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The potential for indirect effects between a weed, one of its biocontrol agents and native herbivores: A food web approach

A.J. Willis [a,1], J. Memmott [b,*]

[a] Co-operative Research Centre for Weed Management Systems and CSIRO Plant Industry, GPO Box 1600, Canberra, ACT 2601, Australia
[b] School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

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Abstract

The safety of biological control is a contentious issue. We suggest that constructing and analyzing food webs may be a valuable addition to standard biological control research techniques, as they offer a means of assessing the post-release safety of control agents. Using preliminary data to demonstrate the value of food webs in biocontrol programs, we quantified the extent to which a key agent has infiltrated natural communities in Australia and, potentially, impacted on non-target species. Using these data, we also demonstrate how food webs can be used to generate testable hypotheses regarding indirect interactions between introduced agents and non-target species. We developed food webs in communities invaded to varying degrees by an exotic weed, bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata*, and a key biocontrol agent for this weed in Australia, the tephritid fly, *Mesoclanis polana.* Three food webs were constructed during springtime showing the interactions between plants, seed-feeding insects and their parasitoids. One food web was constructed in a plot of native Australian vegetation that was free of bitou bush ('bitou-free'), another in a plot of Australian vegetation surrounded by an invasion of bitou bush ('bitou-threatened') and a third from a plot infested with a monoculture of bitou bush ('bitou-infested'). The bitou-free web contained 36 species, the bitou-threatened plot 9 species and the bitou-infested web contained 6 species. One native Australian herbivore attacked the seeds of bitou bush. *M. polana*, a seed-feeding fly, was heavily attacked by native parasitoids, these being more abundant than the parasitoids feeding on the native seed feeders. A surprising result is that none of the three species of native parasitoids reared from *M. polana* were reared from any of the native herbivores. The food webs revealed how a highly host-specific biocontrol agent, such as *M. polana* has the potential to change community structure by increasing the abundance of native parasitoids. The webs also suggest that indirect interactions between *M. polana* and native non-target species are possible, these been mediated by shared parasitoids. The experiments necessary to determine the presence of these interactions are outlined.

Keywords: Environmental weed; Biological control; Bitou bush; *Chrysanthemoides monilifera*; *Mesoclanis polana*; Non-target impact

1. Introduction

Alien species pose a significant threat to global biodiversity, second only to habitat loss (McNeely, 1997; Schmitz and Simberloff, 1997; Walker and Steffen, 1997). Alien plants are a particularly serious threat given their ability to displace native plants (Frankel et al., 1995; Groves and Willis, 1999; McKnight, 1993), change the structure and composition of ecological communities (Fogarty and Facelli, 1999; Mullet and Simmons, 1995; Woods, 1993), and alter a range of ecosystem processes, such as nutrient cycling and disturbance regimes (Mack and D'Antonio, 1998; Vitousek, 1990). A widely used tool in alien plant management is biological control.

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[*] Corresponding author. Fax: +44 0 117 925 7374.
E-mail addresses: tony.willis@health.gov.au (A.J. Willis), Jane.Memmott@bris.ac.uk (J. Memmott).
[1] Present address: Office of the Gene Technology Regulator, P.O. Box 100 (MDP 54) Woden ACT 2606, Australia. Fax: +61 0 2627 14 202.

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Currently, however, the safety of biocontrol is a highly contentious issue (Boettner et al., 2000; Ewel et al., 1999; Follett and Duan, 2000; Henneman and Memmott, 2001; Howarth, 1983; Louda et al., 1997; Pearson and Callaway, 2003; Simberloff and Stiling, 1996; Strong and Pemberton, 2000; Thomas and Willis, 1998) with particular concerns about the interactions between biocontrol agents and 'non-target' species. Such interactions can occur either directly, if an agent attacks a non-target host, or indirectly, when the agent affects non-target species via shared natural enemies.

