basicorne* is highly specific to the target weed [*Centaurea solstitialis*, Asteraceae: Cardueae; (Cristofaro et al. 2013)], indicates that risk averse regulatory authorities are preventing the release of safe and potentially effective agents in some jurisdictions.

Concerns have also been raised regarding the potential indirect impacts of weed biocontrol, for example via interactions in food webs (e.g. Carvalheiro et al. 2008; Pearson and Callaway 2005; Willis and Memmott 2005). Although rarely demonstrated experimentally, there are examples where natural enemies of introduced biocontrol agents have interfered with biocontrol efficacy and many other cases where biotic interference has been suspected or blamed for biocontrol failure (Goeden and Louda 1976). Selecting agents that are likely to experience enemy-release should improve the prospective success of a biocontrol program while also minimizing the potential for indirect impacts (e.g. Paynter et al. 2010). Improved predictive ability regarding direct and indirect non-target impacts has the potential to enhance both the safety and the success of weed biocontrol. Here we review selected biological control literature with a focus on New Zealand (henceforth NZ) research to highlight developments aimed at improving host-range testing protocols and the ability to predict biotic interference in weed biocontrol programs.

Direct impacts on non-target hosts

A recent systematic global review of non-target attack in weed biocontrol programs indicated that significant negative impacts on non-target species occur rarely

and the few cases documented are the result of historic releases that would not be permitted under current regulatory regimes (Suckling and Sforza 2014). This indicates that current host-range testing protocols are assessing risk adequately. Although it could still be argued that the number of detected cases may be a fraction of those that have occurred (Simberloff and Stiling 1996) because systematically collected national survey data from countries that practice weed biocontrol is largely lacking. For example, Suckling and Sforza's (2014) review indicated that, world-wide only 43 of 512 (8%) arthropod agents released attack non-target plants. In NZ, where systematic surveys have been conducted, eight out of 33 (24%) arthropod agents surveyed are known to attack non-target plants (Paynter et al. 2004) (Table 1). This difference is likely due to greater sampling effort, rather than the NZ flora being uniquely susceptible to non-target attack. According to Suckling and Sforza's (2014) damage scale, none of the NZ examples have affected crops and the five (15%) agents that attack native plant species only cause minimal or minor damage.

Although it is possible that Suckling and Sforza (2014) may have underestimated the number of cases of non-target attack, it seems unlikely that there could be any examples of hitherto undetected attack causing major impacts on non-target plants, given the large amount of research on non-target attack in the last two decades. Moreover, non-target survey work in NZ indicated several ways by which the environmental safety of weed biocontrol could be improved. For example, unexpected non-target attack from the gorse pod moth *Cydia succedana* (Denis and Schiffermüller) (Lepidoptera: Tortricidae) indicated that (1) while choice tests generally represent a more natural scenario than no-choice tests, there are situations in which choice tests can be unreliable, and (2) only a tested population of an agent should be released. *Cydia succedana* has two generations in southern England coinciding with the main flowering periods of two gorse species: *Ulex europaeus* L. (Fabales: Fabaceae) in spring and *Ulex minor* Roth (Fabales: Fabaceae) in summer. In NZ, *U. minor* is an uncommon weed and it was hoped that emergence of the second generation of *C. succedana* would coincide with the autumn flowering period of *U. europaeus* (Paynter et al. 2008a). Instead, *C. succedana* emergence has remained poorly synchronized with autumnal flowering of *U. europaeus*, and *C. succedana*

