

# Predicting parasitoid accumulation on biological control agents of weeds

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## Summary

1. Natural enemies may reduce the effectiveness of weed biocontrol agents and can also cause environmental damage, for example to a shared native insect host through apparent competition. Indeed, successful biocontrol may rely on enemy-free space and avoidance of apparent competition in the area where the biocontrol agent is introduced.

2. We surveyed parasitism in 28 insects released for weed biocontrol in New Zealand (NZ). We reviewed the global literature and databases to complement this survey, and to collate records of these insects being parasitized in their area of origin. We also collated records of native insects that feed on weeds targeted for biocontrol in NZ to test Lawton's (1985) hypothesis that, to find enemy-free space, selected agents should 'feed in a way that is different' and 'be taxonomically distinct' from native herbivores in the introduced range.

3. We found that 19, mostly native, parasitoid species attack 10 weed biocontrol agents in NZ, of which 15 were confined to five agents that possessed 'ecological analogues', defined as a native NZ insect that belongs to the same superfamily as the agent and occupies a similar niche on the target weed. Parasitoid species richness in NZ was positively correlated to richness in the area of origin. However, only agents with ecological analogues contributed significantly to this pattern.

4. A review of NZ weed biocontrol programmes indicated that parasitism is significantly associated with the failure of agents to suppress weed populations.

5. *Synthesis and applications.* Although our conclusions are based on an unavoidably limited data set, we conclude that biocontrol agents that escape attack from parasitoids are more likely to suppress weed populations and should be less likely to have significant indirect non-target effects in food webs. Biocontrol practitioners can reduce the chance of weed biocontrol agents attracting species-rich parasitoid faunas after introduction by (i) selecting agents that have species-poor parasitoid faunas in their area of origin, and/or (ii) avoiding agents that have 'ecological analogues' awaiting them in the introduced range.

**Key-words:** apparent competition, enemy-free space, food web, non-target effects, parasitoid, weed biocontrol agent

## Introduction

Two-thirds of weed biocontrol agents that establish fail to suppress their target weed (McFadyen 1998), and this failure can be a result of natural enemies (Goeden & Louda 1976). These natural enemies, such as parasitoids may cause environmental damage, for example to a shared native insect host through apparent competition (Carvalho *et al.* 2008).

Concerns for environmental safety have triggered tighter regulation of biocontrol world-wide (Sheppard *et al.* 2003). In

New Zealand (NZ), biocontrol introductions are administered by the Environmental Risk Management Authority, which evaluates the risks, costs and benefits of introducing biocontrol agents (Barratt & Moeed 2005), including their potential impacts on food webs. Information regarding the potential parasitoids of a candidate biocontrol agent is, however, often unreliable. For example, the parasitic Hymenoptera of the NZ biogeographic region are poorly known (Berry 2007). Biocontrol practitioners have, therefore, sought to make predictions by identifying factors that influence parasitism. For example, Harris (1991) argued that gall midges should be given a low priority as biocontrol agents because they readily

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acquire parasitoids, and Hill & Hulley (1995) noted that parasitism varied according to level of concealment. A broad analysis showed that the numbers of primary parasitoid species acquired by insect herbivores in their introduced range are correlated with the numbers of primary parasitoid species attacking them in their area of origin (Cornell & Hawkins 1993). So, should herbivorous insects with a high diversity of natural enemies in their area of origin be passed over as potential weed biocontrol agents? Paradoxically, weed biocontrol practitioners argue that many herbivorous insects are kept rare by natural enemies in their areas of origin and can become excellent weed biocontrol agents in the 'enemy-free space' of the introduced range (Strong, Lawton & Southwood 1984; Hunt-Joshi, Root & Blossey 2005). Furthermore, agents that are kept rare in their area of origin may be more effective because their target weeds have had little selection to evolve resistance to them (Myers, Higgins & Kovacs 1989).

Lawton (1985) stated that enemy-free space and avoidance of apparent competition in the introduced range may be critical for weed biocontrol agent success and recommended that selected agents should 'feed in a way that is different' and 'be taxonomically distinct' from native herbivores in the introduced range.

We addressed these issues by surveying the parasitoid fauna of weed biocontrol agent species in NZ and testing the following hypotheses:

- 1 Parasitoid richness increases with the time that an agent has been present in the introduced region.
- 2 Weed biocontrol agents that have rich parasitoid complexes in their area of origin should accumulate more parasitoid species in the introduced range than species which have no or few parasitoids that attack them in their area of origin.
- 3 Agents that 'feed in a way that is similar' and are 'taxonomically close' to the native fauna should be susceptible to parasitism.
- 4 Parasitism has reduced the effectiveness of weed biocontrol agents in NZ.

## Materials and methods

### LITERATURE REVIEW AND SURVEYS

Information regarding parasitism (in the area of origin and in NZ) of insect species introduced into NZ for the biological control of invasive weeds, and their ability to suppress weeds in NZ, was obtained by reviewing published literature and conducting field surveys.

Differences in sampling effort may confound comparisons between regions because sampling effort should correlate with parasitoid richness on host species. We, therefore, followed Cornell & Hawkins (1993) example by compiling records from single studies (generally those conducted in weed biocontrol programmes), rather than summary lists, which may be inflated by the inclusion of rare or unusual host-records. For example, Cameron (1935) compiled literature records of 12 primary parasitoids that attack the cinnabar moth *Tyria jacobaeae*, but only reared seven primary parasitoid species from English material, implying that the other parasitoids were either very rare or only rarely attack *T. jacobaeae*.

Surveys in NZ were performed during 2003–2009 (1–14 sample localities per agent, depending on availability). The life stages surveyed matched the stages from which parasitoids were reared in the area of origin: larvae (or nymphs) of all species and pupae of most species were collected, while eggs and adults were surveyed less extensively (Table 1). Larvae and pupae of external feeders were hand-collected. Larvae and pupae of gall-formers, leaf-miners, seed and stem-borers were sampled by collecting infested plant parts. With root and rosette-borers, plants were dug up and potted for subsequent rearing. Agents were reared in sealed, ventilated containers that prevented any emerging parasitoids from escaping. The numbers of biocontrol agents and parasitoids that emerged were recorded until emergences ceased. Species which diapause as pupae were stored in a cool room (c. 10 °C and natural day length for 3–4 months), prior to returning them to room temperature and allowing adults and, if present, parasitoids to emerge the following year. Parasitoids were identified to genus or species (Table 2).

### DEFINITION OF AN ECOLOGICAL ANALOGUE

We defined an ecological analogue as a native NZ insect that (i) is taxonomically related to the agent (see 'Taxonomy' below); (ii) has a similar lifestyle niche; and (iii) feeds on the target weed. We used the feeding guild and taxonomic criteria of Lawton (1985) plus a third criterion: the native analogue had to have been recorded feeding on the target weed. Lawton (1985) used this third criterion implicitly as well because the target weed he discusses is itself a native plant and he is referring to analogues in the native insect herbivore fauna on that plant. To identify ecological analogues, we consulted the Plant-SyNZ™ data base (<http://www.crop.cri.nz/home/plant-synz/database/databasehome.php>) and NZ weed faunal surveys (Syrett 1993; Winks, Fowler & Smith 2004) to locate records of native NZ insects attacking introduced weeds in NZ.

