

REVIEW

Introduced weeds pollinated by introduced bees: Cause or effect?

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In the present review we attempt to synthesize evidence for a causative relationship between the presence of non-native bee pollinators and the successful establishment and spread of introduced weed species. Using data drawn from the literature and from our own survey conducted in New Zealand, we show that introduced bees favor foraging on introduced plant species, and that in some cases they depend totally on these plants as sources of nectar and pollen. It is also apparent that the flowers of many introduced plants are visited, exclusively or predominantly, by introduced bees. Accepting that visitation does not necessarily imply pollination, and not all plants require pollination to reproduce, we review relationships between seed set of exotic weeds and visitation by introduced pollinators. Although few studies have been carried out, we show that those reported so far all point to increased seed set when introduced plants are visited by non-native bee species. There is clear evidence for a positive link between the spread of weeds and the presence of introduced bees. Nevertheless, ecologists have neglected this aspect of weed population biology and remarkably few studies have been conducted on the importance of pollinator availability in the management of weed species. We suggest several avenues along which future research can be conducted and highlight how the management of present and future weed species may be influenced by this research.

Keywords: *Apis mellifera*, *Bombus* spp., invasive weeds, weed control, weed management.

INTRODUCTION

The introduction (deliberate or accidental) of non-indigenous species to new habitats has become an increasingly important aspect of global environmental change (Mack *et al.* 2000). The spread of exotic weed species has caused significant economic and ecological problems throughout many parts of the world (Manchester & Bullock 2000). The problem has been particularly acute in Australia and New Zealand, where both agricultural systems and native plant communities have been greatly affected by the introduction of European-origin weeds such as *Echium plantagineum* L., *E. vulgare* L., *Chondrilla juncea* L. and *Hieracium pilosella* L. (Grigulis *et al.* 2001; Hanley & Groves 2002; Meurk *et al.*

2002; Lamoureaux *et al.* 2003). However, significant problems associated with the spread of non-native plants are also apparent in southern Africa, North America and Asia. Even the UK, considered to be one of the least affected regions (Crawley 1997), is now host to several important weed species (Manchester & Bullock 2000; Willis & Hulme 2002).

One often cited reason for the dramatic spread of alien weeds is release from natural enemies (Crawley 1997). Freed from their natural suite of herbivores, plants emerging in an alien environment are able to grow and reproduce without the limiting effects of tissue loss or seed predation, and so gain a competitive advantage over native species. Support for this hypothesis comes from the many examples of successful biological control of alien weed species by specialist insect herbivores: for example, the control of *Eichornia crassipes* (Martius) by *Neochetina bruchi* Hustache, *Opuntia* spp. by *Cactoblastis cactorum* (Bergroth), and *Hypericum perforatum* L. by *Chrysolina quadrigemina* (Suffrian). These examples underscore the close relationship between plants and the

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many insect herbivores that evolved alongside them within their native range. However, while some insects are detrimental to plant fitness, others are an integral part of the reproductive biology of the same plants.

Pollinating insects are vital to the continued existence of most plant species. Although some taxa are able to reproduce, either vegetatively or through self- or wind-pollination, most angiosperms rely on the transmission of pollen by an animal vector from a second plant in order to set seed and reproduce. Sometimes invading weed species do have access to native generalist pollinators in their new environment. *Impatiens glandulifera* Royle, for instance, which relies on pollination by bumblebees in its native Himalayas, is also visited and presumably pollinated by several indigenous bumblebee species in the UK (Chittka & Schurkens 2001). Similarly, the northern European weeds *Lupinus polyphyllus* Lindl. and *Rhododendron ponticum* (L) are both pollinated by European bumblebees, even though these plants are native to North America and Asia, respectively (Cross 1975; Pohtio & Teras 1995). However, other weed species known to rely exclusively on native insects for pollination may find themselves in environments where native insects are incapable of providing this service. One such species, *Lupinus arboreus* Sims., has large zygomorphic flowers that have to be forced apart to expose the stamens and stigma. Only large, powerful bees are able to do this; in its native California *L. arboreus* is pollinated by bumblebees. Interestingly, in New Zealand where bumblebees were introduced from the UK in the late nineteenth century, *L. arboreus* is a serious weed species. In nearby and climatically similar Tasmania (Australia), the species has remained generally scarce for many decades since its introduction. However, the recent introduction of the bumblebee *Bombus terrestris* L. may affect the status of *L. arboreus* here. Seed set in areas recently colonized by this bumblebee has increased dramatically, and it is likely that *L. arboreus* may become as problematic in Tasmania as it is in New Zealand now that it has an effective pollinator (Stout *et al.* 2002).