Table 1 Non-target attack observed in New Zealand weed biocontrol programs

Agent (year of first introduction)	Target weed	Non-target attack plant(s)	Non-target impacts
Coleoptera			
Chrysomelidae			
<i>Agasicles hygrophila</i> Selman and Vogt (1981) (Coleoptera: Chrysomelidae)	<i>Alternanthera philoxeroides</i> (Mart.) Griseb. (Caryophyllales: Amaranthaceae)	<i>Alternanthera denticulata</i> ^a R. Br. <i>A. nahuia</i> Heenan and de Lange (Caryophyllales: Amaranthaceae)	Rare minor spillover. Non-target plants were not recognized as present in NZ when <i>A. hygrophila</i> was introduced ^{c,d} . Retrospective testing indicated predictable spillover attack ^e
<i>Bruchidius villosus</i> F. (1987)	<i>Cytisus scoparius</i> (L.) Link	<i>Cytisus proliferus</i> L. f. (Fabales: Fabaceae)	Minor impacts ^b
<i>Cassida rubiginosa</i> Müller (2008)	Thistles (mainly <i>Cirsium arvense</i> (L.) Scop. (Asterales: Asteraceae)	<i>Cynara scolymus</i> L. (Asterales: Asteraceae) ^f	Minor spillover. Anticipated risk considered acceptable by regulatory authorities when approval for release was granted ^g
<i>Chrysolina hyperici</i> Forster (1943); <i>C. quadrigemina</i> L. (1963)	<i>Hypericum perforatum</i> L.	NZ native <i>Hypericum</i> species ^h	Minor impacts. Retrospective testing indicated non-target attack was predictable ⁱ
Diptera			
Agromyzidae			
<i>Phytomyza vitalbae</i> Kaltenbach (1996)	<i>Clematis vitalba</i> L. (Ranunculales: Ranunculaceae)	<i>Clematis foetida</i> Raoul and <i>C. forsteri</i> J.F.Gmel (Ranunculales: Ranunculaceae) ^j	Minor spillover. Anticipated risk considered acceptable by regulatory authorities when approval for release was given ^j
Lepidoptera			
Erebidae			
<i>Tyria jacobaeae</i> L. (1929)	<i>Jacobaea vulgaris</i> Gaertn. (Asterales: Asteraceae)	Native <i>Senecio</i> species (Asterales: Asteraceae) ^k	Minor spillover. Affected plant species were omitted from the original host range testing ^k
Tortricidae			
<i>Cydia succedana</i> (Denis & Schiffermüller) (1992)	<i>Ulex europaeus</i> L.	Exotic weeds related to <i>U. europaeus</i> ^l	Minor but unexpected attack ^l

^a Updated from Paynter et al. (2004)^b Sheppard et al. (2006)^c Webb et al. (1988)^d Heenan and de Lange (2004)^e Paynter, unpublished data^f Paynter et al. (2015b)^g ERMA (2007)^h Paynter et al. (2004)ⁱ Groenteman et al. (2011)^j Paynter et al. (2008b)^k Fowler et al. (2004)^l Paynter et al. (2008a)

attacks other non-native summer flowering Fabaceae in NZ, such as *Lotus corniculatus* L. (Fabales: Fabaceae) (Paynter et al. 2008a). Both choice and

no-choice tests were done prior to the release of *C. succedana* in NZ and no-choice starvation tests indicated that *C. succedana* sourced from England

should be highly host-specific. However, moths collected in Portugal were also released in NZ. Retrospective testing indicated that *C. succedana* sourced from Portugal have a broader host-range than English moths, explaining the non-target attack. This study also indicated that choice tests underestimated the risk of non-target attack because Portuguese moths exhibited a very strong preference for *U. europaeus* over *L. corniculatus* in choice oviposition tests, but there was no significant difference in the number of eggs laid on *U. europaeus* and *L. corniculatus* in no-choice tests. In this case no-choice tests were a better predictor of the field host-range of *C. succedana* due to asynchrony between the agent and the target weed in the field (Paynter et al. 2008a).

Predicting the risk of non-target attack from host-specificity tests

Paynter et al. (2015b) noted that the fundamental host-range for development can usually be reliably determined by no-choice laboratory tests, but uncertainties remain regarding the ability to predict the field (also termed realized or ecological) host-range of an agent. As the field host-range is commonly narrower than the fundamental host-range, it follows that no-choice tests may overestimate risks (van Klinken 2000). Developing means to reliably predict the field host-range may, therefore, enable practitioners to differentiate between safe and risky species and avoid rejecting safe agents.

Open field tests conducted in the native range of the candidate agent are generally considered the most natural form of host-range testing (e.g. Marohasy 1998). But they are logistically difficult and interpretation can be problematic because the presence of the primary host may cause females to be unresponsive to lower-ranked potential hosts (Paynter et al. 2015b).

