Population dynamics of the invasive weed *Lupinus arboreus* in Tasmania, and interactions with two non-native pollinators

D GOULSON & E L ROTHERAY

School of Biological and Environmental Sciences, University of Stirling, Stirling, UK

Summary

The factors that determine which plant species become invasive weeds are not well understood and there have been few studies of population dynamics in the early stages of invasion. Here, we examine changes in population size, pollinator visitation and seed set of the tree lupin, *Lupinus arboreus*, in Tasmania between 1999 and 2010. *Lupinus arboreus* is a native of California that has become a major environmental weed in New Zealand and Chile, but has not yet become a serious weed in Tasmania. Our data suggest that the main pollinators of *L. arboreus* are honeybees and the bumblebee, *Bombus terrestris*, which invaded in 1992. There was no clear evidence for an impact of the arrival of bumblebees. *Lupinus arboreus* population size increased by 76% between 1999 and 2010, despite weed control pro-grammes. Populations appeared to be unstable; 43% of populations detected in 1999 were extinct by 2010, but this was more than offset by establishment of new populations. Inland populations tended to be smaller and were more likely to go extinct, compared with coastal populations, and some coastal populations had increased fourfold in 11 years. Large populations in 2010 tended to have higher seed set than smaller populations. The overall rate of increase suggests that *L. arboreus* may become a major environmental weed in Tasmania. Control of expanding populations is likely to become more difficult if, as we observed, seed set increases with population size.

Keywords: Allee effect, *Apis mellifera*, *Bombus terrestris*, invasive species, *Lupinus arboreus*, pollination, population size, seed set.

Introduction

The threats to biodiversity and agriculture posed by non-native species are well established (Simberloff & Rejmanek, 2011). In Australia, there are currently more than 2000 species of non-native plants established in the wild (Rozefelds *et al.*, 1999). It is estimated that introduced plants cost the Australian agricultural industry $4 billion per annum in control measures and lost yields (Sindel, 2000).

While some non-native plants are highly invasive, the majority remain scarce and cause few problems. It is not always easy to predict or explain which species thrive and which do not in a particular non-native environment (e.g. Gasso *et al.*, 2010); aside from the suitability of the abiotic conditions, weediness may be limited by the availability of mutualists including pollinators, seed dispersers and soil microbiota (Richardson *et al.*, 2000; Stokes *et al.*, 2006). Some non-native plants remain at low levels for many years and then increase in

Correspondence: Professor D Goulson, School of Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK.
Tel: 0044 1786 467 759; Fax: 0044 1786 467 843; E-mail: dave.goulson@stir.ac.uk

abundance; these are sometimes known as 'sleeper weeds' (Groves, 2006). However, there are few documented examples and it is often not clear what triggered the population increase. Given the large numbers of non-native plant species present at low levels in most natural ecosystems, it is important to improve our understanding of the likelihood that these plants might become serious weeds.

Lupinus arboreus Sims. (Fabaceae) is a short-lived woody perennial, native to the sandy coastal areas and canyons of California (Abrams, 1964). In its native range, it is pollinated primarily by honeybees (*Apis mellifera*) and *Bombus vosnesenskii* (Barbour *et al.*, 1973; Kittelson & Maron, 2000). However, given that honeybees are not native to the Americas, it seems likely that the plant coevolved with bumblebee pollinators. When introduced outside its native range, *L. arboreus* can become a major invasive weed. For example, in New Zealand, *L. arboreus* is listed among the worst 33 environmental weeds (Donovan, 1990; Williams & Timmins, 1990), forming very large stands in coastal areas, along river banks and road verges (Sullivan *et al.*, 2009). It is also regarded as one of the most aggressive and harmful non-native weeds in Chile (Molina-Montenegro *et al.*, 2008). In New Zealand, *L. arboreus* is pollinated by bumblebees and honeybees, both introduced in the nineteenth century (Hanley & Goulson, 2003), while in Chile, it is pollinated primarily by the native bumblebee *Bombus dahlbomi* and by introduced honeybees (Molina-Montenegro *et al.*, 2008).