The feeding guild and taxonomic criteria broadly reflect knowledge regarding host selection by parasitoids: most parasitoids are oligophagous, attacking related taxa of hosts (Strand & Obrycki 1996), whereas others attack hosts in a range of higher level taxonomic groups that share feeding niches/guilds (Messing 2001). The third criterion of feeding on the target host encompasses several parasitoid behaviour and spatial co-occurrence factors. Many parasitoids locate hosts by responding to visual and chemical cues provided by the host plants of their prey species (Eben *et al.* 2000); occurrence of analogues on the same individual host plants may just give native parasitoids close physical proximity to introduced herbivores; at larger scales, if the analogue's utilization of the target weed is widespread then native parasitoids are likely to have overlapping geographic ranges with the introduced biocontrol agents. Specifications included in our definition of an ecological analogue are:

- 1 Feeding guild: To allow comparison with previous studies, we classified insects into guilds based on the larval feeding habits using Cornell & Hawkins (1993) categories, plus one additional category (root-feeder).
- 2 Taxonomy: Only one agent was congeneric with a native insect species. Therefore, we tested whether defining the ecological analogue within the same family, superfamily or order as the agent, explained the most variance in our analyses (below).

### ANALYSIS

We used data from the literature review and field surveys to test the hypothesis that introduced herbivores should acquire parasitoids over time by performing a Spearman's rank correlation to investigate

**Table 1.** Numbers of parasitoid species attacking weed biocontrol agents in NZ ( $P_{NZ}$ ) and in their area of origin ( $P_{AO}$ ), and the numbers of individuals reared during field surveys in NZ

Biocontrol agent (and NZ ecological analogues)	Agent feeding guild	Year of release in NZ	$P_{NZ}$ $P_{AO}$		Stages reared	No. of agents reared	No. of parasitoids reared	Maximum % mortality due to parasitoids
			$P_{NZ}$	$P_{AO}$				
<i>Agasicles hygrophila</i>	E	1982	0 <sup>a</sup>	1 <sup>b</sup>	ELPA	916	0	0
<i>Agonopterix umbellana</i>	E	1990	0	10 <sup>c</sup>	L	431	0	0 (62) <sup>c</sup>
<i>Arcola malloi</i>	SB	1982	0	6 <sup>d</sup>	L	48	0	0 (38.5) <sup>d</sup>
<i>Arytainilla spartiophila</i>	E	1993	0	0 <sup>e</sup>	NA	200	0	0 (0) <sup>e</sup>
<i>Aulacidea subterminalis</i>	GF	1999	0	2 <sup>f</sup>	LP	153	0	0 (42.9) <sup>f</sup>
<i>Botanophila jacobaeae</i>	FB	1936	0 <sup>g</sup>	7 <sup>h</sup>	LP	2842 <sup>pp</sup>	0 <sup>pp</sup>	0 (51) <sup>h</sup>
<i>Bruchidius villosus</i>	SB	1987	1 <sup>i</sup>	4 <sup>j</sup>	ELPA	7313	511	18.4 (56.4) <sup>j</sup>
<i>Chrysolina hyperici</i>	E	1943	0	5 <sup>k</sup>	LA	226	0	0
<i>Chrysolina quadrigemina</i>	E	1963	0	2 <sup>l</sup>	EL	121	0	0 (40) <sup>l</sup>
<i>Cydia succedana</i>	SB	1992	0	?	L	613	0	0
<i>Exapion ulicis</i>	SB	1931	1 <sup>i</sup>	6 <sup>m</sup>	LP	757	9	2.3 (82.3) <sup>m</sup>
<i>Lema cyanella</i>	E	1983	0	2 <sup>n</sup>	LA	121	0	0
<i>Lochmaea suturalis</i>	E	1997	0 <sup>o</sup>	2 <sup>p</sup>	ELPA	311 <sup>pp</sup>	0 <sup>pp</sup>	0 (53.2) <sup>p</sup>
<i>Longitarsus jacobaeae</i>	RF	1983	0	1 <sup>q</sup>	LP	1054	0	0
<i>Macrolabis pilosellae</i>	GF	2002	0	1 <sup>r</sup>	LP	99	0	0 (80.3) <sup>r</sup>
<i>Pempelia genistella</i> ( <i>Uresiphita polygonalis</i> <sup>S</sup> )	E	1998	1	1 <sup>t</sup>	L	60	1	1.6
<i>Phytomyza vitalbae</i> ( <i>Phytomyza clematadi</i> <sup>U</sup> )	LM	1996	8 <sup>u</sup>	13 <sup>v</sup>	LP	838	103	58 ('high') <sup>v</sup>
<i>Procecidochares utilis</i>	GF	1958	1 <sup>w</sup>	6 <sup>x</sup>	LP	83	126	100
<i>Procecidochares alani</i>	GF	2001	1	?	LP	216	105	68.2
<i>Rhinocyllus conicus</i>	FB	1973	1 <sup>y</sup>	7 <sup>z</sup>	ALP	2849	0	16.8 <sup>y</sup> (71) <sup>z</sup>
<i>Sericothrips staphylinus</i> ( <i>Thrips obscuratus</i> <sup>AA</sup> )	E	1990	0	0 <sup>bb</sup>	NA	1500	0	0 (0) <sup>bb</sup>
<i>Tortrix</i> s.l. sp. ' <i>chrysanthemoides</i> ' ( <i>'Cnephasia' jactatana</i> ; <i>Ctenopseustis obliquana</i> <sup>CC</sup> )	LR	2007	3	6 <sup>dd</sup>	EL	303	23	14.7
<i>Trichosirocalus horridus</i>	RB	1979	0 <sup>ee</sup>	4 <sup>ff</sup>	LPA	210	0	0 (< 1) <sup>ff</sup>
<i>Tyria jacobaeae</i> ( <i>Nyctemera annulata</i> <sup>GG</sup> )	E	1929	3 <sup>hh</sup>	7 <sup>ii</sup>	LP	265	0	78 (60) <sup>ii</sup>
<i>Urophora cardui</i>	GF	1994	0	4 <sup>jj</sup>	LP	342	0	0 (100) <sup>kk</sup>
<i>Urophora solstitialis</i>	GF	1990	0	2 <sup>ll</sup>	LP	590	0	0
<i>Urophora stylata</i>	GF	1999	0	3 <sup>mm</sup>	LP	638	0	0 (29.2) <sup>mm</sup>
<i>Zeuxidiplosis giardi</i>	GF	1961	1 <sup>nn</sup>	5 <sup>l</sup>	LP	390	175	40.8 (87) <sup>l</sup>

Ecological analogues are for native insects in the same superfamily as the agent (see text for details);  $P_{NZ}$  combines published literature and current surveys. Agent feeding guild: E, external feeder; SB, stem-borer; GF, gall-former; FB, flower-borer; RF, root-feeder; LM, leaf-miner; LR, leaf-roller; RB, rosette-borer. Stages reared: E, eggs; L, larvae; N, nymphs; P, pupae; A, adults. Mortality includes both mortality resulting from parasitism and from host-feeding by parasitoids and is the maximum percentage recorded in the published literature or the current surveys; figures in parentheses are the values recorded in the area of origin, if available.