Quantitative food webs provide a powerful means of identifying both the presence of direct non-target effects (e.g., Henneman and Memmott, 2001) and generating testable hypotheses concerning the importance of indirect non-target effects (Memmott, 1999; Morris et al., 2004). The role of natural enemies in mediating indirect effects, such as apparent competition, between alternative hosts has received considerable theoretical attention (e.g., Bonsall and Hassell, 1997; Holt, 1984; Holt and Kotler, 1987), but in only a few cases has their impact been quantified under field conditions (Morris et al., 2004; Morris et al., 2001; Settle and Wilson, 1990). Settle and Wilson (1990) revealed that the invasion of an alien herbivore disrupted a resident host–parasitoid interaction in California. They linked the decline in populations of the grape leafhopper, *Erythroneura elegantula*, to the invasion of the variegated leafhopper, *E. variabilis*, and the ensuing increase of the shared parasitoid, *Anagrus epos*. Schonrogge et al. (1996) suggested that alien herbivores, in general, can increase the abundance of native parasitoids and thereby put native hosts at risk. If weed biocontrol agents are attacked by native parasitoids—and there is evidence that many of them are (Hawkins and Marino, 1997)—then they could increase the abundance of native parasitoids which could, in turn, have a detrimental effect on native herbivores, i.e., a negative indirect effect.

The aim of this paper was to demonstrate the value of food webs as a tool in biocontrol programs. It provides an example of the type of approach that could be taken to better characterize food webs either before and after biological control releases have been made. Specifically, the paper uses preliminary food web data to explore the practicality of food webs for assessing the presence of direct target and non-target effects of biocontrol agents and the likelihood of indirect, unintended effects. Using data from an ongoing project running in Australia as an example, the objectives of the work are threefold: (1) to compare the structure of a food web in weed-free, weed invaded and weed-dominated plots; (2) to determine if direct target and non-target effects are occurring between the weed biocontrol agent and the plants in the community; (3) to determine if there is the potential for indirect non-target effects and, if so, to outline the manipulative experiments needed to prove if these indirect effects are occurring.

2. Methods

2.1. The weed and the biocontrol agent

Bitou bush, *Chrysanthemoides monilifera* ssp. *rotundata* (DC.) T. Norl (Asteraceae), a spreading, woody shrub, and 1–2 m tall that forms a virtual monoculture in invaded habitats of south-eastern Australia. Bitou bush was introduced to Australia from South Africa in the early 1900s, and was deliberately planted for dune stabilization in coastal New South Wales. Although, deliberate plantings ceased in the late 1960's, bitou bush continues to spread naturally and now infests over 70,000 ha of eastern Australia, from southern Queensland to Victoria, threatening the integrity of unique ecological communities and the viability of at least 6 endangered plant species (NSW Threatened Species Conservation Act 1995). Biological control has been used against bitou bush, which commonly hosts two biocontrol agents, a seed-feeding fly, *Mesoclanis polana* Munro (Diptera:Tephritidae) (Edwards et al., 1996) and a leaf-tip feeding moth, *Comostolopsis germana* Prout (Lepidoptera:Geometridae) (Holtkamp, 1993). Both species are recent releases and passed the current safety tests required for biocontrol agents for weeds in Australia.

2.2. The field site

Our study sites were two coastal headlands, about 3 km apart, 15 km north of Coffs Harbour on the central-northern coast of New South Wales, Australia. The northern most headland (30°8.9′S, 153°12.1′E) is being invaded by a dense infestation of bitou bush. By contrast, the southern headland (30°10.9′S, 153°12.1′E) currently, hosts relatively few bitou bush plants (Armstrong, 1996). We selected three study plots at these two sites as they offered the potential to construct food webs in communities differing principally in the extent of bitou bush invasion. With the exception of two shrubs, *Acacia sophorae* (Labill.) R.Br and *Banksia integrifolia* L.f., growing to about 1.5 m in height, the native plant communities at the field sites are approximately 15 cm tall and dominated by *Themeda triandra* Forsk. interspersed with approximately 30 common forb or low-growing shrub species. Each field site, and two adjacent coastal headlands, host the only remaining populations of *Zieria prostrata*, an endangered endemic shrub (Briggs and Leigh, 1996) that is limited geographically to these headlands (Hogbin and Peakall, 1999), and *Thesium australe* R.Br, which is also endangered (Briggs and Leigh, 1996).

2.3. Construction of quantitative food webs

In November (spring) 1998 we established three plots, each 10 × 10 m: (1) a 'bitou-free' plot on the southern headland comprising native vegetation; (2) a 'bitou-threatened' plot on the northern headland comprising native vegetation, whose integrity was threatened by an adjacent (<3 m) large and spreading infestation of bitou bush; (3) a 'bitou-infested' plot also on the northern headland, that hosted a virtual monoculture of bitou bush. The underlying rationale of the sampling sites was to study a gradient of bitou infestation. Plants were sampled in each plot along four 10 × 1 m transects, by collecting every fruit within the transect and by allocating each species to one of three abundance categories: common, rare and the absent from the plot, but the present in the adjacent area. Because of the density of bitou bush and its seeds, we subsampled the bitou-dominated plot with two 10 × 1 m transects. The data were then standardized to express abundance in the same units for all three plots. Some plant species observed in the headland communities were not represented in our study plots. Consequently, we supplemented the transect samples by collecting from these unrepresented species when possible.