Paynter et al. (2015b) tested the hypothesis that quantifying 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. They concluded that this approach can help predict risk of non-target attack because there was a clear threshold score above which non-target attack became likely and below which non-target attack did not occur. This ‘threshold score’ approach has been adopted by NZ regulatory authorities. The release of a leaf beetle

Chrysolina abchasica (Weise) (Coleoptera: Chrysomelidae) for the biological control of tutsan, *Hypericum androsaemum* L. (Malpighiales: Hypericaceae), was recently approved despite native NZ *Hypericum* species being within its fundamental host-range, on the basis that the combined risk scores for native *Hypericum* species were well below the predicted threshold for non-target attack. It was not possible to import and grow native NZ *Hypericum* species for use in field tests in Georgia, where *C. abchasica* is native (Hugh Gourlay, pers. comm.), so approval to release *C. abchasica* in NZ would not have been possible without the development of the Paynter et al. (2015b) approach to laboratory host-range testing. *Chrysolina abchasica* will be closely monitored to test the prediction that native *Hypericum* species will not become permanent field hosts.

Host-range testing could potentially be further refined by developing a more rigorous basis for determining the amount of replication required to assess risk. Withers et al. (2013) used a range of statistical tools to investigate the risk that the buddleia leaf weevil *Cleopus japonicus* (Wingelmüller) (Coleoptera: Curculionidae) might attack native *Hebe speciosa* (A. Cunn.) Andersen (Lamiales: Plantaginaceae) plants. The power analyses performed by Withers et al. (2013) focused on trying to detect relatively rare events. For example, they calculated that ca. 300 replicates would be required to have a 80% chance of detecting survival if only 2% of *C. japonicus* larvae could develop to pupation on *H. speciosa*. This is about an order of magnitude higher than the amount of replication per test plant species currently used in NZ. However, the analysis by Paynter et al. (2015b) indicated that the lowest relative survival rate above which non-target attack was reported was 0.34 (i.e. percentage survival on the non-target plant was 34% of the survival level on the target weed; Fig. 1a Paynter et al. 2015b). The level of replication required to detect a risky candidate agent is therefore likely to be significantly lower than suggested by Withers et al. (2013), but will vary depending on the survival rate on the target plant. For example, assuming a threshold relative survival rate of 0.34, it will be necessary to detect a survival rate of ca. 27% on a test plant if the survival rate on the target weed is 80%. Intuitively it seems likely that current levels of replication are adequate, given that examples of unexpected non-target attack are rare (Suckling and Sforza 2014).

However, greater replication may be desirable to ensure reliable estimates of relative performance are generated when predicting whether a fundamental host plant is likely to be utilized in the field.

As noted by Louda et al. (2003), ecological studies can also refine risk, although there are relatively few examples worldwide of potentially risky agents being approved for release on the basis of ecological studies. The most common cases are where climate matching has indicated potential non-target hosts occur in regions with climates that are unsuitable for the candidate agent (e.g. Hasan and Delfosse 1995).

There is a risk that biocontrol agents could rapidly evolve altered use of fundamental hosts through quantitative genetic changes, although evidence is lacking (van Klinken and Edwards 2002). This hypothetical risk has resulted in at least one candidate agent being rejected. Manrique et al. (2014) demonstrated that rearing *Paectes longiformis* Pogue (Lepidoptera: Noctuidae), a candidate agent for *Schinus terebinthifolia* Raddi (Sapindales: Anacardiaceae) in Florida, exclusively on the native *Rhus aromatica* Aiton (Sapindales: Anacardiaceae) for multiple generations resulted in enhanced performance on the potential non-target plant. It is hard to predict whether there would be a selection pressure for *P. longiformis* to perform better on *Rhus aromatica* had *P. longiformis* been released. For example, *S. terebinthifolia* is an abundant weed and it may be unlikely that populations of *P. longiformis* could persist exclusively on *Rhus aromatica* for multiple generations. Another advantage of using quantitative host-range testing data is that evidence for rapid evolution could be obtained retrospectively by comparing the relative performance of agents collected from the non-target hosts with the original host-testing data or with agents collected from the original source population (Paynter et al. 2015b).