<sup>a</sup>Stewart (1996); <sup>b</sup>Maddox (1968); <sup>c</sup>Hill *et al.* (1995); <sup>d</sup>Vogt *et al.* (1992); <sup>e</sup>Watmough (1968); <sup>f</sup>G. Grosskopf, (personal communication); <sup>g</sup>Hoy (1958, 1960); <sup>h</sup>Miller (1970); <sup>i</sup>Syrett *et al.* (1999); <sup>j</sup>Parnell (1966); <sup>k</sup>Cox (2007); <sup>l</sup>Wilson (1943); <sup>m</sup>Davies (1928); <sup>n</sup>Schmitt (1988); <sup>o</sup>Peterson *et al.* (2004); <sup>p</sup>Waloff (1987); <sup>q</sup>Windig (1991); <sup>r</sup>Grosskopf & Murphy (1999); <sup>s</sup>Leen (1995); <sup>t</sup>Quicke & Shaw (2004); <sup>u</sup>Paynter *et al.* (2008a); <sup>v</sup>Hill *et al.* (2001); <sup>w</sup>Hill (1989); <sup>x</sup>Bess & Haramoto (1959); <sup>y</sup>Murray *et al.* (2002); <sup>z</sup>Gassmann & Louda (2001); <sup>aa</sup>Teulon & Penman (1990); <sup>bb</sup>R. L. Hill (personal communication); <sup>cc</sup>Winks *et al.* (2004); <sup>dd</sup>Scott & Brown (1992); <sup>ee</sup>Barratt *et al.* (1997); <sup>ff</sup>Boldt & Campobasso (1981); <sup>gg</sup>Gaskin (1966); <sup>hh</sup>Helson (1974); <sup>ii</sup>Cameron (1935); <sup>jj</sup>Schlumprecht (1989); <sup>kk</sup>Eber & Brandl (1994); <sup>ll</sup>Zwölfer & Arnold-Rinehart (1994); <sup>mm</sup>Redfern *et al.* (1992); <sup>nn</sup>Syrett (1989).

Numbers of agents reared are from the current survey except: <sup>oo</sup>published literature only; <sup>pp</sup>published literature and current surveys combined.

whether the parasitoid richness (i.e. number of parasitoid species reared per species) of weed biocontrol agents in NZ ( $P_{NZ}$ ) increased according to their residence times (time since the biological control agent was introduced). To test the hypothesis that species should be more likely to accumulate parasitoids in NZ if they (i) have a high diversity of parasitoids in their area of origin, and (ii) possessed an ecological analogue, we performed an analysis of covariance by correlating parasitoid richness in the area of origin ( $P_{AO}$ ) with parasitoid richness in NZ ( $P_{NZ}$ ) and also using the grouping factor 'ecological analogue present', with two values, yes or no. Two agents for which native range parasitism data was lacking (Table 1) were excluded from this analysis.

## Results

### LITERATURE REVIEW AND FIELD SURVEYS

We found literature records for and/or we surveyed 28 of the 30 insects established in NZ for the biological control of weeds, as of December 2008 (the exceptions were *Cleopus japonicus* Wingelmüller and *Platyptilia isodactyla* Zeller that have only very recently established). The details are summarized in Table 1 and below.

**Table 2.** Parasitoid species reared from NZ weed biocontrol agents

Parasitoid	Status	Host(s)
<i>Pteromalus sequester</i>	Accidental introduction	<i>Exapion ulicis</i> ; <i>Bruchidius villosus</i>
<i>Aucklandella</i> sp.	Native	<i>Pempelia genistella</i>
<i>Chrysocharis</i> sp.	Native	<i>Phytomyza vitalbae</i>
<i>Diglyphus isaea</i>	Biocontrol agent	<i>Phytomyza vitalbae</i>
<i>Neochrysocharis</i> 'sp. 1'	Native	<i>Phytomyza vitalbae</i>
<i>Neochrysocharis</i> 'sp. 2'	Native	<i>Phytomyza vitalbae</i>
<i>Opius</i> sp. 'PC'	Native	<i>Phytomyza vitalbae</i>
<i>Opius cinerariae</i>	Native	<i>Phytomyza vitalbae</i>
<i>Pnigalio soemius</i>	Accidental introduction	<i>Phytomyza vitalbae</i>
<i>Proacrias</i> 'sp.'	Native	<i>Phytomyza vitalbae</i>
<i>Megastigmus</i> 'sp.'	Native <sup>a</sup>	<i>Procecidochares utilis</i> ; <i>P. alani</i>
<i>Microctonus aethioides</i>	Biocontrol agent	<i>Rhinocyllus conicus</i>
<i>Trichogrammatoidea</i> sp.	Native	<i>Tortrix s.l.</i> sp. <i>chrysanthemoides</i>
<i>Dolichogenidea tasmanica</i>	Native <sup>a</sup>	<i>Tortrix s.l.</i> sp. <i>chrysanthemoides</i>
<i>Trigonospila brevifascies</i>	Biocontrol agent	<i>Tortrix s.l.</i> sp. <i>chrysanthemoides</i>
<i>Echthromorpha intricatoria</i>	Native <sup>a</sup>	<i>Tyria jacobaeae</i>
<i>Pales casta</i>	Native	<i>Tyria jacobaeae</i>
<i>Pales nyctemeriana</i>	Native	<i>Tyria jacobaeae</i>
<i>Torymoides</i> 'sp.'	Native	<i>Zeuxidiplosis giardi</i>

<sup>a</sup>Regarded as native by taxonomists, but probably recently self-introduced from Australia (see text for details).

### Literature records of parasitism in New Zealand

Syrett *et al.* (1999) reported that the broom seed-beetle *Bruchidius villosus* and gorse seed-weevil *Exapion ulicis* were parasitized by an accidentally introduced parasitoid *Pteromalus sequester*, which also parasitizes both species in their native European ranges.

Barratt *et al.* (1997) investigated non-target attack by *Microctonus aethioides*, a parasitoid introduced into NZ for biological control of the pasture pest weevil *Sitona discoideus*, and found that it attacked adult thistle receptacle weevils *Rhinocyllus conicus*, but did not attack the thistle crown weevil *Trichosirocalus horridus*.

The devil weed gall-fly *Procecidochares utilis* pupae were reported to be parasitized by a wasp *Megastigmus sp.* in 1972, 14 years after the introduction of *P. utilis* (Hill 1989). It is the same species reported to parasitize *P. utilis* in Australia, the assumed origin of *Megastigmus sp.* populations in NZ (Hill 1989).

Three parasitoids attack *T. jacobaeae* in NZ (Helson 1974); an ichneumonid *Echthromorpha intricatoria* attacks the pupae and two native tachinid flies *Pales (Cerosomyia) casta* and *P. nyctemeriana* attack as much as 53–78% of the larvae (Miller 1970). *Echthromorpha intricatoria* was first recorded in NZ in 1915 (Gourlay 1964) and is native to Australia. Both *P. casta* and *E. intricatoria* also attack the related native moth *Nyctemera annulata* (Helson 1974), which occupies a similar

niche to *T. jacobaeae* on native *Senecio* spp. and also attacks ragwort *Jacobaea vulgaris* Gaertn. in NZ.