Fruit and seed heads (for Asteraceae) were returned to the laboratory for rearing using standard techniques (Memmott and Godfray, 1994; Memmott et al., 1994). We collected 2342 seeds from the plots (Table 1), and reared them individually in the laboratory to establish plant–herbivore and herbivore–parasitoid associations. All insects were identified subsequently, or morphotyped by taxonomists at the Australian National Insect Collection. Sampling took place over a four-day period—a sufficient time to provide a spring 'snapshot' of the food web.

3. Results

3.1. Food web structure

In total, we sampled seeds from 20 plant species (Table 1). From these plants we sampled 12 species of seed predator (Table 1) and from these herbivores we sampled 12 species of hymenopteran parasitoid or hyperparasitoid species. The three plots clearly hosted different levels of species richness (Table 2). The bitou-free plot had 33 species, twice the species richness of the 15 species bitou-threatened plot. The bitou-infested plot was very species-poor, hosting only six taxa. The fact that the bitou-free plot was on a different headland to the bitou-threatened and bitou-infested plots may account for some of the differences. However, these two

Table 2
Species richness in the three plots

Plot	Species richness			
	Plant	Herbivore	Parasitoid	Total species
Bitou-infested	1	2	3	6
Bitou-threatened	8	2	5	15
Bitou-free	19	5	9	33

Table 1
The seed species and the seed predators

Plant	Family	Number of seeds	Seed herbivores
Platysace ericoides	Apiaceae	50	
Bidens pilosa	Asteraceae	20	
Bracteantha bracteata	Asteraceae	261	Diptera: Tephritidae: *Spaeniscus* sp. Coleoptera: *Olanea* sp. Lepidoptera, Pyralidae, *Homoeosoma vagella* (Zeller) Lepidoptera, Cosmopterigidae, *Pyroderces* sp
Chrysanthemoides monilifera	Asteraceae	1522	Diptera: Cecidomyiidae: *Lestodiplosis* sp.1 Diptera: Tephritidae: *Mesoclanis polana*
Senecio pinnatifolius	Asteraceae	4	
Polymeria calycina	Convolvulaceae	5	
Hibbertia aspera	Dilleniaceae	442	Diptera: Cecidomyiidae: *Lestodiplosis* sp.2 Curculionidae: *Agestra punctulata* (Blackburn) Unknown/Hibbertia seed herbivore
Podolobium scandens	Fabaceae	105	
Pultenaea villosa	Fabaceae	192	Lepidoptera, Pyralidae, *Etiella behrii* (Zeller)
Goodenia rotundifolia	Goodeniaceae	14	
Scaevola canlendulacea	Goodeniaceae	2	
Hypericum gramineum	Hypericacea	3	
Acacia sophorae	Mimosaceae	31	
Tricoryne elatior	Phormiaceae	3	
Themeda triandra	Poaceae	11	
Banksia integrifolia	Proteaceae	53	Coleoptera: Melanterius ventralis (Lea) Diptera: Cecidomyiidae: *Lestodiplosis* sp.2
Boronia polygalifolia	Rutaceae	9	
Zieria prostrata	Rutaceae	338	Unknown seed herbivore
Thesium australe	Santalaceae	5	
Pimelea linifolia	Thymelaeaceae	33	

headlands were only 3 km apart and chosen because they appeared similar in all respects except for their level of bitou bush invasion. Although species counts and lists are useful in determining the magnitude, taxonomic composition and distribution of biodiversity, they say little about its maintenance and dynamics (Godfray et al., 1999). To obtain such information, data on the interactions between species, as well as their identities and population densities are required. The interactions between the plants, herbivores, and parasitoids are shown in a quantitative food web for each plot (Fig. 1).