The relationship between *B. terrestris* and *L. arboreus* in Tasmania highlights the important role pollinating insects may play in the spread of exotic weeds. Nevertheless, despite this and several other examples in the literature documenting preferential visitation of alien weed species by introduced bees, there remains some debate regarding the exact role exotic bees play in the reproduction and spread of introduced weed species (Butz Hury 1997).

In the present review we examine the relationship between the spread of alien weeds and the introduc-

tion of exotic bee species and attempt to shed some light on the following aspects of this relationship: (i) Do exotic bees preferentially forage upon introduced weed species? (ii) Does the presence of exotic bees facilitate the successful spread of forage species through increased reproductive vigor? (iii) Is the distribution of exotic bees limited by the availability of preferred forage species?

We do not consider here the wider ecological impact that introduced bees may have in new environments (e.g. competition with native pollinators, transmission of pathogens) as these have been dealt with in greater detail elsewhere (Butz Hury 1997; Goulson 2003a).

GLOBAL DISTRIBUTION OF EXOTIC BEES

The native range of bumblebees (*Bombus* spp.) is largely confined to the temperate northern hemisphere (Goulson 2003b). However, bumblebees have been deliberately introduced to various countries around the world, often in order to enhance the pollination of introduced crop plants. New Zealand for instance, has four well-established *Bombus* species; *B. terrestris*, *B. hortorum* (L), *B. subterraneus* (L) and *B. ruderatus* (Fabr.), following introductions in 1885 and 1906 from the UK that were intended to improve pollination of the clover, *Trifolium pratense* L. (Hopkins 1914; Macfarlane & Gurr 1995). More recently, *B. terrestris* has colonized Tasmania, probably from New Zealand, and has since spread out to occupy a substantial portion of the island (Stout & Goulson 2000; Hingston *et al.* 2002). Feral populations of *B. terrestris* have also become established in Israel and Japan following escapes from commercial colonies used for pollination in glasshouses (Dafni & Shmida 1996; Dafni 1998). *B. ruderatus* was introduced to Chile in the early 1980s, again for pollination of *T. pratense* (Arretz & MacFarlane 1986), and within 10 years had spread into Argentina (Abrahamovich *et al.* 2001).

The honeybee (*Apis mellifera* L) is native to Africa, western Asia, and south-east Europe (Michener 1974), but has become naturalized throughout much of the rest of the world and is now among the most widespread and abundant insects on earth. The European strain of the honeybee appears to be adapted to temperate and Mediterranean climates, and feral populations occur throughout Asia, North America, the southern half of South America and Australasia. The African race, *A. mellifera scutellata* Lepeletier, is associated with tropical forests and savannas and has spread throughout the neotropics and into North America following its introduction to Brazil in 1957.

The only other bees to have been deliberately introduced to new regions in substantial numbers are members of the Megachilidae. The most widespread is *Megachile rotundata* (F), a native of Eurasia frequently used commercially for pollination of alfalfa (Bohart 1972). *M. rotundata* was introduced successfully to New Zealand in order to pollinate alfalfa (Donovan 1975), and has since become established in southern Australia (Woodward 1996). In North America the species now forms populations as far apart as California and Florida (Frankie *et al.* 1998; Pascarella *et al.* 1999). At least two other exotic Megachilidae are established in California (*M. apicalis* Spinola and *M. concinna* (Smith)) (Frankie *et al.* 1998).

VISITS TO WEED SPECIES BY EXOTIC BEES

Within their native range, different bee species exhibit marked preferences for particular flowers, often those with which they have coevolved and which possess a suitable morphology, enabling them to efficiently access rewards (Fussell & Corbet 1992; Waser *et al.* 1996; Goulson 2003b). There is, however, also a substantial body of evidence showing that this association is maintained when pollinators and plants are moved outside their native range. One study in Canada showed that 75% of the pollen collected by honeybees came from introduced plants (Stimec *et al.* 1997), and a similar preference by honeybees for non-native plants is also apparent in Argentina (Telleria 1993). In Australia the Megachilid *Megachile rotundata* also appears to feed exclusively from introduced plants (Woodward 1996).