In Tasmania, *L. arboreus* was deliberately introduced in the 1920s to help stabilise sand dunes and prevent their spread, and the first records of this species occurring naturalised in the bush are from the early 1940s (Stout *et al.*, 2002). By 1955, scattered but extensive populations were recorded (Raphael, 1955). Populations occur both in inland areas disturbed by anthropogenic activity (road verges, railway cuttings, quarries, brownfield sites) and in coastal dune systems (Stout *et al.*, 2002). Prior to the arrival of bumblebees, it seems probable that *L. arboreus* was pollinated primarily by honeybees, which were introduced to Tasmania in 1826 (Doull, 1973). Tasmania lacks any native bee species heavy enough to operate the pump mechanism of the flower and Stout *et al.* (2002) recorded very few visits to *L. arboreus* by native bees.

It is not clear why *L. arboreus* has become a major weed in New Zealand and Chile, but not in Tasmania. One obvious explanation may be the historical lack of bumblebees. However, in 1992, one bumblebee species, *B. terrestris,* invaded Tasmania from New Zealand (very probably facilitated by humans) (Semmens *et al.*, 1993; Stout & Goulson, 2000; Goulson *et al.*, 2002; Goulson, 2003; Schmid-Hempel *et al.*, 2007). Prompted by this

invasion, Stout *et al.* (2002) studied 20 populations of *L. arboreus* in 1999, recording their population size, bee visitation rates and seed set. They found that visitation rates by both *A. mellifera* and *B. terrestris* were correlated with seed set at the population level, while native bees were too small to manipulate flowers to extract pollen (Stout *et al.*, 2002). Their conclusions were equivocal; on the one hand, the historical lack of bumblebees provided the most obvious explanation for the failure of *L. arboreus* to become a major weed in Tasmania as it has elsewhere, but on the other hand, *A. mellifera*, which was introduced to Tasmania before *L. arboreus* (Ziegler, 1993), provides an alternative pollinator, albeit not one with which the plant coevolved.

Here, we describe a follow-up study where we revisit the 20 populations studied by Stout *et al.* (2002), 11 years after their visit, to establish whether *L. arboreus* populations have grown in the intervening years and to examine how bee visitation patterns and seed set have changed, with a view to establishing whether the introduction of bumblebees has had a substantial impact on the population dynamics of this invasive weed species.

Methods

Study species

Lupinus arboreus produces relatively large (14–18 mm) bright yellow flowers in whorls on racemes (Jepson, 1951). Flowers are protandrous and insect visits are usually necessary to fertilise flowers, which are generally not capable of automatic self-pollination or apomictic seed production (Knuth, 1908; Richards, 1986; Kittelson & Maron, 2000). Flowers of *L. arboreus* are nectarless, but are visited by bees for pollen. The flower mechanism has a pump arrangement, whereby the thickened ends of the stamens press out strings of pollen from the tip of the keel when a heavy insect lands on the flower (Knuth, 1908).

Data collection

In November and December 1999, Stout *et al.* (2002) surveyed a 1306 km route by car for *Lupinus arboreus* populations (Fig. 1). The route roughly circumnavigated Tasmania, taking in the major climatic zones and a range of different biotopes. Surveying from a car is a crude technique that may fail to detect non-flowering populations and which is biased towards populations close to roads. However, given that *L. arboreus* are up to 2-m tall and that established plants tend to be in full flower at this time, it is probable that most populations
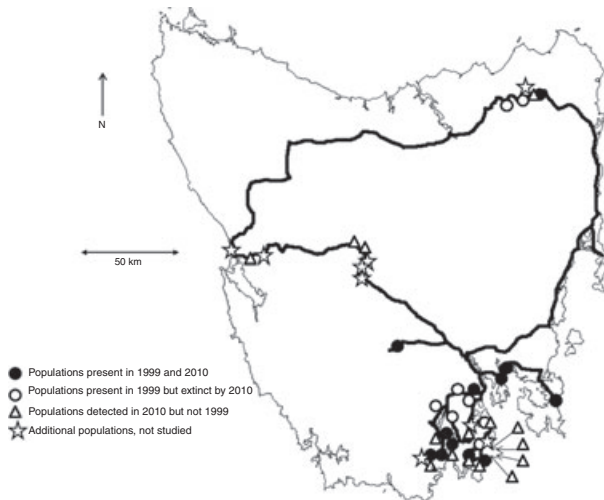
Fig. 1 Survey route and locations of *L. arboreus* populations.