Parasitoids, predators and diseases

Parasitism

In NZ, ten out of 28 (35%) arthropod weed biocontrol agents surveyed were found to be hosts to 19 parasitoid species (Paynter et al. 2010). The majority of parasitoid species belong to the Hymenoptera, which are poorly described in NZ (Berry 2007), making predictions regarding the risk of future agents

being hosts to parasitoids problematic (Paynter et al. 2010). Nevertheless, a method for predicting the likelihood of parasitism was developed by Paynter et al. (2010), who found that parasitoid species richness on weed biocontrol agents in NZ was positively correlated to richness in the area of origin. However, only agents with native ‘ecological analogues’ (i.e. a native NZ insect that is taxonomically related to the agent, and has a similar lifestyle niche and feeds on the target weed) contributed significantly to this pattern. This ‘native analogue’ approach has subsequently been used to prioritize candidate biocontrol agents in NZ. For example, a potentially host-specific moth, *Lobesia coccophaga* Falkovitch (Lepidoptera: Tortricidae), was recently given low priority for biocontrol of Japanese honeysuckle *Lonicera japonica* (Thunb.) (Dipsacales: Caprifoliaceae), due to presence of native analogues (native tortricid moths) feeding on *L. japonica* in NZ that are likely to be hosts of parasitoids that are capable of attacking and potentially reducing the impact of *L. coccophaga* (Paynter et al. 2017).

Not all parasitized agents listed by Paynter et al. (2010) possess a native analogue. For example, some agents are parasitized by exotic parasitoids that have no known native hosts. Nevertheless, the analogue approach could be expanded as there is evidence that the presence of a parasitized ‘introduced analogue’ (defined here as an introduced herbivore that is taxonomically related to the subsequent agent, and has a similar lifestyle niche and feeds on the target weed or a congeneric plant) indicates the risk of any subsequent introductions being parasitized. For example *Procecidochares alani* introduced into NZ in 2001 to control *Ageratina riparia* (Regel) R.M. King and H. Rob. (Asterales: Asteraceae), is parasitized by *Megastigmus* sp. (Hymenoptera: Torymidae), which was already known to attack a congeneric agent *P. utilis*, which was introduced into NZ in 1958 to control *A. adenophora* (Spreng.) R.M. King and H. Rob. (Asterales: Asteraceae) (Paynter et al. 2010).

Preliminary investigation reveals that releasing agents that are analogues of already-released parasitized agents appears to be a relatively frequent occurrence. McFadyen and Jacob (2004) listed 54 international records of parasitism of weed biocontrol agents which contains eight (~15%) examples of parasitized agents which were released after a parasitized ‘introduced analogue’.

Predation

Predation is much harder to detect than parasitism as parasitoids can be reared, while predators generally have to be ‘caught in the act’ or their prey items detected using molecular techniques (e.g. Chen et al. 2000). Therefore, predation is likely to be under-recorded. In NZ, there are mostly anecdotal observations of predation on only 17 out of 39 (~43%) arthropod agents confirmed to have established by December 2014 (Supplementary information, Table S1).

The native analogue approach appears less useful for predicting predation, perhaps because most predators are generalists (Petráková et al. 2015). Nevertheless, there are two examples in NZ where introduced biocontrol agents are attacked by oligophagous predators that prey on analogous native hosts: the gorse spider mite *T. lintearius* is attacked by a native coccinellid beetle *Stethorus bifidus* (Kapur) (Coleoptera: Coccinellidae), which naturally attacks native *Tetranychus* species, feeding on native *Carmichaelia* species (Fabales: Fabaceae); the Scotch broom gall mite *Aceria genistae* Nalepa (Tribidiformes: Eriophyidae) is attacked by predatory mites that also occur in the galls of *Aceria carmichaeliae* Lamb (Tribidiformes: Eriophyidae) found on native brooms (*Carmichaelia* species), with the main predators being *Typhlodromus caudiglan* Schuster (Mesostigmata: Phytoseiidae) and *Zetzellia maori* González-Rodríguez (Tribidiformes: Stigmaeidae) (Mala 2013). Furthermore, the predators associated with *T. lintearius* and *A. genistae* in NZ are closely-related to predators which feed on these species in their native ranges indicating that native range surveys of natural enemies could help predict the food webs associated with species that possess analogous native species: in England, the main predator of *T. lintearius* was reported to be *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) (Kirby 2006) and, in France, a predatory phytoseiid mite *Typhlodromus pyri* Scheuten (Mesostigmata: Phytoseiidae) was commonly found preying on *A. genistae* (Q. Paynter, pers. obs.). Therefore, with hindsight, predation of *T. lintearius* and *A. genistae* in NZ was predictable and it could be argued that the potential impact of these predators was predictable as well: predation is considered the main reason why outbreaks of *T. lintearius* fail to persist in NZ (Peterson et al. 2000) yet

extremely damaging outbreaks of *A. genistae* have endured in NZ since it was introduced in 2008, perhaps because *A. genistae* mites are smaller than their phytoseiid predators so that there is a refuge from predation within the highly convoluted gall-like leaf curls (Z-Q Zhang, pers. comm.). In the native range, the status of both agents is similar to the situation in NZ: *Tetranychus lintearius* is considered to be uncommon in Europe (Kirby 2006; van Eynhoven 1967), whereas *A. genistae* is common in the Cévennes region of France, where it appears to be one of the few natural enemies capable of killing *Cytisus scoparius* (L.) Link (Fabales: Fabaceae) plants (Hosking 1990).