In a recent survey of flower use by the four species of introduced bumblebees in New Zealand (Table 1), we recorded few visits to native species and a clear preference for introduced plants (Goulson & Hanley unpubl. data). Of the 36 species visited by bumblebees, only three were native, despite the fact that we surveyed areas throughout the South Island and included both farmland and native vegetation. Visits to native flowers comprised just 1.2% of all visits recorded. Our data lend support to previous studies in New Zealand. MacFarlane (1976) recorded *Bombus terrestris* on 400 exotic plants, but the same bumblebee only visited 19 native species. Moreover, the three other introduced *Bombus* species have previously been shown to feed exclusively on exotic rather than native plant species (Donovan 1980). New Zealand honeybees also rely almost exclusively on introduced plants for pollen during most of the season (Pearson & Braiden 1990). Preferences for non-native plants presumably occur because introduced bees tend to gain more rewards by visiting flowers with which they are coadapted.

In addition to the marked preference shown by introduced bees for exotic plant species, many non-native plants have close plant–pollinator associations with the same insects. Stout *et al.* (2002) showed the close relationship between bumblebees and the pollination of *Lupinus arboreus* in Tasmania. Furthermore, in North America honeybees are the main pollinators of wild radish, *Raphanus sativus* L. (Stanton 1987) and purple loosestrife, *Lythrum salicaria* L. (Mal *et al.* 1992).

The most commonly visited plant species recorded in our survey, *Trifolium pratense*, was deliberately introduced to New Zealand as a pasture crop. This species, like *Lotus corniculatus* and *Trifolium repens*, is highly dependant on insects, particularly bumblebees, for pollination (Knuth 1906; Grime *et al.* 1988) but has declined in abundance in New Zealand due to changes in agricultural practices (W. Lee *Pers. comm.*). However, we also found substantial numbers of bumblebees visiting several important weed species, including *Lupinus arboreus*, *L. polyphyllus*, *Cirsium vulgare*, *Cytisus scoparius* and *Echium vulgare*. Each of these species is known to depend substantially or exclusively on insect pollinators in order to reproduce (Table 1) and all are major weeds (Williams & Timmins 1990).

Although our results lend further support to the contention that exotic bees are important pollinators of various weeds (Stanton 1987; Mal *et al.* 1992; Sugden *et al.* 1996; Stout *et al.* 2002; Goulson 2003a), this clear preference for introduced weed species is insufficient in itself to determine whether the spread of weeds is in fact facilitated by exotic bees (Butz Huryn & Moller 1995; Butz Huryn 1997; Goulson 2003a). Although several problematic weed species represent important nectar and pollen sources for exotic bees, they are also quite able to reproduce successfully in the absence of pollinators. In Canada, *Taraxacum officinale* L. is both a common weed and an important nectar source for honeybees, yet the species is apomictic and does not require pollination for seed set to occur (Grime *et al.* 1988). Similarly, several of the weed species we observed bumblebees foraging on in New Zealand are capable of self-pollination or apomictic reproduction (e.g. *Cirsium vulgare*, *C. arvense*, *Hypericum perforatum*, *Mimulus guttatus*). Indeed, Butz Huryn (1997) argues that most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic, or primarily reproduce vegetatively.

In addition to demonstrating the clear foraging preference introduced bees have for introduced plants, we also need to demonstrate that enhanced reproduction in weeds is actually facilitated by the presence of exotic bee species. The most obvious way to do this is to examine

Table 1. Forage preferences of four introduced bumblebee (*Bombus*) species to the South Island of New Zealand