● Populations present in 1999 and 2010
○ Populations present in 1999 but extinct by 2010
△ Populations detected in 2010 but not 1999
☆ Additional populations, not studied

close to the road were detected. Twenty-eight populations were detected in 1999, of which 20 (10 inland and 10 coastal) were studied in more detail. For these twenty populations, population size was estimated and visitation rates by insects were recorded for 10 min on each of six replicate patches of flowers. For each patch, the number of racemes, the number and identity of visiting insects and the number of racemes visited per insect were recorded. All observations were made between 09:45 and 16:00, in clear weather. In addition, seed set was scored for the lowest 10 florets on 10 randomly selected racemes from each of five randomly selected plants. Some florets fail to set seed entirely, leaving a readily detected scar on the stalk of the raceme. For those that produced a seed pod, the number of seeds per pod was counted. The mean number of seeds produced per floret (including florets that produced no seeds) was used in the analyses. These data are reported in Stout *et al.* (2002).

In December 2010, we resurveyed the same route for *L. arboreus* using the same method. At locations where *L. arboreus* had been found in 1999, searches on foot were performed as necessary to establish whether they still persisted. Where populations remained, population size, insect visitation and seed set were recorded, exactly as carried out in 1999. Both flowering and non-flowering plants were recorded. For any additional populations that were detected, only population size was recorded.

Changes in population size between the two survey dates were examined using a generalised linear mixed model. Inspection of residuals confirmed that the data were best described by a negative binomial distribution, which was fitted using a log link in SPSS version 19.0. Population size was the dependent variable, with year and location (coastal versus inland) and the interaction between them included as explanatory factors. Site was

included as a random effect, because we had two population measures per site (for 1999 and 2010). To examine whether visitation rates by the two bee species or seed set had altered between the two study periods in 1999 and 2010, means per site were compared using paired *t*-tests, after confirming approximation to normality of the data using Kolmogorov–Smirnov tests. Annual population growth rate ($\lambda = (N$ in 2010$/N$ in 1999$)^{(1/11 \text{ years})}$) was calculated for each population, excluding those which had gone extinct by 2010. A Pearson's product-moment correlation was used to examine whether sites with high population growth rates tended to have more bee visitors. Finally, we used linear regressions to examine whether population growth rate could be predicted by seed set in either 1999 or 2010.

Results

In total, 28 populations of *L. arboreus* were detected along the 1999 survey route (8 were not studied other than to record their presence). Of these, 16 were still present in 2010 and 12 had gone extinct. However, an additional 15 populations were detected, bringing the total number of populations detected in 2010 to 31.

Of the 10 coastal and 10 inland populations of *L. arboreus* that were studied in detail in 1999, two of the coastal and six of the inland populations had gone extinct by 2010. Populations that went extinct over this period tended to be those which were smallest in 1999 (mean ± SE; 24.1 ± 8.5 and 157.9 ± 42.7 for extinct versus surviving populations, respectively, $t_{18} = 2.51$, $P = 0.022$).

Overall, population size increased over time (generalised linear mixed model, $\chi^2_1 = 12.9$, $P < 0.001$), but there was a strong interaction between time and population location, with inland populations tending to increase less than coastal populations ($\chi^2_1 = 8.81$, $P = 0.003$) (Fig. 2). In 1999, the 20 populations comprised 2088 plants (mean ± SE; 104.4 ± 29.5). Despite the eight extinctions, the total number of plants present at these 20 sites had increased to 3680 by 2010 (mean ± SE; 184 ± 67.8, or 307 ± 99.0, if extinct populations are excluded). In both 1999 and 2010, inland populations tended to be smaller than coastal (dune) populations (mean ± SE; 31.0 ± 10.0 and 177.8 ± 48.8, for inland versus coastal populations, respectively, $t_{18} = 2.95$, $P = 0.009$ for 1999; 36.5 ± 15.5 and 322.8 ± 92.3, for inland versus coastal populations, respectively, $t_{25} = 3.17$, $P = 0.004$ for 2010).

Annual population growth rates varied from 0.68 to 1.16 for populations, which survived across the period, with seven populations increasing, one remaining unchanged and four declining. There was no significant
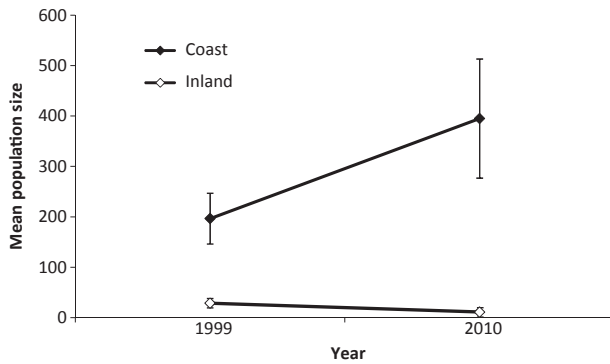
Fig. 2 Population change between 1999 and 2010 for populations of *L. arboreus*. Each point is a mean ± SE based on 10 populations.

correlation between annual population growth rate and populations size in 1999 ($r = 0.457$, n.s.).

