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Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania

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Abstract

Exotic plant invasions threaten ecological communities world-wide. Some species are limited by a lack of suitable pollinators, but the introduction of exotic pollinators can facilitate rapid spread. In Tasmania, where many non-native plants are naturalised, exotic honeybees (*Apis mellifera*) and bumblebees (*Bombus terrestris*) have become established. We determined how these species affect the pollination of *Lupinus arboreus*, an invasive, nitrogen-fixing shrub, which is rarely visited by native pollinators. The proportion of flowers setting seed and the number of ovules fertilised per flower were positively related to the visitation rates of both exotic bee species. There was no effect of bee visitation rates on the proportion of seeds aborted prior to maturity, possibly due to post-fertilisation environmental constraints. We conclude that the spread of *B. terrestris* may not alter the fecundity of *L. arboreus* because of the pollination service provided by *A. mellifera*, and discuss potential interactions between these two bee species. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: *Apis mellifera*; Australia; *Bombus* spp.; Environmental weeds; Pollinator limitation

1. Introduction

Increasing numbers of non-native plant species are becoming naturalised in exotic habitats world-wide, often with negative impacts on the biodiversity of the ecological communities they invade (Weber, 2000). There are currently >2000 species of non-native plants growing wild in Australia and it is estimated that in Tasmania, one third of plant species present have been introduced from other countries or mainland Australia (Rozefelds et al., 1999). Indeed, since 1970, 159 new plant taxa have been recorded as naturalised in Tasmania, bringing the total number of exotic weed species in the state to over 740 (Rozefelds et al., 1999). If suitable pollinators, seed dispersers and symbiotic microbiota are present, and in the absence of natural enemies and other constraints, these exotic plant species can become both environmental and agricultural weeds (Richardson et al., 2000). Exotic plant species can compete with and displace native plants and animals, and can substantially alter ecosystem processes (for example fire occurrence and frequency, nutrient cycling etc.) (Randall, 1996). Throughout Australia, it is estimated that introduced plants cost the agricultural industry $4 billion per annum in control measures and lost yields (Sindel, 2000). In Tasmania, a state that has large areas of internationally protected habitats [United Nations Educational Scientific and Cultural Organisation (UNESCO) World Heritage Areas], exotic weeds pose a major agricultural and environmental problem (Rozefelds et al., 1999).

Recently, concern has centred on so-called "sleeper weeds". These are plants that are not currently environmental or agricultural weeds, but have the potential to become so with changes in ecological factors such as climate, habitat or pollinator visitation. In Tasmania, such species may be affected by the recent establishment of an exotic pollinator species, the bumblebee, *Bombus terrestris* (L.) (Hymenoptera, Apidae). There are no bumblebee species native to Australia, but this species was first sighted in Hobart, Tasmania, in 1992. It is thought to have originated from populations in New Zealand (Semmens et al., 1993), where several species of

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British bumblebee were intentionally released in 1885 and 1906 to pollinate crops (Hopkins, 1914). The means by which these bumblebees travelled to Tasmania is unknown but *B. terrestris* is now common and widespread throughout south-eastern Tasmania (Stout and Goulson, 2000; Goulson, Stout and Kells, unpublished data) and many individuals have also been observed in the south-west and north of the island (Pete Godfrey, personal communication).

Originally native to Britain, this species of bumblebee visits a wide range of flower species, including many of Tasmania's exotic weed species from Europe and North America (Semmens, 1996; Hingston and McQuillan, 1998; Stout and Goulson, 2000). *B. terrestris* workers are larger and heavier than any native Tasmanian bees. They also have longer tongues that enable them to forage from plants with deep corolla tubes that are not accessible to the shorter-tongued native bees (Goulson and Stout, unpublished data). *B. terrestris* is also bigger than the other exotic pollinator that is common and widespread throughout Tasmania, *Apis mellifera* L. (Hymenoptera, Apidae). *A. mellifera* has been common throughout temperate Australia since its introduction in the early 1800s (Laurie, 1863; Bailey, 1982; Gross and Mackay, 1998). Furthermore, unlike *A. mellifera*, *B. terrestris* is able to 'buzz-pollinate' species with poricidal anthers (Buchmann, 1983). Hence, exotic plant species previously suffering from pollen limitation due to a lack of suitable pollinators (particularly those adapted for pollination by large hairy bees), may experience a higher quality and quantity of pollination with the establishment of *B. terrestris*. This, in turn, may increase the seed production of these exotic weeds, and could enable certain plant species to become an environmental problem.