St John's wort gall midge *Zeuxidiplosis giardi* larvae were parasitized by *Torymoides sp.* (Syrett 1989) that is probably native (J. A. Berry, pers. comm.). Torymid wasps attack native NZ gall midges, e.g. *Dasyneura hebefolia* is a host of *Dimeromicrocrus* (= *Torymoides*) sp. (Valentine 1967).

### Surveys

No new cases of parasitism were discovered on previously surveyed biocontrol agent species. However, four biocontrol agents, not previously surveyed, were found to be parasitized. An ichneumonid wasp (*Aucklandella* sp.) was reared from silken tents containing gorse hard shoot moth *Pempelia genistella* Duponchel larvae. Little is known about *Aucklandella* sp., although Berry (1990) reared *Aucklandella* sp. from the silken tents of a native moth *Hierodoris atychioides*. Mist flower gall-fly *Procecidochares alani* Steyskal was parasitized by *Megastigmus sp.*, which also attacks *P. utilis* in NZ (Hill 1989). Boneseed leafroller *Tortrix s.l.* sp. *chrysanthemoides* eggs were parasitized by a wasp *Trichogrammatoidea* sp. Two native species of *Trichogrammatoidea* are known from NZ including *T. bactrae*, which has been reared from *Epiphyas postvittana* eggs, while other, unidentified material has been reared from eggs of several moths including *Planotortrix excessana* (Noyes & Valentine 1989). *Tortrix s.l.* sp. *chrysanthemoides* larvae were parasitized by *Trigonospila brevifascies* Hardy and a braconid wasp *Dolichogenidea tasmanica* (Cameron). *Trigonospila brevifascies* was deliberately introduced from Australia to control tortricid orchard pests (Thomas 1975) and attacks various non-target hosts (Munro & Henderson 2002); *D. tasmanica* is self-introduced (Munro & Henderson 2002). Finally, six native (eulophid and braconid) and two exotic eulophid parasitoids were reared from old man's beard leaf-miner *Phytomyza vitalbae* larvae and pupae (previously reported in Paynter *et al.* 2008a). Five of the native parasitoids also attack a closely related native leaf-miner *Phytomyza clematadi* (Paynter *et al.* 2008a). The exotic parasitoids were: *Pnigalio soemius* (misidentified previously as *P. pectinicornis*), which was accidentally introduced c. 1950 with its host, the oak leaf-miner (Thomas & Hill 1989) and *Diglyphus isaea*, which was deliberately introduced to control exotic leaf-miner pests (McGregor 1989). Parasitism of *P. vitalbae* was relatively low (6%; Paynter *et al.* 2008a). However, more larvae are killed by female eulophids host-feeding than by parasitism (Hill, Wittenberg & Gourlay 2001) and c. 50% of *P. vitalbae* mines were subject to predation (Paynter *et al.* 2008a).

No obligate hyperparasitoids were reared or mentioned in literature records of parasitism in NZ. Parasitoids assumed to be rearing contaminants are listed in Table S1 (Supporting information).

### ANALYSIS OF FACTORS ASSOCIATED WITH PARASITISM

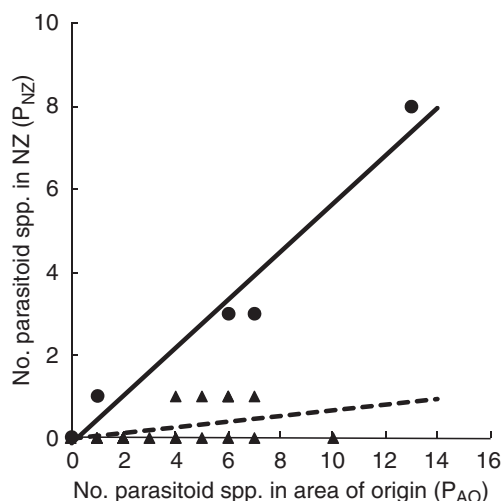
Nineteen, mostly native, parasitoid species were reared from 10 of the 28 biocontrol agent species surveyed. P<sub>NZ</sub> was not

correlated to years since agent introduction (Spearman's rank correlation,  $r_s = 0.064$ , d.f. = 26,  $P = 0.748$ ).

Defining an ecological analogue as a native insect in the same superfamily as a biological control agent, resulted in the recognition of five agents with ecological analogues (Table 1) that were attacked by 15 of the 19 parasitoids identified (Table 2). We assume that species that are not parasitized in the area of origin are unlikely to be parasitized in the introduced range, regardless of the presence of an analogue. A Fisher's exact test, therefore, examined the difference between the categories 'analogue present AND parasitized in area of origin' (Y/N) and parasitized in NZ (Y/N) and indicated the associations between these categories was non-random ( $P = 0.0088$ ). All four species that possessed both an analogue and were parasitized in their area of origin were parasitized in NZ, compared with only 5 of the remaining 22 species [two agents for which native range parasitism data was lacking (Table 1) were excluded from this analysis].

The analysis of covariance explained 92.4% of the variance in parasitoid richness in NZ ( $P_{NZ}$ ), which was positively correlated to richness in the area of origin ( $P_{AO}$ ; ANCOVA  $F_{1,22} = 145.5$ ,  $P < 0.001$ ), but only agents with ecological analogues contributed significantly to this pattern (Fig. 1; ANCOVA on effect of analogue presence:  $F_{1,22} = 91.77$ ,  $P < 0.001$ ;  $P_{AO}$ /analogue interaction;  $F_{1,22} = 69.93$ ,  $P < 0.001$ ). The same relationships were significant when we omitted the potentially influential *P. vitalbae* data point: ANCOVA  $P_{AO}$ :  $F_{1,21} = 18.87$ ,  $P < 0.001$ ; effect of analogue presence:  $F_{1,21} = 49.40$ ,  $P < 0.001$ ;  $P_{AO}$ /analogue interaction:  $F_{1,21} = 21.57$ ,  $P < 0.001$ .

Defining an ecological analogue as a native insect within the same family as the biocontrol agent excluded *P. genistella/Uresiphita polygonalis* (Felder) (Table 1) and explained marginally less variance (91.9%). The same relationships were



**Fig. 1.** Number of parasitoid species attacking weed biocontrol agents in New Zealand ( $P_{NZ}$ ) vs. in their areas of origin ( $P_{AO}$ ) for agents categorized as having a native analogue in same insect superfamily (see text for details) either present in NZ (circles, solid line;  $P_{NZ} = 0.577 * P_{AO} - 0.116$ ) or absent (triangles, dashed line;  $P_{NZ} = 0.068 * P_{AO} - 0.022$ ).

significant:  $P_{NZ}$  was positively correlated to  $P_{AO}$  (ANCOVA  $F_{1,22} = 135.58$ ,  $P < 0.001$ ; effect of analogue presence  $F_{1,22} = 78.85$ ,  $P < 0.001$ ;  $P_{AO}$ /analogue interaction  $F_{1,22} = 70.33$ ,  $P < 0.001$ ).