Plant species	Origin	Pollination mechanism	<i>B. terrestris</i>		<i>B. hortorum</i>		<i>B. ruderatus</i>		<i>B. subterraneus</i>		Total
			Pollen	Nectar	Pollen	Nectar	Pollen	Nectar	Pollen	Nectar	
<i>Trifolium pratense</i> L.	Europe	Insect ¹	28	146	402	140	100	14	6	887	
<i>Echium vulgare</i> L.	Europe	Insect ²	63	233	19	107	9	93	6	530	
<i>Lotus corniculatus</i> L.	Europe	Insect (self) ³	66	24	15		8	1	6	119	
<i>Trifolium repens</i> L.	Europe	Insect ³	23	78	3	3	1	1	1	110	
<i>Cirsium vulgare</i> (Savi) Ten.	Europe	Insect (self) ¹		26		11				38	
<i>Hypericum perforatum</i> L.	Europe	Apomictic ¹	20		4		11	2		37	
<i>Lupinus polyphyllus</i> Lindl.	North America	Insect ⁴	15	3	2	1	1			28	
<i>Cirsium arvense</i> (L.) Scop.	Europe	Insect (self) ¹	2	22					1	25	
<i>Digitalis purpurea</i> L.	Europe	Insect (self) ³		1	6	13		1	4	25	
<i>Lupinus arboreus</i> Sims.	North America	Insect ⁵	17	5	2		1			25	
<i>Medicago sativa</i> L.	Europe	Insect (self) ³	12	8						20	
<i>Cytisus scoparius</i> L.	Europe	Insect ³	19							19	
<i>Mimulus guttatus</i> DC.	North America	Insect (self) ⁵	3	2	2	3	1			11	
<i>Vicia sativa</i> L.	Europe	Insect (self) ³		11						11	
<i>Prunella vulgaris</i> L.	Europe	Insect ¹		1	8	1				10	
<i>Cabystegia sylvestris</i> (Willd.)	Europe	Insect ¹		1		9				9	
<i>Leycesteria formosa</i> Wallr.	Asia		1	3	2				2	8	
<i>Hypochoeris radicata</i> L.	Europe	Insect ¹	1	5						6	
<i>Buddleia davidii</i> Franch.	Asia	Insect ⁵		2		3				5	
<i>Lathyrus tuberosus</i> L.	Europe	Insect ³		4		1				5	

Table 1. (Cont.)

Plant species	Origin	Pollination mechanism	<i>B. terrestris</i>		<i>B. hortorum</i>		<i>B. ruderals</i>		<i>B. subterraneus</i>		Total
			Pollen	Nectar	Pollen	Nectar	Pollen	Nectar	Pollen	Nectar	
<i>Coronilla varia</i> L.	Europe	Insect ³	1	3							4
<i>Hypericum calycinum</i> L.	Europe		4								4
<i>Rosa canina</i> L.	Europe	Insect (self) ³	2			1					3
<i>Verbascum nigrum</i> L.	Europe	Insect ⁵	1		1			1			3
<i>Verbascum thapsus</i> L.	Europe	Insect (self) ⁵	1		2						3
<i>Centaurea cyanus</i> L.	Europe	Insect (self) ³	2								2
<i>Cichorium intybus</i> L.	Europe	Insect (self) ³						2			2
<i>Ulex europaeus</i> L.	Europe	Insect (self) ¹	1	1							2
<i>Antirrhinum majus</i> L.	Europe	Insect (self) ⁵	1								1
<i>Centaureum erythraea</i> Rafn.	Europe	Self (insect) ¹		1							1
<i>Impatiens glandulifera</i> Royle	Asia	Insect (self) ¹					1				1
<i>Parentucellia viscosa</i> (L.) Caruel	Europe		1								1
<i>Tilia cordata</i> Miller	Europe	Insect ⁵					1				1
Native species											
<i>Metrosideros excelsa</i> (Sol.) Gaertn.				8							8
<i>Phormium tenax</i> Forst.				5							5
<i>Hebe cantabrigiensis</i> Armst.				1							1

One-hour timed searches were conducted in 70 sites, predominantly in the Canterbury and Otago regions during January 2003. Numbers are counts of bees collecting nectar or pollen. In addition to showing bumblebee feeding preferences (pollen and nectar) on different plants, the origin of non-native plants is shown together with the pollination mechanism of each of the non-native species where known. Sources for the latter are: ¹ Grime *et al.* (1988); ² Rademaker *et al.* (1997); ³ Knuth (1906); ⁴ Williams (1987); ⁵ Clapham *et al.* (1987).

the relationship between weed fecundity and bee visitation.

WEED FECUNDITY AND EXOTIC BEES

Surprisingly little is known about the pollination biology of weed species in new environments and it is unclear whether inadequate pollination is commonly a limiting factor (Richardson *et al.* 2000). As already noted, several weed species are incapable of self-fertilization, and so clearly rely on insect pollinators in order to set seed. This group includes *Lupinus arboreus* and *Cytisus scoparius*, both of which are self-incompatible and rely entirely on pollination by bumblebees in order to reproduce (Stout 2000; Stout *et al.* 2002). We have already seen how seed set in *Lupinus arboreus* has been increased in Tasmania as a result of the recent introduction of *Bombus terrestris* (Stout *et al.* 2002). Another member of the Fabaceae, *Ulex europeus*, is also thought to depend on honeybee and bumblebee pollination. MacFarlane *et al.* (1992) showed that the lack of pollinators in the New Zealand Chatham Islands, where honeybees and bumblebees are absent, significantly reduced the rates of successful seed set in this species.