One such plant species is *Lupinus arboreus* Sims. (Fabaceae), a shrubby plant native to the sandy coastal areas and canyons of California (Abrams, 1964). *L. arboreus* is an invasive species that fixes nitrogen and enriches the soil, facilitating the invasion of other plants and the possible displacement of native plant species (Maron and Conners, 1996; Pickart et al., 1998; Naeem et al., 1999). In California, rodent granivores limit *L. arboreus* seed survival and seedling emergence, and heavy insect herbivory of roots and foliage can kill off whole stands of plants (Molloy et al., 1991; Strong et al., 1995; Maron and Conners, 1996; Maron and Simms, 1997), but population growth may not be controlled in this way in Tasmania.

L. arboreus is classified as one of the worst 33 environmental weeds in New Zealand (Williams and Timmins, 1990). It was intentionally introduced into Tasmania in the 1920s to help stabilise sand dunes and prevent their spread and the first records of this species occurring as naturalised in the bush are from the early 1940s (Andrew Rozefelds, Tasmanian Herbarium, personal communication) and by 1955 scattered but extensive populations were recorded (Raphael, 1955). *L. arboreus* is thought to be spreading where it is naturalised, but not at a great rate. In New Zealand, which has a similar climate to Tasmania and several established bumblebee species, the plant is now extremely abundant (Donovan, 1990; Williams and Timmins, 1990). It has the potential to become an environmental weed in Tasmania and, in the mid- to long-term, poses a threat to sandy, often disturbed, dune systems (Tim Rudman, Flora Protection Officer, DPIWE, Tasmania, personal communication).

L. arboreus produces relatively large (14–18 mm) bright-yellow flowers in whorls on racemes (Jepson, 1951) which, in Tasmania, are presented from November to February. 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 and Maron, 2000). Although *L. arboreus* flowers are nectarless, they 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). In California, *L. arboreus* is pollinated by a native bumblebee species, *Bombus vosnesenskii*, and the introduced honeybee, *A. mellifera* (Barbour et al., 1973). In Tasmania, native bees may be too small to manipulate flowers to extract pollen, and so may not visit and pollinate this species. *A. mellifera* is common throughout Tasmania, but a preliminary investigation in January 1999 suggested that the additional pollination facilitated by recently established *B. terrestris* might increase seed production (Stout and Goulson, unpublished data).

The current study comprises a more detailed investigation of the pollination of *L. arboreus* in Tasmania and examines the potential for this species to become a more serious environmental weed as *B. terrestris* spreads through the state. We studied pollinator behaviour and seed production in populations of *L. arboreus* at sites with a range of *B. terrestris* densities. However, populations of *L. arboreus* in Tasmania are highly variable in size. Pollinator attraction is known to be influenced by the size of the floral array (Klinkhamer et al., 1989; Robertson and Macnair, 1995; Stout, 2000) and this can subsequently affect pollination and seed production (Klinkhamer and de Jong, 1990; de Jong et al., 1992; Karron et al., 1995; Kato and Hiura, 1999). Variation in plant population size therefore has the potential to confound effects resulting from the abundance of bees. Therefore, we also analysed pollinator attraction and pollination success in relation to plant population size.

Specifically, we tested the following hypotheses:

1. Exotic bees are the primary pollinators of *L. arboreus* in Tasmania.

2. The proportion of flowers setting seed, the number of ovules fertilised per pod and post-fertilisation seed abortion are influenced by bee visitation rates.
3. Population size affects the attraction of pollinators and subsequently pod formation, ovule fertilisation and seed abortion.