Defining an ecological analogue as a native insect within the same order as the biocontrol agent recognized 6 agents with ecological analogues (the 'superfamily analogues' listed in Table 1 plus *Agonopterix umbellana* (F.) due to the presence of several native tortricid leafroller species that feed on gorse in NZ) and explained much less variance (57.5%).  $P_{NZ}$  was again positively correlated to  $P_{AO}$  (ANCOVA  $F_{1,22} = 26.03$ ,  $P < 0.001$ ), as was the effect of analogue presence (ANCOVA  $F_{1,22} = 7.23$ ,  $P < 0.05$ ), but the  $P_{AO}$ /analogue interaction was not significant (ANCOVA  $F_{1,21} = 3.63$ , NS).

#### IMPACT OF PARASITISM

We reviewed the success of biocontrol programmes and of individual agents in NZ, in relation to parasitism (Table 3). Excluding programmes that are too recent to assess, nine insect agents are classified as successful, or partially successful, of which only one is parasitized, while 8 of the 15 insects classified as unsuccessful are parasitized (Table 3). A one-tailed Fisher's exact test confirmed the hypothesis that agent success was negatively associated with parasitism ( $P = 0.048$ ).

#### Discussion

The lack of correlation between parasitoid richness and residence time indicates that, as previously noted from South Africa (Hill & Hulley 1995), susceptible weed biocontrol agents rapidly accumulate parasitoids. Our analyses indicate that ecological analogues are a major source of parasitoids capable of rapidly colonizing novel biocontrol agent hosts. Agents that are heavily parasitized in their areas of origin may, therefore, find enemy-free space after introduction if they lack ecological analogues in the herbivore fauna they are introduced into. If analogues exist, however, then weed biocontrol practitioners may do well to avoid agents that are parasitized in their areas of origin: these species are likely to accumulate parasitoids, potentially reducing their performance and creating the possibility of indirect non-target impacts in food webs (e.g. Willis & Memmott 2005). Analogues could be identified without substantially increasing the operating costs of a weed biocontrol programme because target weeds should be surveyed in the introduced range during the early stages of a biological control programme (Wapshere, Delfosse & Cullen 1989).

Compared with successful agents, a high proportion of agents that have failed to suppress their target weeds in NZ are parasitized. Our conclusions, however, are based on an unavoidably limited data set and the relative importance of parasitism as a key factor for biocontrol failure requires further study. For example, Hawkins, Thomas & Hochberg (1993) noted that parasitoids that kill fewer than c. 40% of their hosts rarely control that host and few NZ weed biocontrol agents were parasitized to that extent (Table 1). Our surveys, however, were designed to determine parasitoid diversity.

Table 3. Success of weed biocontrol agents confirmed established in NZ by December 2008

Target weed	Agent(s) to which success attributed	Other agent(s) released	Notes
Successful programmes			
Heather <i>Calluna vulgaris</i> (L.) Hull	<i>Lochmaea suturalis</i> Thomson		Considered an incipient success: heather patches are being killed by <i>L. suturalis</i> outbreaks at several localities <sup>a</sup>
Mist flower <i>Ageratina riparia</i> R.M. King & H. Rob.	<i>Entyloma ageratinae</i> Barreto and Evans	<i>Procecidochares alani</i> <sup>a</sup>	<i>E. ageratinae</i> destroyed mist flower stands before <i>P. alani</i> impact was measured <sup>d</sup>
Ragwort <i>Jacobaea vulgaris</i> Gaertn.	<i>Longitarsus jacobaeae</i>	<i>Botanophila jacobaeae</i> <i>Tyria jacobaeae</i> <sup>b</sup>	In most regions, <i>L. jacobaeae</i> controls ragwort <sup>c</sup> . Asynchrony with host plant limits <i>B. jacobaeae</i> <sup>c</sup> . <i>T. jacobaeae</i> outbreaks are not sustained due to parasitism and predation <sup>e</sup>
St John's wort <i>Hypericum perforatum</i> L.	<i>Chrysolina hyperici</i> <i>C. quadrigemina</i>	<i>Zeuxidiplois giardi</i> <sup>a</sup>	Complete control due to <i>Chrysolina</i> beetles <sup>b</sup> . <i>Z. giardi</i> is highly localized around Nelson (South Island) <sup>f</sup>
Partially successful programmes			
Alligator weed <i>Alternanthera philoxeroides</i> Griseb.	<i>Agasicles hygrophila</i> <i>Arcola malloi</i>		Good control of weed floating in still water, but not terrestrial weed <sup>g</sup>
Mexican Devil weed <i>Ageratina adenophora</i> (Spreng.) King & H. Rob.	<i>Cercospora eupatorii</i> Peck	<i>Rhinocyclus conicus</i> <sup>a</sup>	Relative importance of agents is unknown but <i>P. utilis</i> has declined due to parasitism <sup>k</sup>
Nodding thistle <i>Carduus nutans</i> L.	<i>Proceidochares utilis</i> <sup>*</sup> <i>Trichosirocaltus horridus</i> <i>Urophora solstitialis</i>		Models <sup>l</sup> indicate that <i>T. horridus</i> and <i>U. solstitialis</i> are responsible for partial success <sup>h</sup>
Long-term programmes considered unsuccessful to date			
California thistle <i>Cirsium arvense</i> (L.) Scop.			
Gorse <i>Ulex europaeus</i> L.		<i>Lema cyanella</i> <i>Urophora cardui</i> <i>Agonopterix umbellana</i> <i>Cydia succedana</i> <i>Exapion ulicis</i> <sup>a</sup> <i>Pempelia genistella</i> <sup>b</sup> <i>Sericothrips staphylinus</i> <i>Tetranychus lintearius</i> Dufour <i>Phytomyza vitalbae</i> <sup>b</sup> <i>Phoma clematidina</i> Thüm.) Boerema <i>Arytainilla spartiophila</i> <i>Bruchidius villosus</i> <sup>a</sup>	<i>L. cyanella</i> is confined to one locality <sup>m</sup> . Palatable <i>U. cardui</i> stem galls are eaten by sheep and cattle, limiting its abundance <sup>n</sup> <i>C. succedana</i> and <i>E. ulicis</i> are ineffective because they do not attack the autumn/winter seed crop <sup>o</sup> . <i>T. lintearius</i> outbreaks do not persist due to predation <sup>o</sup> ; <i>P. genistella</i> is rare and highly localized. <i>A. umbellana</i> and <i>S. staphylinus</i> are abundant at some localities, but their impacts are unknown
Old Man's Beard <i>Clematis vitalbae</i> L.			Insufficient damage for control <sup>p</sup>
Scotch broom <i>Cytisus scoparius</i> (L.) Link			<i>A. spartiophila</i> impact is minor, possibly due to predation. <i>B. villosus</i> destroys c. 70% of seed at early release sites, which is insufficient to control broom <sup>c</sup>
Ongoing programmes too early to assess success			
Boneseed <i>Chrysanthemoides monilifera</i> (L.) Norlindh		<i>Tortrix s.l. sp. chrysanthemoides</i> <sup>b</sup>	Patchy establishment on the North Island; no establishment on the South Island despite multiple releases
Hieracium <i>Pilosella officinarum</i> (L.) F.W.Schultz & Sch.Bip.		<i>Aulacidea subterminalis</i> <i>Macrolabis pilosellae</i> <i>Urophora stylata</i>	Impact of agents not measured, they are common at some early release sites
Scotch thistle <i>Cirsium vulgare</i> (Savi) Ten.			Impact not measured

Successful programmes: no other control methods required where biocontrol agents are well established; partially successful programmes: substantial biocontrol impacts, but other control options still required. Long-term programmes: first agents released > 10 years ago; programmes too early to assess success: first agents released < 10 years ago.