The bitou-free and the bitou-threatened webs are dwarfed by the bitou-infested web, (Fig. 1). Seed production was considerably higher in the latter, with a total of 1522 seeds per 40 m^2 (4 × 10 m transects) in the bitou-infested plot compared to 956 seeds in the bitou-free plot and 625 seeds in the bitou-threatened. Not only is seed production higher in the bitou-infested plot, but seed herbivory is also higher: 73% of bitou seeds were attacked by seed herbivores whereas only 54 and 22% of seeds were attacked in the bitou-free and bitou-threatened plots. We recorded only one native herbivore species, *Lestodiplosis* sp.1 (Diptera:Cecidomyiidae), directly associated with bitou bush. Twenty one percent of the herbivores sampled from bitou bush seeds (out of a total of 1112 herbivores sampled) were parasitized by native parasitoids, whereas 45 and 47% of native herbivores were parasitized in the bitou-free and bitou-threatened webs, respectively. However, we were unable to establish whether the parasitoids in the bitou-infested web were reared from the native *Lestodiplosis* species or from *M. polana* as it was impossible to determine what was happening inside the bitou bush seeds without dissection, which would have destroyed both the seed and any larvae within. However, as *Lestodiplosis* constituted less than 4% of the herbivores reared from bitou bush, we assumed that the majority of parasitoids were from *M. polana*. Indeed, the most abundant parasitoid in the bitou-infested web is in the genus *Eupelmus*, a genus known to parasitise *M. polana* at high rates elsewhere in New South Wales (Holtkamp, pers. comm.). This very common parasitoid reared from *M. polana* is a native Australian species that has included this alien herbivore in its host range.

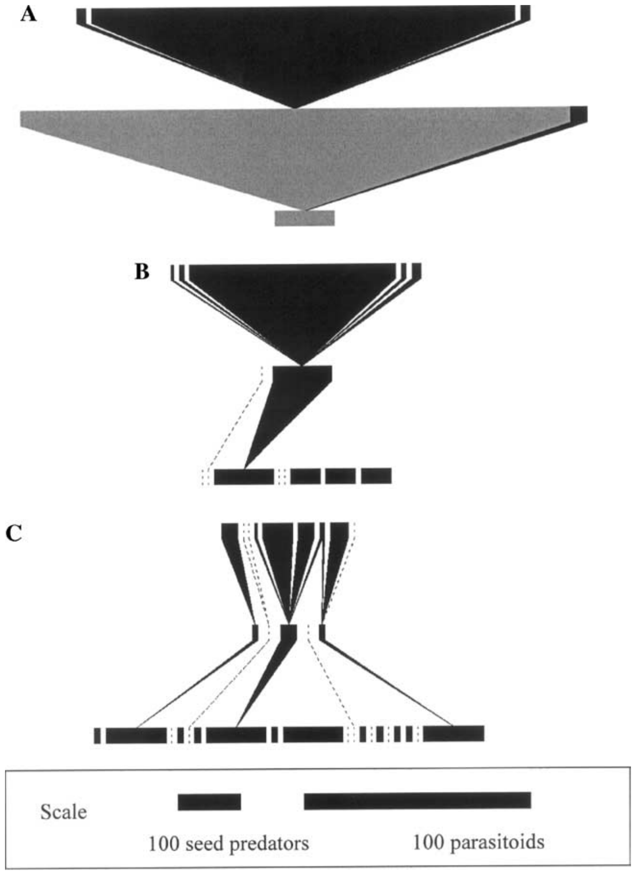

Fig. 1. The three food webs from the study drawn to scale to highlight the relative abundances of different species and trophic levels within the community. (A) The bitou-dominated; the plant is bitou and the main herbivore is *M. polana*; (B) The bitou-threatened plot; (C) The bitou-free plot. Each species of plant and insect is represented by a rectangle: plants are shown on the bottom level, herbivores on the middle level and parasitoids on the top level. The width of the rectangles and the size of the interaction between them, is proportional to their abundance at the field site. The species shown as dotted lines were not found in the plots, but were sampled from the adjacent area. Native species are shown in black, alien species in grey. The three webs are drawn to the same scale to facilitate comparison and show the number of insects reared per 40 m^2. The herbivore and parasitoid scale bars show 100 individuals and the plants are put into three classes: abundant, rare and only found outside the plot (large box, small box, and dotted line, respectively).

3.2. Are there direct target and non-target effects?

As reported above, 73% of bitou seeds were attacked by *M. polana* (the intended target interaction). No direct non-target effects were observed between the biocontrol agent, *M. polana*, and the native vegetation, i.e., *M. polana* was not recorded as feeding on any native plants. Given the legal requirements and scientific expectations for safety testing biocontrol agents today, this latter result is not surprising.

3.3. Is there the potential for indirect non-target effects between M. polana and native herbivores, mediated by shared natural enemies?