2. Methods

2.1. Study sites

During November and December 1999, 20 populations of *L. arboreus* were monitored throughout Tasmania, at sites with a range of densities of *B. terrestris* (Fig. 1, Table 1). Most naturalised populations of *L. arboreus* are in the south-east of the state, but there are isolated populations in the west (near Strahan) and north east (near Derby). It was not possible to visit the populations at Strahan, but populations near Derby were included in this study.

2.2. Pollinator visits

At each site, six small patches (on average 36.5 racemes per patch) of *L. arboreus* flowers were observed for 10 mins each. The number of pollinators attracted (*B. terrestris*, *A. mellifera* and native pollinators) and the number of racemes visited by each individual were recorded. All observations were made between 09:45 and 16:00, in clear weather. We tested whether the time of day that observations were made affected the average abundance of bees (*B. terrestris*, *A. mellifera* and all bees combined) at three periods during the day (morning 09:45–11:50, midday 11:50–13:55 and afternoon 13:55–16:00) using a single-factor ANOVA.

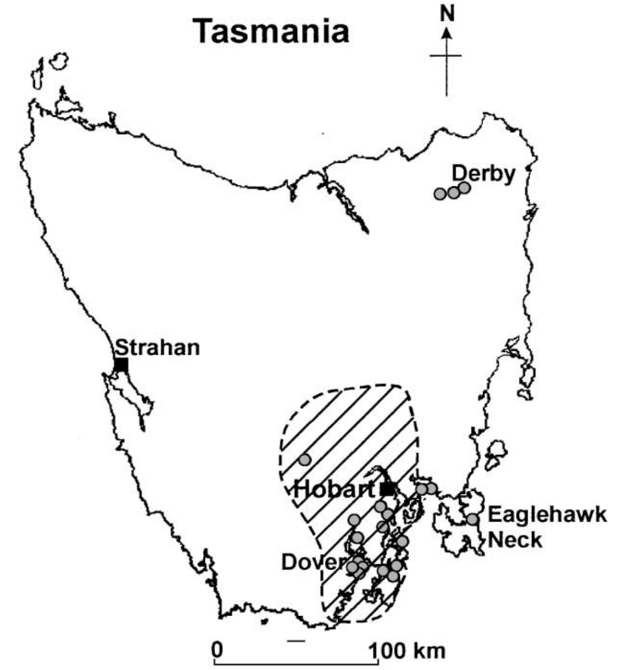

Fig. 1. The distribution of populations of *Lupinus arboreus* used in this investigation (filled circles). The shaded area represents where *Bombus terrestris* was established and common at the time of the study. Filled squares represent named towns.

Two measures of bee visitation rate were calculated for all bees combined and for *B. terrestris* and *A. mellifera* separately. Firstly, the number of bees attracted to each patch of flowers was divided by the number of racemes in the patch to give an average number of bees attracted per raceme per site per hour (henceforth 'bees per flower'). Secondly, the number of racemes visited was divided by the number of racemes in the patch to give the the average proportion of racemes visited per site per hour (henceforth 'proportion of flowers visited').

2.3. Seed set

Two weeks after observations were made, the sites were revisited and seeds were counted in ten pods on each of five flower racemes on each of five plants previously observed (except site 4 which had only three large, flowering plants, all of which were sampled). Dehiscence does not occur until five weeks after pollination (Kittelson and Maron, 2000). If flowers did not set any seeds, pods did not form, but scars on the raceme stem indicated that the flower had failed to set seed. Since observations of bee behaviour had been made at the beginning of the flowering period of *L. arboreus*, and flowering starts at the base of the racemes, the lowest ten pods or scars were examined on each raceme. Many pods contained aborted seeds that were larger than the unfertilised ovules, but failed to develop properly. These were also counted.