<sup>a</sup>Parasitized; <sup>b</sup>Parasitized and ecological analogue present. *Entyloma ageratinae*, *Cercospora eupatorii* and *Phoma clematidina* are fungal pathogens, *Tetranychus lintearius* is a mite. Note that *Cleopus japonicus* and *Platyptilia isodactyla* are excluded as they were not surveyed for parasitoids.

<sup>c</sup>Landcare Research, unpublished data; <sup>d</sup>Barton et al. (2007); <sup>e</sup>Gourlay et al. (2008); <sup>f</sup>Dymock (1985); <sup>g</sup>Miller (1970); <sup>h</sup>Fowler et al. (2000); <sup>i</sup>Syrett (1989); <sup>j</sup>Roberts & Sutherland (1989); <sup>k</sup>Hill (1989); <sup>l</sup>Shea & Kelly (2004); <sup>m</sup>Gourlay (2004); <sup>n</sup>Paynter et al. (2008b); <sup>o</sup>Peterson et al. (2000); <sup>p</sup>Paynter et al. (2006).

Percentage parasitism samples are unreliable indicators of total parasitoid impact per host generation and the meticulous methods required for accurate estimates (Van Driesche *et al.* 1991) were beyond the scope of this study.

In addition to their relevance to biocontrol, our findings have implications for assessing the biosecurity risk posed by accidental introductions of insect herbivores. We hope that the results from this study will encourage researchers to test our findings.

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## References

- Barratt, B.I.P. & Moed, A. (2005) Environmental safety of biological control: policy and practice in New Zealand. *Biological Control*, **35**, 247–252.
- Barratt, B.I.P., Evans, A.A., Ferguson, C.M., Barker, G.M., McNeill, M.R. & Phillips, C.B. (1997) Laboratory nontarget host range of the introduced parasitoids *Microctonus aethioides* and *Microctonus hyperodae* (Hymenoptera: Braconidae) compared with field parasitism in New Zealand. *Environmental Entomology*, **26**, 694–702.
- Barton, J., Fowler, S.V., Gianotti, A., Winks, C.J., de Beurs, M., Arnold, G.C. & Forrester, G.J. (2007) Successful biological control of mist flower (*Ageratina riparia*) in New Zealand: agent establishment, impact and benefits to the native flora. *Biological Control*, **40**, 370–385.
- Berry, J.A. (1990) Two parasitoid complexes: *Hierodoris atychioides* (Butler) (Lepidoptera: Oecophoridae) and *Icerya purchasi* Maskell (Homoptera: Margarodidae). *New Zealand Entomologist*, **13**, 60–62.
- Berry, J.A. (2007) Alysiinae (Insecta: Hymenoptera: Braconidae). *Fauna of New Zealand*, **58**, 95 pp.
- Bess, H.A. & Haramoto, F.H. (1959) Biological control of Pamakani *Eupatorium adenophorum*, in Hawaii by a tephritid gall fly, *Procecidochares utilis*. 2. Population studies of the weed, the fly and the parasites of the fly. *Ecology*, **40**, 244–249.
- Boldt, P.E. & Campobasso, G. (1981) Biology of two weevils, *Ceutorhynchus trimaculatus* and *Trichosirocalus horridus*, on *Carduus* spp. in Europe. *Environmental Entomology*, **10**, 691–696.
- Cameron, E. (1935) A study of the natural control of ragwort (*Senecio Jacobaea* L.). *Journal of Ecology*, **23**, 265–322.
- Carvalho, L.G., Buckley, Y.M., Ventim, R., Fowler, S.V. & Memmott, J. (2008) Apparent competition can compromise the safety of highly specific biocontrol agents. *Ecology Letters*, **11**, 690–700.
- Cornell, H.V. & Hawkins, B.A. (1993) Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *American Naturalist*, **141**, 847–865.
- Cox, M.L. (2007) *Atlas of the Seed and Leaf Beetles of Britain and Ireland (Coleoptera, Bruchidae, Chrysomelidae, Megalopodidae and Orsodacnidae)*. Pisces publications, Newbury, Berks. UK.
- Davies, W.M. (1928) The bionomics of *Apion ulicis* Forst. (gorse weevil) with special reference to its role in the control of *Ulex europaeus* in New Zealand. *Annals of Applied Biology*, **15**, 263–386.
- Dymock, J.J. (1985) *Population Dynamics of the Seedfly, Pegohylemyia Jacobaeae (Hardy) (Diptera: Anthomyiidae), and its Potential as a Biological Control Agent of Ragwort, Senecio Jacobaea L.* PhD thesis, Massey University, Palmerston North, New Zealand.
- Eben, A., Benrey, B., Sivinski, J. & Aluja, M. (2000) Host species and host plant effects on preference and performance of *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae). *Biological Control*, **29**, 87–94.
- Eber, S. & Brandl, R. (1994) Ecological and genetic spatial patterns of *Urophora cardui* (Diptera: Tephritidae) as evidence for population structure and biogeographical processes. *Journal of Animal Ecology*, **63**, 187–199.
- Fowler, S.V., Syrett, P. & Hill, R.L. (2000) Success and safety in the biological control of environmental weeds in New Zealand. *Austral Ecology*, **25**, 553–562.
- Gaskin, D.E. (1966) *The Butterflies and Common Moths of New Zealand*. Whitcombe & Tombs Ltd, Auckland, New Zealand.