In 1999, bumblebees were still largely confined to the south-east of Tasmania; they were absent from seven of the 20 *L. arboreus* populations surveyed. By 2004–2005, bumblebees had been recorded throughout Tasmania (Hingston, 2006) and our personal observations suggest that they are abundant throughout the island, wherever suitable flowers are present. We recorded them visiting nine of the 10 *L. arboreus* populations for which pollinator observations were made in 2010. However, visitation rates by bumblebees had not changed significantly between 1999 and 2010 (mean visits per raceme per hour ± SE; 1.46 ± 0.697 and 1.25 ± 0.380 for 1999 and 2010, respectively, paired *t*-test, $t_9 = 0.386$, n.s.).

Honeybees were recorded at 11 of 20 sites in 1999 and just two of 10 sites in 2010 (Table 1). Visits by honeybees declined from a mean of 1.08 ± 0.50 visits per raceme per hour in 1999 to just 0.0023 ± 0.0016 visits in 2010. However, this difference was not significant, with large variation between sites and many sites where no honeybees were recorded in both years (paired *t*-test, $t_9 = 2.167$, $P = 0.58$).

In 2010, mean seed set per floret per site was not correlated with visitation rate of either bee species (Pearson product-moment correlation, $r^2 = 0.243$, d.f. $= 10$, n.s. and $r^2 = 0.428$, d.f. $= 10$, n.s. for bumblebees and honeybees respectively), although it should be noted that our power to detect any relationship was reduced by the smaller sample size in 2010 ($n = 10$ compared with $n = 20$ in 1999). Annual population growth was not significantly correlated with honeybee, bumblebees or total bee visitation rates in either 1999 or 2010 (Pearson product-moment correlations, $r^2 < 0.521$ in all cases, all n.s.). At some sites, honeybees appear to have been replaced by bumblebees between 1999 and 2011 (sites 12, 13, 15, 17 and 19, Table 1). Mean seed set per floret per site was not significantly different between

1999 and 2010 (paired *t*-test, $t_9 = 2.24$, n.s.), although sites in which honeybees had been replaced by bumblebees since 1999 tended to exhibit a slight but non-significant increase in seed set compared with sites where bumblebees were present in both study years ($t_8 = 1.93$, $P = 0.089$).

Mean seed set per floret in 1999 and 2010 was strongly positively correlated ($r^2 = 0.725$, d.f. $= 10$, $P = 0.018$, Fig. 3). Also, population size in 2010 was positively correlated with seed set in 2010 ($r^2 = 0.677$, d.f. $= 10$, $P = 0.031$, Fig. 4). Annual population growth between 1999 and 2010 was not predicted by seed set in 1999 (linear regression, $r^2 = 0.002$, $n = 12$, n.s.), but was predicted by seed set in 2010 ($r^2 = 0.696$, $n = 12$, $P = 0.001$).

Discussion

The broad picture of abundance derived from comparing our 1999 and 2010 population surveys suggests that *L. arboreus* populations are unstable, being prone to extinctions or rapid population increases. During this period, the number of populations detected rose from 28 to 31, with 12 populations present in 1999 going extinct by 2010, but 15 new populations appearing. Overall, populations had significantly increased; the total number of plants detected had increased by c. 76%, and population size had approximately tripled in those populations which had survived from 1999 to 2010. The populations that had gone extinct tended to be those that were smallest in 1999, while those which had grown most tended to be those which were largest in 1999. The location of populations appears to have a strong influence on their population biology; inland populations tend to be smaller than those on coastal dunes (in both 1999 and 2010) and 6 of 10 inland populations went extinct.