Whilst a relatively small proportion of the bitou bush herbivores are parasitized (21 vs 45 and 47%), the abundance of the *M. polana* provides a large resource for parasitoids. Consequently, there are many more parasitoids in the bitou-infested plot than in the bitou-free plot (contrast the parasitoid trophic level in Fig. 1A with Figs. 1B and C). A surprising result is that none of the native parasitoids reared from bitou bush were reared from any of the native herbivores. We would have expected to rear these parasitoids from native seed predators of the Asteraceae because of the frequency with which this plant family is attacked by tephritid seed predators (Edwards et al., 1996). In particular, it is surprising that we found none of these parasitoids associated with the native tephritid *Spaeniscus* sp. (Table 1) sampled from *Bracteantha bracteata*.

While at this stage entirely speculative, it is possible that *M. polana* is impacting indirectly and adversely on native Australian herbivores. For example, *M. polana* hosts a large population of native Australian parasitoids which, while not identified in our snapshot sampling, must have some native hosts. A parasitoid maintained at high densities on a common biocontrol insect (such as, the *Eupelmus* species on *M. polana*) can potentially drive a rare non-target species to extinction via apparent competition (Holt and Hochberg, 2001). The density dependence, which would vitiate such an effect in a simple two species interaction, is lacking in these cases (Simberloff and Stiling, 1996). While we cannot exclude other causes, including the possibility that our sampling snapshot may not have detected the native herbivores, an explanation for the very low abundance of the native tephritid, *Spaeniscus* sp. is that apparent competition is occurring between this species and *M. polana* via shared native parasitoids. *Spaeniscus* sp. is the most likely native host for the native parasitoids attacking *M. polana* as it is the most closely related.

4. Discussion

While extensive data exists on the distributions of alien species, and their impact upon native species as competitors, prey species, predators, pollinators, and parasites and even their impact upon ecosystem properties, there is extraordinarily little data on how aliens are accommodated in food webs. Indeed, we are only aware of three published datasets: Schonrogge and Crawley (2000) working in the UK, Henneman and Memmott (2001) working in Hawaii, and Munro and Henderson (2002) working in New Zealand. Cornell and Hawkins (1993) compared the structure and diversity of 87 parasitoid complexes associated with alien herbivores with those on the same herbivore species in their native regions. Overall parasitoid attack rates were generally lower on hosts as invaders than on hosts as natives, a pattern that appears to be repeated here—the parasitism rate on *M. polana* is 21 vs 45% on native seed feeders overall. We now examine factors that could bias the data, before exploring how the food webs we constructed may reveal some indirect non-target effects. We end by identifying the steps that would be required to determine whether, or not, non-target effects are important in this community. These steps underscore the value of food webs as a hypothesis-generating tool for applied ecological disciplines such as biological pest control.

4.1. Limitations of the study

As plant–herbivore–parasitoid food webs are temporally dynamic (Memmott et al., 1994), a limitation was the short time frame during which we sampled the community. In comparison to the sampling regimes used in other food web studies, we have data describing the community for about six weeks, from sampling to final rearings. We are confident nevertheless, that this provided an accurate snap shot of the community during November 1998. Given that there are approximately 30 common forb or low-growing shrub species at the site and we collected seeds from 20 of these, one-third of the seed species present at the site remain unsampled. This was because our sampling period did not coincide with their seeding phenology and future work at the site should obviously include sampling these missing species. We would also have preferred to replicate the three types of plot. Although this ideal is achieved only rarely in food web studies (Cohen et al., 1993), it is particularly important if treatment effects (here, the presence or the absence of bitou bush) are to be distinguished from spatial or other confounding effects. Finally, estimating percent parasitism is not free from methodological problems (e.g., Vandriesche, 1983; Vandriesche et al., 1991). If, however, the aim is to compare food webs (as is the case here) then any confounding effects are obviously the same within the webs. Consequently, the structure of the webs can still be compared. While acknowledging that these limitations may affect our conclusions, we argue strongly that although not perfect, the data meet our aim of illustrating how food webs are an effective tool for exploring ecological issues relating to biocontrol and how they can be used to develop testable hypothesis—in this case, concerning the role of indirect non-target effects.

4.2. The food web structure

Our data show, perhaps not surprisingly, that the structure of the three food webs are very different (Fig. 1). A reticulate food web in the bitou-free web is replaced by simpler, species-poor web in the bitou-threatened plot, and by a food chain in the bitou-infested plot. Native parasitoids have attacked *M. polana* and are building up to large numbers in the community. The species richness of the bitou-threatened plot is less than the bitou-free plot despite the fact that both plots are uninvaded by bitou bush. One explanation for this may lie in the fact that the bitou-threatened plot is on a headland where the area available for native vegetation has been diminished by a bitou invasion. The fact that fewer species are found at the native may be due to simple island biography effects: the smaller area of native habitat is host to smaller numbers of species.