Both honeybees and the yellow star thistle (*Centaurea solstitialis* L.) were introduced to North America at approximately the same time in the 1800 s. The latter has now invaded over 4 million hectares of pasture in the western USA and is one of the most economically important weeds in the region (Gerlach 1997). A recent study by Barthell *et al.* (2001) examined the relationship between honeybees and seed set in *C. solstitialis* at three sites in California. Not only were honeybees the most frequent visitors to *C. solstitialis* at all three sites, but there was also a significant correlation between visit rates and the average number of viable seeds produced by *C. solstitialis*. Furthermore, the selective exclusion of honeybees from flower heads reduced seed set significantly, highlighting the importance of honeybees to the reproductive ecology of this species.

In Queensland, Australia, Goulson and Derwent (unpubl. data) examined the pollination ecology of *Lantana camara* L and in particular its relationship with honeybees. *L. camara*, a woody shrub native to South America, is among the most widespread and troublesome exotic weeds of the old-world tropics (Morton 1994; Anon. 2000). In Australia alone, *L. camara* currently covers approximately 40 000 km² of forest, including national parks, and costs an estimated A\$10 million per year to control. A further A\$7.7 million is spent on losses to the livestock industry due to decreased

stocking densities and the deaths of approximately 1500 cattle per year through poisoning (Anon. 2000). Goulson and Derwent (unpubl. data) not only demonstrated that *L. camara* requires cross-pollination in order to set fruit, but that seed set is limited by pollinator abundance. At many sites, particularly in southern Queensland, honeybees were the only flower visitors recorded and seed set was strongly correlated with honeybee abundance throughout the areas studied. While many more studies are required on this important topic, it seems clear from the evidence gathered so far that for some weeds introduced bees are a strong catalyst for their spread in new environments.

WEED ABUNDANCE AND THE DISTRIBUTION OF EXOTIC BEES

The importance of non-native plant species to the success of exotic bee species has received little attention, but can be inferred from the close relationship between preferred food plants and their bee pollinators. Recent declines in the numbers and diversity of European bumblebee species have been attributed to the loss of flower rich pastures and the resulting reduction in the abundance of key forage plants (Carvell 2002; Goulson & Derwent unpubl. data).

For some introduced bees therefore we might expect their distribution and abundance to be closely tied in with the availability of alien food plants. This seems to be exactly the case in New Zealand where our recent survey (Goulson & Hanley unpubl. data) found a decline in the distribution of *Bombus ruderatus* and *B. subterraneus* relative to the earlier study of Macfarlane and Gurr (1995). Both bumblebee species rely greatly on non-native Fabaceae, such as *Trifolium pratense* and *Lotus corniculatus*, for pollen (Table 1), and both food plants have declined greatly in abundance in New Zealand due to changing agricultural practices (W. Lee pers. comm.).

For other bees however, their generalist nature makes them less reliant on specific plant species. Both *Bombus terrestris* and *Apis mellifera* have more polylectic foraging habits than many bee species, meaning that they are able to feed from a range of non-native and native plant species (Buchmann 1996; Dafni & Shmida 1996; Butz Huryn 1997; Hingston *et al.* 2002; Goulson 2003a). Although both species may benefit greatly from the presence of alien weed species, their continued spread is unlikely to be strongly constrained by the absence of introduced plants. Our study in New Zealand showed that *B. terrestris* remained as widespread as it was in Macfarlane and Gurr's (1995) survey, fed from more

plants than the other *Bombus* species, and was the only bumblebee found foraging on native plant species (Table 1). It was also the only bumblebee species to occur in areas dominated by native vegetation, notably along the south-west coast, although it tended to be scarce in such areas. Similarly, *B. terrestris* is rare or absent in the World Heritage area in the south-west of Tasmania, where native vegetation predominates (Goulson *et al.* 2002), although the most recent survey suggests that it may be slowly invading this area (Hingston *et al.* 2002).

Although the successful spread of the two most commonly introduced bee species may only be partly influenced by the presence of introduced weeds, forage availability could still influence the establishment success of non-native bee species. This relationship is important because the number and distribution of introduced bees may have far-reaching effects on the population biology of future weed introductions. Clearly some exploratory work needs to focus on the relationship between forage availability and bee population size. However, more pressing still is the need to examine how the presence of exotic bees affects the fecundity and spread of alien weeds.