- Gassmann, A. & Louda, S.M. (2001) *Rhinocyllus conicus*: initial evaluation and subsequent ecological impacts in North America. *Evaluating Indirect Ecological Effects of Biological Control* (eds E. Wajnberg, J.K. Scott & P.C. Quimby), pp. 147–183. CABI International, Wallingford, Oxon, United Kingdom.
- Goeden, R.D. & Louda, S.M. (1976) Biotic interference with insects imported for weed control. *Annual Review of Entomology*, **21**, 325–342.
- Gourlay, E.S. (1964) Notes on New Zealand insects and records of introduced species. *New Zealand Entomologist*, **3**, 45–51.
- Gourlay, A.H. (2004) Classical biological control of Californian thistle: the New Zealand story. *Proceedings of 14th Australian Weeds Conference* (eds B.M. Sindel & S.B. Johnson), pp. 374–377. Weed Society of New South Wales, Sydney.
- Gourlay, A.H., Fowler, S.V. & Rattray, G. (2008) Is ragwort flea beetle (*Longitarsus jacobaeae*) performance reduced by high rainfall on the West Coast, South Island, New Zealand? *Proceedings of the XII International Symposium on Biological Control of Weeds* (eds M.H. Julien, R. Sforza, M.C. Bon, H.C. Evans, P.E. Hatcher, H.L. Hinz & B.G. Rector), pp. 545–551. CAB International, Wallingford, UK.
- Grosskopf, G. & Murphy, S. (1999) *Investigations on Potential Biocontrol Agents of Mouse-ear Hawkweed, Hieracium pilosella L.* Annual report 1999. Unpublished report, CABI Bioscience, Delémont, Switzerland.
- Harris, P. (1991) Classical biocontrol of weeds: its definitions, selection of effective agents, and administrative-political problems. *The Canadian Entomologist*, **123**, 827–849.
- Hawkins, B.A., Thomas, M.B. & Hochberg, M.E. (1993) Refuge theory and biological control. *Science*, **262**, 1429–32.
- Helson, G.A.H. (1974) Beneficial insects. Cinnabar moth and ragwort seed fly. *New Zealand Journal of Agriculture*, **128**, 56–59.
- Hill, R.L. (1989) *Ageratina adenophora* (Sprengel) R. King & H. Robinson, Mexican devil weed (Asteraceae). *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987* (eds P.J. Cameron, R.L. Hill, J. Bain & W.P. Thomas), pp. 317–320. CAB International and DSIR, Wallingford, UK.
- Hill, M.P. & Hulley, P.E. (1995) Host-range extension by native parasitoids to weed biocontrol agents introduced to South Africa. *Biological Control*, **5**, 297–302.
- Hill, R.L., O'Donnell, D.J., Gourlay, A.H. & Speed, C.B. (1995) Suitability of *Agonopterix ulicetella* (Lepidoptera: Oecophoridae) as a control for *Ulex europaeus* (Fabaceae: Genisteae) in New Zealand. *Biocontrol, Science & Technology*, **5**, 3–10.
- Hill, R.L., Wittenberg, R. & Gourlay, A.H. (2001) Biology and host range of *Phytomyza vitalbae* and its establishment for the biological control of *Clematis vitalba* in New Zealand. *Biocontrol, Science & Technology*, **11**, 459–473.
- Hoy, J. (1958) The collection of *Hylemyia seneciella* (Meade) (Diptera, Muscidae) for shipment to Australia. *New Zealand Journal of Science*, **1**, 417–22.
- Hoy, J. (1960) Collection of *Hylemyia seneciella* (Meade) (Diptera, Muscidae) in 1959 season. *New Zealand Journal of Science*, **3**, 100–2.
- Hunt-Joshi, T.R., Root, R.B. & Blossy, B. (2005) Disruption of weed biological control by an opportunistic mirid predator. *Ecological Applications*, **15**, 861–870.
- Lawton, J.H. (1985) Ecological theory and choice of biological control agents. *Proceedings, VI International Symposium on the Biological Control of Weeds, Vancouver, Canada, 1984*, (ed E.S. Delfosse), pp. 13–26. Agriculture Canada, Ottawa.
- Leen, R. (1995) Biology of *Uresiphita reversalis* (Guenée) and comparison with *U. polygonalis maoralis* (Felder). *Journal of the Lepidopterist's Society*, **49**, 163–170.
- Maddox, D.M. (1968) Bionomics of an alligator weed flea beetle, *Agasicles* sp. in Argentina. *Annals of the Entomological Society of America*, **61**, 1300–1305.
- McFadyen, R.E.C. (1998) Biological control of weeds. *Annual Review of Entomology*, **43**, 369–393.
- McGregor, P.G. (1989). Agromyzidae, leaf miners (Diptera). *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987* (eds P.J. Cameron, R.L. Hill, J. Bain & W.P. Thomas), pp. 45–49. CAB International and DSIR, Wallingford, UK.
- Messing, R.H. (2001) Centrifugal phylogeny as a basis for non-target host testing in biological control: is it relevant for parasitoids? *Phytoparasitica*, **29**, 187–190.
- Miller, D. (1970) Ragwort *Senecio jacobaeae* L. Biological Control of Weeds in New Zealand 1927–1948. New Zealand Department of Scientific and Industrial Research No. 74, Wellington New Zealand.
- Munro, V.M.W. & Henderson, I.M. (2002) Nontarget effect of entomophagous biocontrol: shared parasitism between native lepidopteran parasitoids