To determine whether flowers in populations that received more bee visits were more likely to set seed, the proportion of flowers setting seed was calculated for each site. This was regressed against the number of bees per flower and the proportion of flowers visited (for all bees combined, *B. terrestris* and *A. mellifera*) using a logistic regression with binomial errors in GLIM (Crawley, 1993).

The mean number of ovules fertilised per pod per site was calculated and compared for sites that were dominated by *B. terrestris* and sites that were dominated by *A. mellifera* using Student's *t*-test. One site (site 20) had no bee visitors during observation periods and was omitted from this particular analysis. We used model II regression analysis to investigate whether increased bee visitation rates were associated with increased ovule fertilisation (Sokal and Rohlf, 1995). Similarly, we regressed the average proportion of aborted seeds per pod per site (excluding flowers which failed to set any seed) against bee visitation rates.

Table 1
Details of *Lupinus arboreus* populations used in this study

Site No.	Site location	Dominant species	Latitude	Longitude	Population size
1	Kingston	BB	42 58′ S	147 20′ E	15
2	C638 btw Dover & Surveyors Bay	BB	43 17′ S	147 03′ E	150
3	Dover beach	BB	43 18′ S	147 01′ E	250
4	Ranelagh	BB	43 00′ S	147 03′ E	3
5	A6 W of Kingston	BB	42 58′ S	147 16′ E	75
6	Craddoc	BB	43 06′ S	147 02′ E	7
7	West Bay Golf Club	BB	43 00′ S	147 18′ S	35
8	A6 SW of Dover	BB	43 18′ S	147 00′ E	25
9	Alonnah, Bruny Island	BB	43 18′ S	147 15′ E	60
10	B66, North Bruny Island	BB	43 09′ S	147 15′ E	8
11	W of Westerway	BB	42 40′ S	146 48′ E	20
12	Adventure Bay, Bruny Island	HB	43 22′ S	147 20′ E	450
13	Seven Mile Beach	HB	42 50′ S	147 31′ E	250
14	A3 nr Branxholm, W of Derby	HB, a	41 11′ S	147 44′ E	20
15	Derby	HB, a	41 08′ S	147 50′ E	100
16	Neck Beach, Bruny Island	HB	43 17′ S	147 20′ E	35
17	NE of Seven Mile Beach	HB	42 52′ S	147 32′ E	400
18	Tonganah	HB, a	41 11′ S	147 38′ E	10
19	Eaglehawk Neck	HB	43 01′ S	147 55′ E	100
20	Surveyors Bay	Neither	43 16′ S	147 06′ E	75

Site numbers correspond with Fig. 2. Dominant bee species: BB = *Bombus terrestris*, HB = *Apis mellifera*, neither = sites where neither species of bee were seen, a = sites where native bees were also seen (see Fig. 2). Population size = number of flowering plants in population.

To determine whether flowers were capable of automatic self-pollination in the absence of insect visitors, 20 racemes at each of two sites were bagged with fine netting to prevent insect visits. These were examined 2 weeks later and seeds were counted.

2.4. Plant population size

Populations of *L. arboreus* ranged from 3 to 450 flowering plants, excluding sterile individuals and seedlings (Table 1), with an average of 104.40 ± 29.52 plants per site (mean ± S.E.). Pearson's product moment correlation coefficients were calculated to test relationships between plant population size (log number of flowering plants in a population) and (1) average visitation rates of *B. terrestris*, *A. mellifera* and all bees combined, (2) proportion of flowers setting seed, (3) average number ovules fertilised, and (4) average proportion of seeds aborted.

3. Results

3.1. Pollinator visits

A total of 144 *B. terrestris*, 132 *A. mellifera* and 10 native bees (two *Exoneura bicolor* Smith, Anthophoridae, two *Leioproctus* sp., Colletidae, and six *Lasioglossum* sp., Halictidae) were observed visiting *Lupinus arboreus* flowers during the investigation. Other flower visitors were rare and were excluded from the analyses (one drone fly (*Eristalis tenax* (L.), Diptera, Syrphidae), one Macleay's swallow tail butterfly (*Graphium macleayanum*, Lepidoptera, Papilionidae) and seven Coleoptera (*Metriorrhynchus rhipidius*, Cantharidae, *Chauliognathus lugubris*, Cantharidae, and *Eleale aspersa*, Cleridae).