These patterns are readily explained. *Lupinus arboreus* is a pioneer species associated with sand dunes and disturbed habitats. Tasmania has extensive areas of coastal dunes that clearly provide large areas of suitable habitat in the long term, so populations in these habitats tend to be large and are unlikely to go extinct. In contrast, inland populations are primarily associated with anthropogenic disturbance (quarries, road cuttings, railway embankments). Such populations are likely to disappear if disturbance ceases and are vulnerable to roadside applications of herbicides, which appear to be frequent. Two of the sites where roadside populations had gone extinct showed signs of herbicide use, and two extant roadside populations contained plants that were dead or dying following recent applications. Populations in disturbed areas may also be destroyed by the disturbance itself; one population had been largely

Table 1 Details of *Lupinus arboreus* populations used in this study, and visitation rates per raceme per hour by bumblebees (bbee) or honeybees (hbee)

Site No.	Site location	Latitude & Longitude	Coast/ Inland	1999 Population size	2010 population size	1999 bbee visitation rate	2010 bbee visitation rate	1999 hbee visitation rate	2010 hbee visitation rate	Population growth rate λ
1	Kingston	42° 58'S 147° 20'E	I	15	15	6.42	2.09	0.12	0	1.00
2	C638 btw Dover & Surveyors Bay	43° 17'S 147° 03'E	C	150	353	3.66	2.22	0	0	1.08
3	Dover beach	43° 18'S 147° 01'E	C	250	779	3.12	3.40	0	0	1.11
4	Ranelagh	43° 00'S 147° 03'E	I	3	0	3		0		–
5	A6 W of Kingston	42° 58'S 147° 16'E	I	75	0	2.76		0.06		–
6	Craddoc	43° 06'S 147° 02'E	I	7	0	2.28		0		–
7	West Bay Golf Club	43° 00'S 147° 18'E	I	35	0	1.86		0.18		–
8	A6 SW of Dover	43° 18'S 147° 00'E	I	25	1	1.74		0		0.75
9	Alonnah, Bruny Island	43° 18'S 147° 15'E	C	60	315	0.6	0.80	0	0	1.16
10	B66, North Bruny Island	43° 09'S 147° 15'E	C	8	0	0.48		0		–
11	W of Westerway	42° 40'S 146° 48'E	I	20	2	0.42	0.00	0	0	0.81
12	Adventure Bay, Bruny Island	43° 22'S 147° 20'E	C	450	912	0.18	2.37	2.28	0.015	1.07
13	Seven Mile Beach	42° 50'S 147° 31'E	C	250	761	0.18	0.05	2.28	0	1.11
14	A3 nr Branxholm, W of Derby	41° 11'S 147° 44'E	I	20	0	0		8.16		–
15	Derby	41° 08'S 147° 50'E	I	100	105	0	0.33	4.68	0.008	1.00
16	Neck Beach, Bruny Island	43° 17'S 147° 20'E	C	35	0	0		1.5		–
17	NE of Seven Mile Beach	42° 52'S 147° 32'E	C	400	412	0	0.04	1.44	0	1.00
18	Tonganah	41° 11'S 147° 38'E	I	10	0	0		1.38		–
19	Eaglehawk Neck	43° 01'S 147° 55'E	C	100	24	0	1.18	0.06	0	0.88
20	Surveyors Bay	43° 16'S 147° 06'E	C	75	1	0		0		0.68

The bumblebee visitation rate is visits per raceme per hour. 2010 visitation rates were not assessed for sites where only one plant remained in 2010.

$\lambda = (N$ in 2010$/N$ in 1999$)$ ^ $(1/11)$.
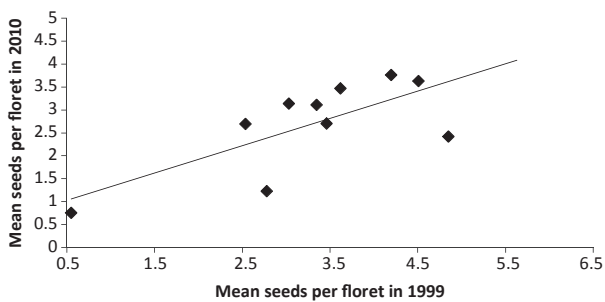
Fig. 3 Relationship between seed set per floret in 1999 and 2010 for 10 populations of *L. arboreus* which survived this period (Pearson product-moment correlation, $r^2 = 0.725$, d.f. = 10, $P = 0.018$).
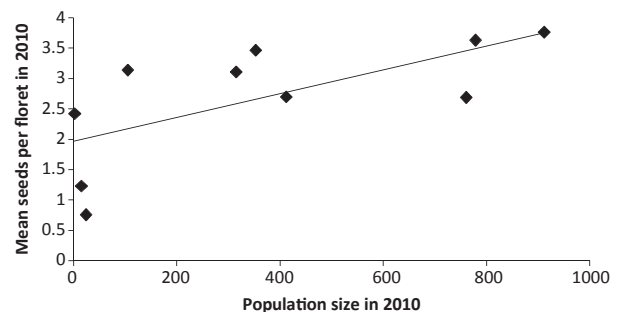
Fig. 4 Relationship between population size in 2010 and mean seed set per floret per site in 2010 ($r^2 = 0.677$, d.f. = 10, $P = 0.031$).