- and the biocontrol agent *Trigonospila brevifacies* (Diptera: Tachinidae) in forest habitats. *Environmental Entomology*, **31**, 388–396.
- Murray, T.J., Barratt, B.I.P. & Fergusson, C.M. (2002) Field parasitism of *Rhinocyllus conicus* Froelich (Coleoptera: Curculionidae) by *Microctonus aethiopooides* Loan (Hymenoptera: Braconidae) in Otago and south Canterbury. *New Zealand Plant Protection*, **55**, 263–266.
- Myers, J.H., Higgins, C. & Kovacs, E. (1989) How many insect species are necessary for the biological control of insects. *Environmental Entomology*, **18**, 541–547.
- Noyes, J.S. & Valentine, E.W. (1989) *Chalcidoidea (Insecta: Hymenoptera) – Introduction, and Review of Genera in Smaller Families*. Fauna of New Zealand Number 18. DSIR Publishing, Wellington, New Zealand.
- Parnell, J.R. (1966) Observations on the population fluctuations and life histories of the beetles *Bruchidius ater* (Bruchidae) and *Apion fuscirostre* (Curculionidae) on broom (*Sarothamnus scoparius*). *The Journal of Animal Ecology*, **35**, 157–188.
- Paynter, Q., Waipara, N., Peterson, P., Hona, S., Fowler, S., Gianotti, A. & Wilkie, P. (2006) The impact of two introduced biocontrol agents, *Phytomyza vitalbae* and *Phoma clematidina*, on *Clematis vitalba* in New Zealand. *Biological Control*, **36**, 350–357.
- Paynter, Q., Martin, N., Berry, J., Hona, S., Peterson, P., Gourlay, A.H., Wilson-Davey, J., Smith, L., Winks, C. & Fowler, S.V. (2008a) Non-target impacts of *Phytomyza vitalbae* a biological control agent of the European weed *Clematis vitalba* in New Zealand. *Biological Control*, **44**, 248–258.
- Paynter, Q., Gourlay, A.H., Oboyski, P.T., Fowler, S.V., Hill, R.L., Withers, T.M., Parish, H. & Hona, S. (2008b) Why did specificity testing fail to predict the field host-range of the gorse pod moth in New Zealand? *Biological Control*, **46**, 453–468.
- Peterson, P.G., McGregor, P.G. & Springett, B.P. (2000) Density dependent prey-feeding time of *Stethorus bifidus* (Coleoptera: Coccinellidae) on *Tetranychus lintearius* (Acari: Tetranychidae). *New Zealand Journal of Zoology*, **27**, 41–44.
- Peterson, P., Fowler, S.V. & Barrett, P. (2004) Is the poor establishment and performance of heather beetle in Tongariro National Park due to the impact of parasitoids, predators or disease? *New Zealand Plant Protection*, **57**, 89–93.
- Quicke, D.L.J. & Shaw, M.R. (2004) Cocoon silk chemistry in parasitic wasps (Hymenoptera, Ichneumonidea) and their hosts. *Biological Journal of the Linnean Society*, **81**, 161–170.
- Redfern, M., Jones, T.H. & Hassell, M.P. (1992) Heterogeneity and density dependence in a field study of a tephritid-parasitoid interaction. *Ecological Entomology*, **17**, 255–262.
- Roberts, L.I.N. & Sutherland, O.R.W. (1989). *Alternanthera philoxeroides* (C. Martius) Grisebach, alligator weed (Amaranthaceae). *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987* (eds P.J. Cameron, R.L. Hill, J. Bain & W.P. Thomas), pp. 325–330. CAB International and DSIR, Wallingford, UK.
- Schlumprecht, H. (1989) Dispersal of the thistle gallfly *Urophora cardui* and its endoparasitoid *Eurytoma serratae* (Hymenoptera: Eurytomidae). *Ecological Entomology*, **14**, 341–348.
- Schmitt, M. (1988) The Criocerinae: biology, phylogeny and evolution. *Biology of Chrysomelidae* (eds P. Jolivet, E. Petitpierre & T.H. Hsiao) pp. 475–495. Kluwer Academic Publishers, Dordrecht.
- Scott, J.K. & Brown, E.M. (1992) Preliminary observations on the biology and host plants of “*Tortrix*” sp. (Lepidoptera: Tortricidae), a possible biological control agent for Chrysanthemoides spp. (Asteraceae). *Journal of the Entomological Society of South Africa*, **55**, 245–253.
- Shea, K. & Kelly, D. (2004) Modeling for management of invasive species: musk thistle (*Carduus nutans*) in New Zealand. *Weed Technology*, **18**, 1338–1341.
- Sheppard, A.W., Hill, R., DeClerck-Floate, R.A., McClay, A., Olckers, T., Quimby, P.C. & Zimmermann, H.G. (2003) A global review of risk-benefit-cost analysis for the introduction of classical biological control agents against weeds: a crisis in the making? *Biocontrol News & Information*, **24**, 91N–108N.
- Stewart, C.A. (1996) *The Effect of Temperature on the Biology and Population Ecology of Agasicles Hygrophila (Coleoptera: Chrysomelidae), a Biological Control Agent of Alligator Weed (Alternanthera Philoxeroides)*. PhD thesis, Lincoln University, New Zealand.
- Strand, M.R. & Obrycki, J.J. (1996) Host specificity of insect parasitoids and predators. *BioScience*, **46**, 422–429.
- Strong, D.R., Lawton, J.H. & Southwood, T.R.E. (1984) *Insects on Plants. Community Patterns and Mechanisms*. Blackwell, Oxford. 313 pp.
- Syrett, P. (1989) *Hypericum perforatum* L., St John’s wort (Clusiaceae). *A Review Of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987* (eds P.J. Cameron, R.L. Hill, J. Bain & W.P. Thomas), pp. 353–356. CAB International and DSIR, Wallingford, UK.
- Syrett, P. (1993) The insect fauna of broom, *Cytisus scoparius*, in New Zealand. *New Zealand Entomologist*, **16**, 75–83.
- Syrett, P., Fowler, S.V., Coombs, E.M., Hosking, J.R., Markin, G.P., Paynter, Q.E. & Sheppard, A.W. (1999) The potential for biological control of Scotch broom (*Cytisus scoparius* (L.) Link) and related species. *Biocontrol News and Information*, **20**, 17N–34N.
- Teulon, D.A.J. & Penman, D.R. (1990) Host records for the New Zealand flower thrips (*Thrips obscuratus* (Crawford) Thysanoptera: thripidae). *New Zealand Entomologist*, **13**, 46–51.
- Thomas, W.P. (1975) Additional notes on leaf rollers. *The Orchardist of New Zealand*, **48**, 354–355.
- Thomas, W.P. & Hill, R.L. (1989) *Phyllonorycter messaniella* (Zeller), oak leaf-miner (Lepidoptera: Gracillariidae). *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987* (eds P.J. Cameron, R.L. Hill, J. Bain & W.P. Thomas), pp. 289–293. CAB International and DSIR, Wallingford, UK.
- Valentine, E.W. (1967) A list of the hosts of entomophagous insects of New Zealand. *New Zealand Journal of Science*, **10**, 1100–1210.
- Van Driesche, R.G., Bellows, T.S., Elkinton, J.S., Gould, J.R. & Ferro, D.N. (1991) The Meaning of percentage parasitism revisited: solutions to the problem of accurately estimating total losses from parasitism. *Environmental Entomology*, **20**, 1–7.
- Vogt, G.B., Quimby, P.C. & Kay, S.H. (1992) Effects of weather on the biological control of alligatorweed in the lower Mississippi Valley region, 1973–83. *USDA Technical Bulletin*, **1766**, 143.
- Waloff, N. (1987) Observations on the heather beetle *Lochmaea suturalis* (Thomson) (Coleoptera, Chrysomelidae) and its parasitoids. *Journal of Natural History*, **21**, 545–556.
- Wapshere, A.J., Delfosse, E.S. & Cullen, J.M. (1989) Recent developments in biological control of weeds. *Crop Protection*, **8**, 227–250.
- Watmough, R.H. (1968) Population studies on two species of Psyllidae (Homoptera : Sternorrhyncha) on broom (*Sarothamnus scoparius* (L.) Wimmer). *Journal of Animal Ecology*, **37**, 283–314.
- Willis, A.J. & Memmott, J. (2005) The potential for indirect effects between a weed, one of its biocontrol agents and native herbivores: a food web approach. *Biological Control*, **35**, 299–306.
- Wilson, F. (1943) The entomological control of St. John’s wort (*Hypericum perforatum* L.) with particular reference to the insect enemies of the weed in southern France. *Bulletin of the Council for Scientific and Industrial Research Australia*, **169**, 87.
- Windig, J.J. (1991) Life-cycle and abundance of *Longitarsus jacobaeae* (Col.: Chrysomelidae), biocontrol agent of *Senecio jacobaeae*. *Entomophaga*, **36**, 605–626.
- Winks, C.J., Fowler, S.V. & Smith, L.A. (2004) Invertebrate fauna of boneseed, *Chrysanthemoides monilifera* ssp. *monilifera* (L.) T. Norl. (Asteraceae: Calenduleae), an invasive weed in New Zealand. *New Zealand Entomologist*, **27**, 61–72.
- Zwölfer, H. & Arnold-Rinehart, J. (1994) The evolution of interactions and diversity in plant-insect systems: the *Urophora-Eurytoma* food web in galls on Palearctic Cardueae. *Biodiversity and Ecosystem Function* (eds E.D. Schulze & H.A. Mooney), pp 245–233. Springer, Berlin Heidelberg New York.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** Parasitoids reared during the field survey, which are considered to be rearing contaminants.

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