The visitation rate of bees per flower was not significantly different according to whether observations were made in the morning, midday or afternoon (*B. terrestris*: $F_{2,18} = 0.489$, $P = 0.621$; *A. mellifera*: $F_{2,18} = 0.130$, $P = 0.880$; all bees combined: $F_{2,18} = 0.183$, $P = 0.834$).

There was an inverse relationship between the number of *B. terrestris* and *A. mellifera* individuals observed at sites (Fig. 2). *B. terrestris* and *A. mellifera* were observed foraging together on *L. arboreus* at only five sites, even though *A. mellifera* are common throughout the area where *B. terrestris* is currently found. Native bees were observed foraging on *L. arboreus* at only three sites, all of which were free of *B. terrestris* at the time of our observations.

3.2. Proportion of flowers setting seeds

The proportion of flowers setting seed significantly increased as visitation rates of all bees combined (*B. terrestris*, *A. mellifera* and native bees) increased (Fig. 3a and b). The proportion of flowers setting seeds was also related positively to the visitation rates of *B. terrestris* (Fig. 3c and d). There were no significant relationships between visitation rates of *A. mellifera* and proportion

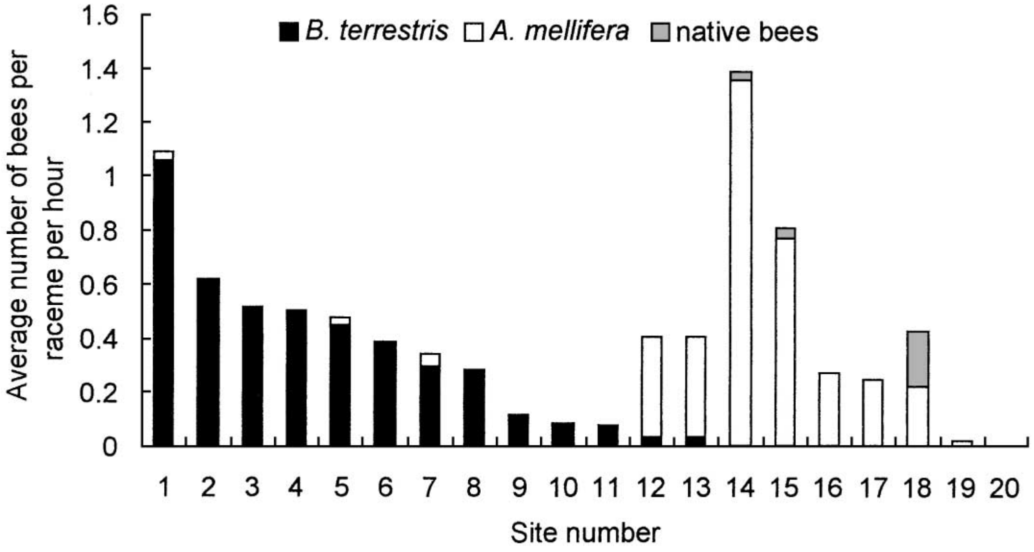

Fig. 2. The average number of *Bombus terrestris*, *Apis mellifera* and native bees per raceme per hour at each site.

of flowers setting seeds (bees per flower: $F_{1,18}=0.249$, $P=0.624$, proportion of flowers visited: $F_{1,18}=0.39$, $P=0.540$). However, when sites dominated by *B. terrestris* were excluded from the analysis, there were significant relationships between *A. mellifera* visitation rates and the proportion of flowers setting seed in the remaining eight sites (Fig. 3e and f).