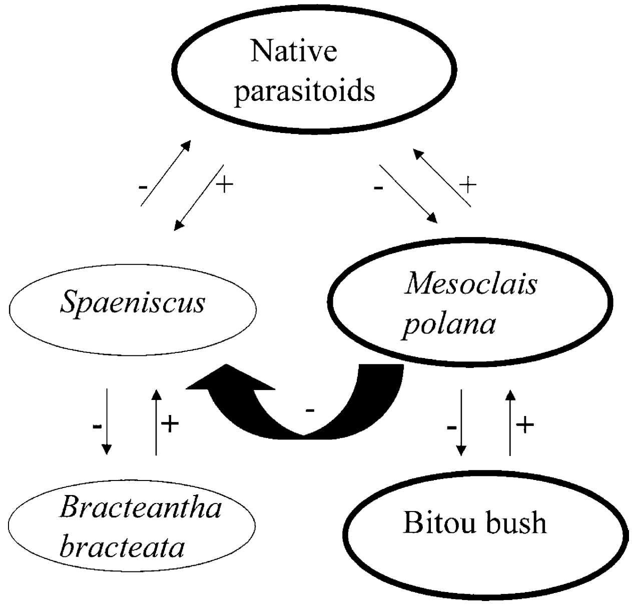

Fig. 2. The predicted current relationship between *M. polana* and *Spaeniscus*, the likely native host of the parasitoids currently attacking *M. polana*. Trophic interactions are shown by narrow black arrows and likely indirect interactions by thick black arrows. The direction of the interactions, negative, and positive or unknown is shown next to each interaction and the size of the circles around the species indicates their relative abundance.

4.3. Next steps

The work presented here is part of a project that was initiated to explore the utility of food webs in biological weed control programs. The data were gathered to establish approximate values for the trophic links between the native and alien components of the community. Subsequent steps associated with the food web approach are outlined below. Unfortunately, undertaking these was beyond the scope of the current project.

(1) The snapshot food webs require more comprehensive sampling to include likely spatio-temporal variation. Ideally, further sampling would focus on larger plots that incorporate both native speices and bitou bush, rather than on the plots we established, which were effectively ‘presence and absence’ plots. More extensive sampling is likely to identify the native hosts of the parasitoids currently attacking *M. polana*.

(2) Field experiments. Fig. 2 summarizes the direct and possible indirect interactions between the two herbivores. Manipulative field experiments are the most robust means of determining whether negative indirect effects, mediated by shared natural enemies, are operating between *M. polana* and the native tephritid *Spaeniscus* sp. These experiments would require manipulating the density of *M. polana* to determine if this influences the population of *Spaeniscus* sp. Ideally, range of *M. polana* infestation densities would be established in plots containing both of the two host plants, bitou bush and *B. bracteata*. While this may be practical in a glasshouses/insectary, it is likely to be technically difficult in the field. Accordingly, it may be more practical to establish plots with *M. polana* either the present or the absent and managed by a systemic insecticide that has been shown not to affect seed production (Adair and Holtkamp, 1999). We hypothesize that, if *M. polana* impacts indirectly on *Spaniscus* sp. via shared parasitoid(s), fewer of the latter species will emerge in the presence of *M. polana*, than in its absence.

5. Conclusion

The ability of biological control agents to disrupt communities was highlighted by Louda et al. (1997). They demonstrated that an exotic seed-feeding agent was displacing native seed feeders associated with non-target host plants. Observations such as, these suggest that quantitative food webs may be a useful tool for biocontrol practitioners, including because of their potential to inform the design of experiments addressing critical questions about the impact of alien organisms on the community. Our study, for example, suggests that there has been an explosion in the population of Australian native parasitoids following the success of the bitou bush seed fly. Is this a temporary ‘boom’ that will abate as populations of the weed decline in size and density? Will the relatively large parasitoid community now associated with bitou bush affect species or interactions elsewhere in the food web adversely and, if so, over what time frame? The development of indirect effects is likely to be a dynamic process. Thus, in the early stages of the invasion, it may be that the native parasitoids which attack *M. polana*, are supported by a large population of a native host such as *Spaeniscus* and these exert an indirect negative impact on *M. polana*. If however, *M. polana* survives and establishes large populations, the tables are effectively turned and it could then exert an indirect negative impact on the native insect. Quantitative food webs provide a very useful tool for identifying the potential for indirect effects, and when backed up with manipulative experiments can identify whether they are simply theoretically plausible, or actually occurring in the field.