Larvae of endophytic feeders appear to be less susceptible to predation than exposed feeders. Arthropod weed biocontrol agents (listed in Supplementary information, Table S1) were classified as having endophytic (e.g. seed, or stem-borers, gall-formers, leaf-miners) or externally-feeding juvenile stages (including partially concealed leaf-tiers). Predation has been reported for only 5/21 (~24%) of endophytic agents released in NZ. By contrast, 12/18 (~67%) of externally-feeding agents have been reported to be subject to predation and the proportion of agents subject to predation varied significantly according to concealment (Supplementary information, Table S1; $P = 0.011$, Fischer’s exact test). Moreover, exposed feeders can be more prone to predation when honeydew-producing Hemiptera are present and attract predatory ants onto host plants (Paynter et al. 2012).

Impact of predation and parasitism

Parasitism was associated with biocontrol failure in NZ, with 8 of 15 (53%) unsuccessful agents being parasitized, while only one of nine successful agents was parasitized (Paynter et al. 2010). Five agent species were found to be heavily parasitized to an extent that is likely to significantly influence their efficacy: the old man’s beard leafminer, *Phytomyza vitalbae* Kaltenbach (Diptera: Agromyzidae), where combined parasitism and predation (attributed to eulophid parasitoids, which eat more prey than they parasitize) rates averaged at least 58%; *Tyria jacobaeae* L. (Lepidoptera: Erebididae) (up to 78% parasitism), *Zeuxidiplosis giardi* (Kieffer) (Diptera: Cecidomyiidae) (41% parasitism); *Procecidochares alani* Steyskaland (Diptera: Tephritidae) (68%

parasitism); and *P. utilis* Stone (Diptera: Tephritidae) (up to 100% parasitism) (Paynter et al. 2010).

Predation is considered to be reducing the efficacy of four agents: *Urophora solstitialis* L. (Diptera: Tephritidae), *Tortrix s.l. sp. chrysanthemoides*, *Urophora cardui* (L.) (Diptera: Tephritidae) and *T. lintearius* (Supplementary information, Table S1). Overall, at least nine agent species are therefore currently impacted by parasitism and/or predation to an extent where it is believed to significantly reduce their impacts on the target weed. This is a significant proportion of agents established in NZ and a major cause of agent failure: of the 39 arthropod weed biocontrol agent species confirmed to be established in NZ by 2014, 16 species are considered to contribute to complete or partial control of their target weeds. The impacts of four species are uncertain and the remaining 19 species are considered to be unsuccessful (Supplementary information, Table S1). Moreover, future surveys may demonstrate that predation has reduced the efficacy of other unsuccessful agents in NZ, such as *Monophadnus spinolae* (Klug) (Hymenoptera: Tenthredinidae), where the cause of failure is currently unknown (Supplementary information, Table S1). Therefore, prioritizing the release of agents that are likely to find enemy-free space (e.g. Fowler et al. 2010) could have a tangible effect on the success rate of weed biocontrol introductions, as well as reducing the risk of unwanted indirect impacts on native food webs.

Disease

Disease is a factor that has affected rearing programs in NZ (Paynter et al. 2015a) although there is little evidence to suggest that it negatively affects weed biocontrol agents in the field in NZ. However, there is increasing awareness that the effects of some diseases may be more subtle compared to the epizootics discussed by Goeden and Louda (1976). For example, a gregarine (sporozoan protozoan) gut parasite of the leaf beetle, *Neolema ogloblini* (Monrós) (Coleoptera: Chrysomelidae), discovered while still in containment, was not lethal but appeared to reduce beetle fecundity, longevity and general vigor, potentially compromising its biological control efficacy (Smith et al. 2013). This pathogen was eliminated from the culture prior to the release of *N. ogloblini*. Since 1984, permission to release agents from containment in NZ

has been made conditional on testing agent cultures for freedom of pathogenic organisms using light microscopy techniques (Paynter et al. 2016). Surveys are currently underway to investigate whether disease is present and impacting on weed biocontrol agent populations in the field.