OVERVIEW AND FUTURE RESEARCH

As a result of the significant ecological and economic costs associated with their presence, a considerable amount of research has focused on the population biology of alien weeds (Hoffmann & Moran 1998; Kriticos *et al.* 1999; Downey & Smith 2000; Willis & Hulme 2002). Often this research takes the form of demographic studies where important aspects of particular stages of weed life history are identified. This information is vital to our understanding of how and why non-native plants become serious weeds, and often allows us to target vulnerable periods of the weed life cycle in order to control their populations. However, to our knowledge, no serious attempt has been made to quantify the role of pollinators on fecundity and population dynamics in introduced plant species.

Because most weed species are short-lived and dependent on high reproductive rates, seed production is a crucial factor in determining their persistence and abundance in the plant community (Grime 2001). Furthermore, given that many invasive weeds rely greatly, or even exclusively on insects for pollination, the presence of pollinators should be crucial to their persistence and spread in new environments. Yet what is most striking from the literature is that surprisingly little work has been performed on the interaction between introduced weeds and introduced pollinators. Only a handful of

published accounts have dealt with the issue over a single field season (MacFarlane *et al.* 1992; Barthell *et al.* 2001; Stout *et al.* 2002) and no long-term studies have been conducted at all. The fact that the small amount of information we do have points to an important causative link between the presence of introduced bees and the spread of weeds highlights the pressing need for ecologists to undertake this kind of research. More attention needs to be focused on how the presence of introduced bees affects weed seed set and fecundity, particularly experimental studies that involve the manipulation of pollinator populations, or more feasibly their access to flowers.

Even for established weed species, information on the role of introduced bees in promoting seed set is of management value. Although it is difficult to see how effective and economically viable exclusion of feral bee populations from target weeds could be undertaken, it is possible to control the activities of commercial beekeepers. Exclusion of honeybee hives from and around national parks or other areas where bee-pollinated weeds have significant economic or ecological effects could reduce significantly seed set and ultimately the population size of the target species. Clear evidence for a causative link between introduced pollinator activity and the spread of weeds may allow us to pre-empt the establishment and spread of introduced plant species that as yet have no effective pollinators in their new environment.

So called 'sleepers' are plant species that have naturalized in a new environment but have failed to expand their populations exponentially (Groves 1999). Usually this is because one key element in the plant's life history prevents it from expanding its population and achieving weed status. In some cases this key element might be effective pollination by non-native bees. The example of increased seed set in Tasmanian populations of *Lupinus arboreus* following the arrival of *Bombus terrestris* shows that pollinator availability may indeed be an important controlling factor (Stout *et al.* 2002). Now that bumblebees have colonized Australia, many more 'sleepers' might be awoken, and even if only one achieves weed status, the economic and environmental costs to that country could be substantial.

Although available information is limited, a positive feedback between the abundance of weeds and bumblebees is probable, because an increase in weed populations may encourage more bumblebees, and vice-versa. Of particular interest is the relationship between plant population size, bee foraging activity and weed fecundity. Because plant aggregation and density can markedly influence bee foraging behavior (Klinkhamer

& de Jong 1990; Cresswell 2000; Ohashi & Yahara 2002) we might well expect that the more common a weed becomes in a new environment, the more likely it is that introduced pollinators will visit the plant, and hence the greater the potential for increased seed set. Related to this is the question of how the availability of introduced forage plants affects the population size and range of introduced bees. These interactions represent an important potential positive feedback mechanism for the spread of invasive weeds. Nevertheless, neither question has yet been addressed for any weed species, actual or potential.

We have shown how introduced bees tend to favor introduced weed species, but accept Butz Huryn's (1997) contention that this alone does not conclusively show that non-native bees are responsible for the spread of weeds. The clear preference demonstrated by introduced bees for non-native plants does provide good circumstantial evidence for a causative relationship. Furthermore, the limited evidence available points towards the fact that visitation by introduced bees does actually increase the fecundity of those weed species studied. Again this is not in itself conclusive proof that insect pollination leads to increased weed populations, as other aspects of the weed's life history might limit the successful colonization of new habitats. Nevertheless, it is clear that the relationship between introduced weeds and introduced bees could lead to the successful spread of the former. Given the considerable environmental and economic costs associated with the spread of invasive weeds (Manchester & Bullock 2000; Williams & West 2000), this relationship would seem to be worthy of far more research than it has so far received.

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