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References

Adair, R.J., Holtkamp, R.H., 1999. Development of a pesticide exclusion technique for assessing the impact of biological control agents for *Chrysanthemoides monilifera*. Biocontrol Sci. Technol. 9, 383–390.

Armstrong, R.A., 1996. Moonee Beach Nature Reserve Pest Management Plan. Report to the New South Wales National Parks and Wildlife Service. New South Wales National Parks and Wildlife Service, Dorrigo.

Boettner, G.H., Elkinton, J.S., Boettner, C.J., 2000. Effects of a biological control introduction on three nontarget native species of saturniid moths. Conserv. Biol. 14, 1798–1806.

Bonsall, M.B., Hassell, M.P., 1997. Apparent competition structures ecological assemblages. Nature 388, 371–373.

Briggs, J.D., Leigh, J.H., 1996. Rare or Threatened Australian Plants. CSIRO Publishing, Collingwood.

Cohen, J.E., Beaver, R.A., Cousins, S.H., Deangelis, D.L., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H., Martinez, N., Omalley, R., Page, L.M., Patten, B.C., Pimm, S.L., Polis, G.A., Rejmanek, M., Schoener, T.W., Schoenly, K., Sprules, W.G., Teal, J.M., Ulanowicz, R.E., Warren, P.H., Wilbur, H.M., Yodzis, P., 1993. Improving food webs. Ecology 74, 252–258.

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. Am. Nat. 141, 847–865.

Edwards, P.B., Adair, J.J., Holtkamp, R.H., 1996. Seedhead tephritids and their parasitoids—can predictions be made about likely parasitism of tephritids introduced into Australia for biological control of Asteraceae. In: Moran, V.C., Hoffmann, J.H. (Eds.), Proceedings of the IX International Symposium on Biological Control of Weeds. Stellenbosch, South Africa, pp. 153–164.

Ewel, J.J., O'Dowd, D.J., Bergelson, J., Daehler, C.C., D'Antonio, C.M., Gomez, L.D., Gordon, D.R, Hobbs, R.J., Holt, A., Hopper, K.R., Hughes, C.E., LaHart, M., Leakey, R.R.B., Lee, W.G., Loope, L.L., Lorence, D.H., Louda, S.M., Lugo, A.E., McEvoy, P.B., Richardson, D.M., Vitousek, P.M., 1999. Deliberate introductions of species: Research needs—Benefits can be reaped, but risks are high. Bioscience 49, 619–630.

Fogarty, G., Facelli, J.M., 1999. Growth and competition of *Cytisus scoparius*, an invasive shrub, and Australian native shrubs. Plant Ecol. 144, 27–35.

Follett, P.A., Duan, J.J., 2000. Nontarget Effects of Biological control. Kluwer Academic Publishers, Norwell Massachusetts.

Frankel, O.H., Brown, A.D.H., Burdon, J.J., 1995. The Conservation of Plant Biodiversity. Cambridge University Press, Cambridge.

Godfray, H.C.J., Lewis, O.T., Memmott, J., 1999. Studying insect diversity in the tropics. Philos. Trans. R. Soc. Lond. B Biol. Sci. 354, 1811–1824.

Groves, R.H., Willis, A.J., 1999. Weeds and loss of native plant biodiversity: some Australian examples. Australian Journal of Environmental Management 6, 156–163.

Hawkins, B.A., Marino, P.C., 1997. The colonization of native phytophagous insects in North America by exotic parasitoids. Oecologia 112, 566–571.

Henneman, M.L., Memmott, J., 2001. Infiltration of a Hawaiian community by introduced biological control agents. Science 293, 1314–1316.

Hogbin, P.M., Peakall, R., 1999. Evaluation of the contribution of genetic research to the management of the endangered plant *Zieria prostrata*. Conserv. Biol. 13, 514–522.

Holt, R.D., 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am. Nat. 124, 377–406.

Holt, R.D., Hochberg, M.E., 2001. Indirect interactions, community modules and biological control: a theoretical perspective. In: Wajnberg, E., Scott, J.K., Quimby, P.C. (Eds.), Evaluating Indirect Ecological Effects of Biological Control. CABI Publishing, pp. 13–34.