destroyed by a housing development. It should be noted that we did not attempt to quantify the number of seeds present in the soil. *Lupinus arboreus* can accumulate a substantial seedbank with seeds able to lie dormant for several years (Maron & Simms, 1997), so that populations that appeared to have gone extinct might revive, particularly if the soil is disturbed.

Tasmania's coastal dunes contain many rare endemic plants (Reid *et al.*, 1999) and the marked increase in the size of *L. arboreus* populations occupying dune systems is thus a cause for serious concern. *Lupinus arboreus* is an invasive pioneer species that fixes nitrogen and enriches the soil, facilitating the invasion of other plants and hence also the displacement of native plant species (Maron & Conners, 1996;

Pickart *et al.*, 1998). Although it is hard to establish events over the last 11 years, it is clear that *L. arboreus* is subject to control programmes at some coastal sites; for example, at Surveyor's Bay, Seven Mile Beach and Adventure Bay, local volunteers are used to clear invasive weeds and extensive replanting of native species within protective cloches was evident. However, these efforts appear to be of limited efficacy; while the population at Surveyor's Bay had declined sharply, the populations at Seven Mile Beach and Adventure Bay have both increased greatly and are now so large that hand weeding would be exceedingly difficult. This may be partly because the seedbank enables this species to repopulate areas from which plants have been cleared.

Of additional concern is the finding that seed set per plant is highest in large populations. We cannot discern whether these populations are large because seed set is high or whether large population size has a positive effect on seed set. The latter might reflect an Allee effect, whereby population growth shows positive density dependence at low numbers (Stephens *et al.*, 1999), although we cannot be certain that higher seed set leads to higher population growth, because other negative density-dependent factors may be in operation. Others have found evidence of Allee effects in invading plants (e.g. Davis *et al.*, 2004). The implication of an Allee effect is that expanding populations may become more difficult to control. The cause of increased seed set in large populations is unclear; large populations do not seem to receive higher numbers of bee visits per raceme per hour, but they may benefit from greater rates of outcrossing.

Has the arrival of bumblebees contributed to the expansion of *L. arboreus* populations? It is difficult to reach a firm conclusion to this question without data on the population trajectory over the ~78 years prior to commencement of our study. If we extrapolate backwards, assuming the overall population growth rate has remained unchanged over time, we obtain predicted past populations of 1185 for 1988, 672 for 1977 and so on back to a population of 40 in 1922, the approximate year of introduction. Thus, there is no evidence that the rate of increase has changed since the arrival of bumblebees, perhaps because honeybees provided an adequate pollination service. Nonetheless, the increase of 76.25% over 11 years, despite the introduction of control programmes at a number of sites, suggests that *L. arboreus* is likely to become a major environmental weed in Tasmania, as it has in New Zealand and Chile, particularly in coastal sites. Control of expanding populations is likely to become progressively more difficult if, as we observed, seed set increases with population size.

Lupinus arboreus is just one of many invasive plants in Tasmania that coevolved with bumblebee pollinators, such as *Rubus fruticosus* L., *Digitalis purpurea* L., *Ulex europaeus* L., *Echium plantagineum* L. and *Cytisus scoparius* (L.) Link (Hanley & Goulson, 2003). Some of these, such as *D. purpurea*, are not pollinated by honeybees and so may exhibit a more marked response to the introduction of a coevolved pollinator. At present, we have a poor understanding of how introduced bees interact with invasive plants. Given that the introductions of non-native bumblebees continue to occur both accidentally (e.g. *B. terrestris* in Japan, Yokoyama & Inoue, 2010), and deliberately (*B. terrestris* in Chile, Montalva *et al.*, 2011), it would be valuable to quantify their likely ecological and economic impacts in more detail.

Acknowledgements

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