3.3. Ovules fertilised per pod

At sites dominated by *B. terrestris* (11 sites), an average of 5.15 (±0.53 S.E.) ovules were fertilised per pod, while at *A. mellifera* dominated sites (eight sites), an average of 3.61 (±0.82 S.E.) ovules were fertilised per pod. This difference was not significant ($t_{17}=1.65$, $P=0.059$), probably because there was high inter-site variability in visitation rates.

The average number of ovules fertilised per pod per site increased as the visitation rates of all bees increased (Fig. 4a and b). The average number of ovules fertilised per pod also increased as rates of *B. terrestris* per flower increased (Fig. 4c) but the relationship with the proportion of flowers visited by *B. terrestris* was not significant (Fig. 4d). There was no relationship between visitation rates of *A. mellifera* and the number of ovules fertilised per pod (bees per flower: $F_{1,18}=0.35$, $P=0.56$, proportion of flowers visited: $F_{1,18}=0.54$, $P=0.47$). However, the relationship became significant when sites where *B. terrestris* were common were excluded from the analyses (Fig. 4e and f).

3.4. Proportion of seeds aborted

The proportion of aborted seeds per pod did not vary with visitation rates of all bees, *B. terrestris* or *A. mellifera* (Table 2). None of the bagged racemes at either site set any seed. All flowers fell from the spikes into the bags without forming pods, indicating that insect visitation is necessary for seed formation in this plant species.

3.5. Plant population size

There were no significant correlations between plant population size and bee visitation rates (for all bees, *B. terrestris* and *A. mellifera* the coefficient r ranged from 0.145 to −0.303, $n=20$, $P>0.05$). Furthermore, plant population size was not related to the proportion of flowers setting seed ($r=-0.05$, $n=20$, $P>0.05$), the average number of ovules fertilised per pod ($r=-0.02$, $n=20$, $P>0.05$) or the proportion of aborted seeds per pod ($r=0.09$, $n=20$, $P>0.05$).

4. Discussion

Pollinator limitation is rarely a major constraint to the spread of introduced entomophilous plants either because asexual propagation occurs or generalist pollinators can provide a pollination service (Valentine, 1978; Richardson et al., 2000). However, when asexual reproduction is limited and floral traits preclude pollination by native floral visitors, plant fecundity is susceptible to changes in abundance of legitimate pollinators (Larson and Barrett, 1999). We found that *L. arboreus* is pollinated by *A. mellifera* and *B. terrestris* in Tasmania, and, during our observations, rarely visited by native bee species or other native pollinators. It is unclear whether this is because native pollinators are excluded from this resource through competitive interactions (Hingston and McQuillan, 1999), or because