Holt, R.D., Kotler, B.P., 1987. Short-term apparent competition. Am. Nat. 130, 412–430.

Holtkamp, R.H., 1993. Parasitoids of *Comostolopsis germana* Prout (Lepidoptera, Geometridae). J. Aust. Entomol. Soc. 32, 387–388.

Howarth, F.G., 1983. Classical Biocontrol: Panacea or Pandora's Box. Proceedings of the Hawaiian Entomological Society 24, 239–244.

Louda, S.M., Kendall, D., Connor, J., Simberloff, D., 1997. Ecological effects of an insect introduced for the biological control of weeds. Science 277, 1088–1090.

Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13, 195–198.

McKnight, B.N., 1993. Biological pollution: The control and impact of invasive exotic species. Indiana Acad. Sci..

McNeely, J., 1997. IUCN International Union for Conservation of Nature and Natural Resources alien invasive species: a framework for action. In: Rubec, C., Lee, G. (Eds.), Conserving Vitality and Diversity: Proceedings of the World Conservation Congress Workshop on Alien Invasive Species. IUCN and Environment Canada, Ottawa, pp. 3–9.

Memmott, J., 1999. Food webs as a tool for studying nontarget effects in biological control. In: Follett, P.A., Duan, J.J. (Eds.), Nontarget Effects of Biological Control. Kluwer Academic Publishers, Dordrecht, pp. 147–167.

Memmott, J., Godfray, H.C.J., 1994. The use and construction of parasitoid webs. In: Hawkins, B.A., Sheehan, W. (Eds.), Parasitoid Community Ecology. Oxford University Press, Oxford, pp. 300–318.

Memmott, J., Godfray, H.C.J., Gauld, I.D., 1994. The structure of a tropical host parasitoid community. J. Anim. Ecol. 63, 521–540.

Morris, R.J., Lewis, O.T., Godfray, H.C.J., 2004. Experimental evidence for apparent competition in a tropical forest food web. Nature 428, 310–313.

Morris, R.J., Muller, C.B., Godfray, H.C.J., 2001. Field experiments testing for apparent competition between primary parasitoids mediated by secondary parasitoids. J. Anim. Ecol. 70, 301–309.

Mullet, T., Simmons, D., 1995. Ecological impacts of the environmental weed sweet pittosporum (*Pittosporum undulatum*) Vent. in dry sclerophyll forest communities. Victoria Plant Protection Quarterly 10, 131–138.

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. Environ. Entomol. 31, 388–396.

Pearson, D.E., Callaway, R.M., 2003. Indirect effects of host-specific biological control agents. Trends Ecol. Evol. 18, 456–461.

Schmitz, D.C., Simberloff, D., 1997. Biological invasions: A growing threat. Issues Sci. Technol. 13, 33–40.

Schonrogge, K., Crawley, M.J., 2000. Quantitative webs as a means of assessing the impact of alien insects. J. Anim. Ecol. 69, 841–868.

Schonrogge, K., Stone, G.N., Crawley, M.J., 1996. Alien herbivores and native parasitoids: rapid developments and structure of the parasitoid and inquiline complex in an invading gall wasp *Andricus quercuscalicis* (Hymenoptera: Cynipidae). Ecol. Entomol. 21, 71–80.

Settle, W.H., Wilson, L.T., 1990. Invasion by the variegated leafhopper and biotic interactions—-parasitism, competition, and apparent competition. Ecology 71, 1461–1470.

Simberloff, D., Stiling, P., 1996. How risky is biological control? Ecology 77, 1965–1974.

Strong, D.R., Pemberton, R.W., 2000. Ecology—biological control of invading species—risk and reform. Science 288, 1969–1970.

Thomas, M.B., Willis, A.J., 1998. Biocontrol—risky but necessary. Trends Ecol. Evol. 13, 325–329.

Vandriesche, R.G., 1983. Meaning of percent parasitism in studies of insect parasitoids. Environ. Entomol. 12, 1611–1622.

Vandriesche, 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. Environ. Entomol. 20, 1–7.

Vitousek, P.M., 1990. Biological invasions and ecosystem processes—towards an integration of population biology and ecosystem studies. Oikos 57, 7–13.

Walker, B., Steffen, W., 1997. An overview of the implications of global change for natural and managed terrestrial ecosystems. 1, URL: http://www.consecol.org/vol1/iss2/art2.

Woods, K.D., 1993. Effects of invasion by *Lonicera tatarica* L on herbs and tree seedlings in 4 New-England forests. Am. Midl. Nat. 130, 62–74.