Discussion

Host-specificity tests and predicting the risk of non-target attack

Paynter et al.'s (2015b) quantitative relative risk approach could provide regulatory authorities with a defensible decision-making mechanism and help ensure that correct decisions are made. Further analyses using datasets from other countries are desirable. For example, by 2010, 49 weed biocontrol agent species had been released in NZ (Fowler et al. 2010) of which only 23 species met the criteria for inclusion in Paynter et al.'s (2015b) analyses (i.e. during host-range testing they developed to adult on potential non-target plant species present in NZ and directed surveys had been conducted to investigate whether these fundamental host plants are also attacked in the field in NZ). By comparison, 94, 242 and 270 weed biocontrol agent species had been released in mainland USA, Australia and South Africa by 2004, 2012 and 2011 respectively (Coombs et al. 2004; Julien et al. 2012; Klein 2011). Much larger data sets from these countries could potentially be generated to (1) rigorously test the reliability of Paynter et al.'s (2015b) approach and (2) refine parameter estimates of the approach, thereby improving confidence when using the approach to predict the risk of non-target attack. Directed surveys to formally assess non-target attack in these countries would be required, before such analyses should proceed, due to the possibility that non-target attack has been under-reported in these countries.

The potential to expand this approach to predict the field host-range of plant pathogen weed biocontrol agents could also be explored. Results of plant pathogen specificity testing are commonly presented as categorical/qualitative damage scores, similar to those first proposed by Mortensen (1984). Globally, pathogens released for the biological control of weeds have apparently only ever caused damage to six non-

target species outdoors, yet those same agents damaged 107 non-target species in pre-release tests conducted indoors (Barton 2012). We therefore hypothesise that a relative risk method for determining the degree of resistance/susceptibility of test plants more quantitatively (for example, by quantifying the number of telia/teliospores on test and host plants) could help predict the field host-range of pathogen agents more reliably. As noted by Barton (2012), directed surveys for non-target damage from pathogens released as classical biological control agents are rare, reiterating the need for directed surveys as non-target attack may be underestimated.

Parasitoids, predators and diseases

Agents at the greatest risk of being attacked by parasitoids can be identified by the presence of analogues. Moreover, although specialist predators are rare, the risk they pose to candidate biocontrol agents is predictable, although the definition of what constitutes a native analogue may need to be broadened from that outlined by Paynter et al. (2010). Native analogues of the gorse spider mite and broom gall mite feed on plants in the same family as the target weeds, rather than the target weed itself.

Few studies have investigated food webs associated with weed biocontrol agents in both native and exotic habitats (Veldtman et al. 2011). The potential utility of using the analogue approach to predict predation might become more apparent if more food web association studies were conducted.

The analogue approach does not predict the level of parasitism or predation that an agent might be subjected to. Applying the approach uncritically might, therefore, result in a potentially effective agent being given an inappropriately low priority for introduction. An excellent suggestion for further refining this methodology is to determine the impact of parasitism on the analogue species, assuming that the candidate agent is likely to suffer a similar level of parasitism should it be released (Greg Wheeler, pers. comm.). Similarly, it may prove useful to determine the level or impact of parasitism or predation in the native range, for example using the techniques described by van Driesche et al. (1991) and Luck et al. (1988), as a potential predictor of the impact of natural enemies in the introduced range for species which possess an analogue.

It may also be informative if the utility of the analogue approach is investigated in other countries. Due to its isolated island status, some taxonomic groups are absent or of low diversity in NZ (Wallis and Trewick 2009). We hypothesize that introduced weed biocontrol agents introduced into continental areas, such as Australia, South Africa and the USA, may be more likely to encounter an analogous native species than agents released in NZ. Comparing agent performance in regions where analogues are present and regions where analogues are absent may be informative.

Finally, more detailed case studies and surveys are needed to investigate whether disease is an unrecognized cause of biocontrol failure and cause of indirect impacts. Not all jurisdictions make pathogen screening a condition for approval to release an agent from containment, so it may be informative to compare and contrast the incidence of disease in weed biocontrol agents in NZ and other countries where pathogen screening is not routinely performed (e.g. Australia; A.W. Sheppard, pers. comm.).

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