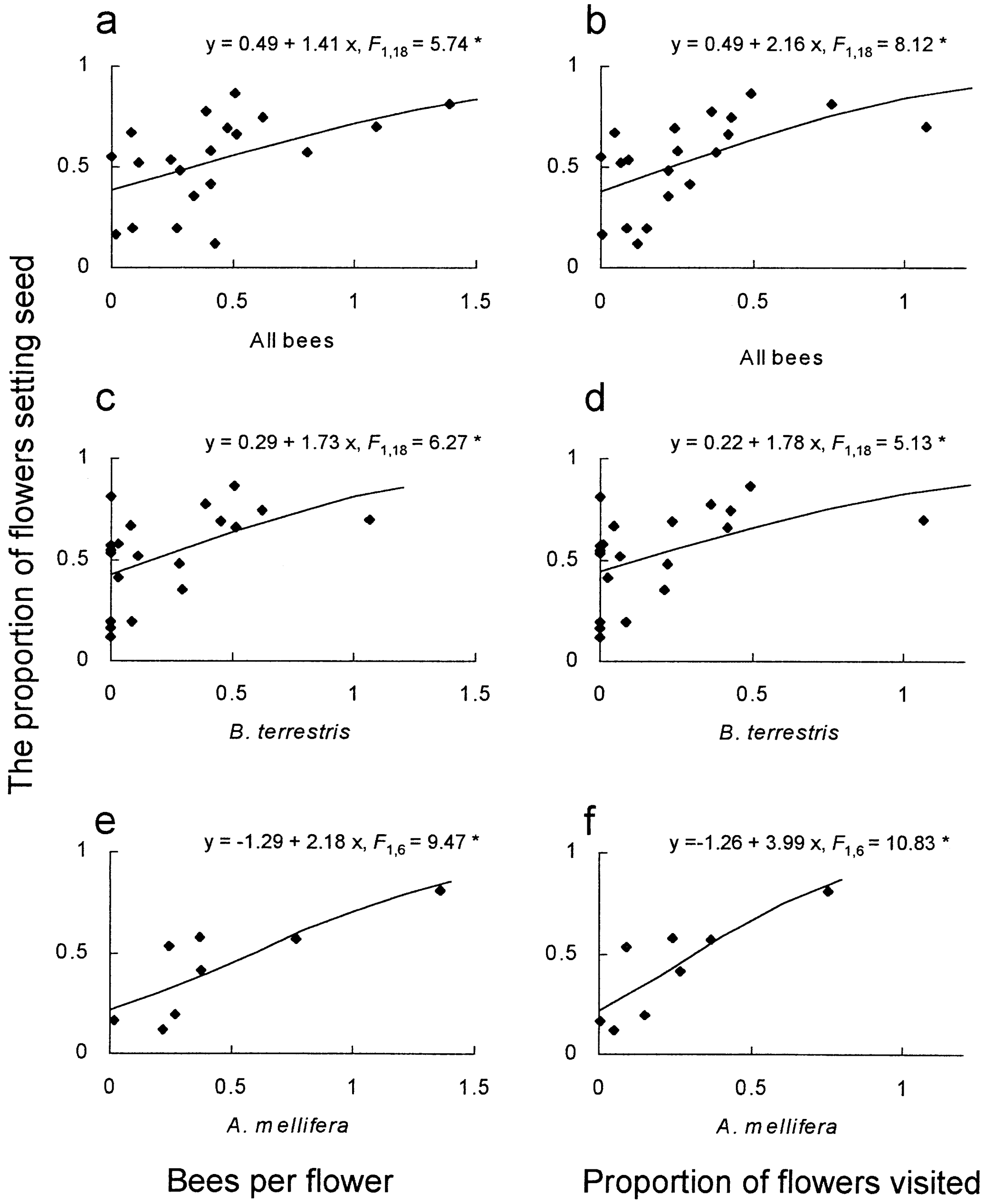

Fig. 3. Relationships between bee visitation rates (bees per flower and proportion of flowers visited) and the proportion of flowers setting seed at each site. Graphs a, b, c and d include all sites; e and f only include sites where *Bombus terrestris* was absent. $*P<0.05$ ($y=\ln(^{p}/_{q})$ where p = number of flowers setting seed, q = number of flowers not setting seed and x = visitation rates of bees).

native bees are too small to manipulate the floral mechanism which releases the pollen, or because they are not attracted to this species as a forage resource.

Where *B. terrestris* individuals were present and common (in south-east Tasmania), they appeared to be the primary pollinators of *L. arboreus*. However, where there were no *B. terrestris* (in other parts of Tasmania), *A. mellifera* successfully pollinated flowers. The average number of ovules fertilised per pod was not significantly different among sites dominated by *B. terrestris* and those dominated by *A. mellifera*. Therefore, it may be concluded that the spread of *B. terrestris* may not increase ovule fertilisation of *L. arboreus* plants in Tasmania, because of the pollination *L. arboreus* already receives from *A. mellifera*. However, regression analysis revealed that bumblebee visitation rates can be used to predict the proportion of flowers setting seed and the number of ovules fertilised at all sites, whereas honeybee visitation rates can only be used to predict seed set and ovule fertilsation at sites with no bumblebees. Seed production and the visitation rates of *B. terrestris* and *A. mellifera* were highly variable among sites, and the higher average number of ovules fertilised in sites dominated by *B. terrestris* may indicate an important

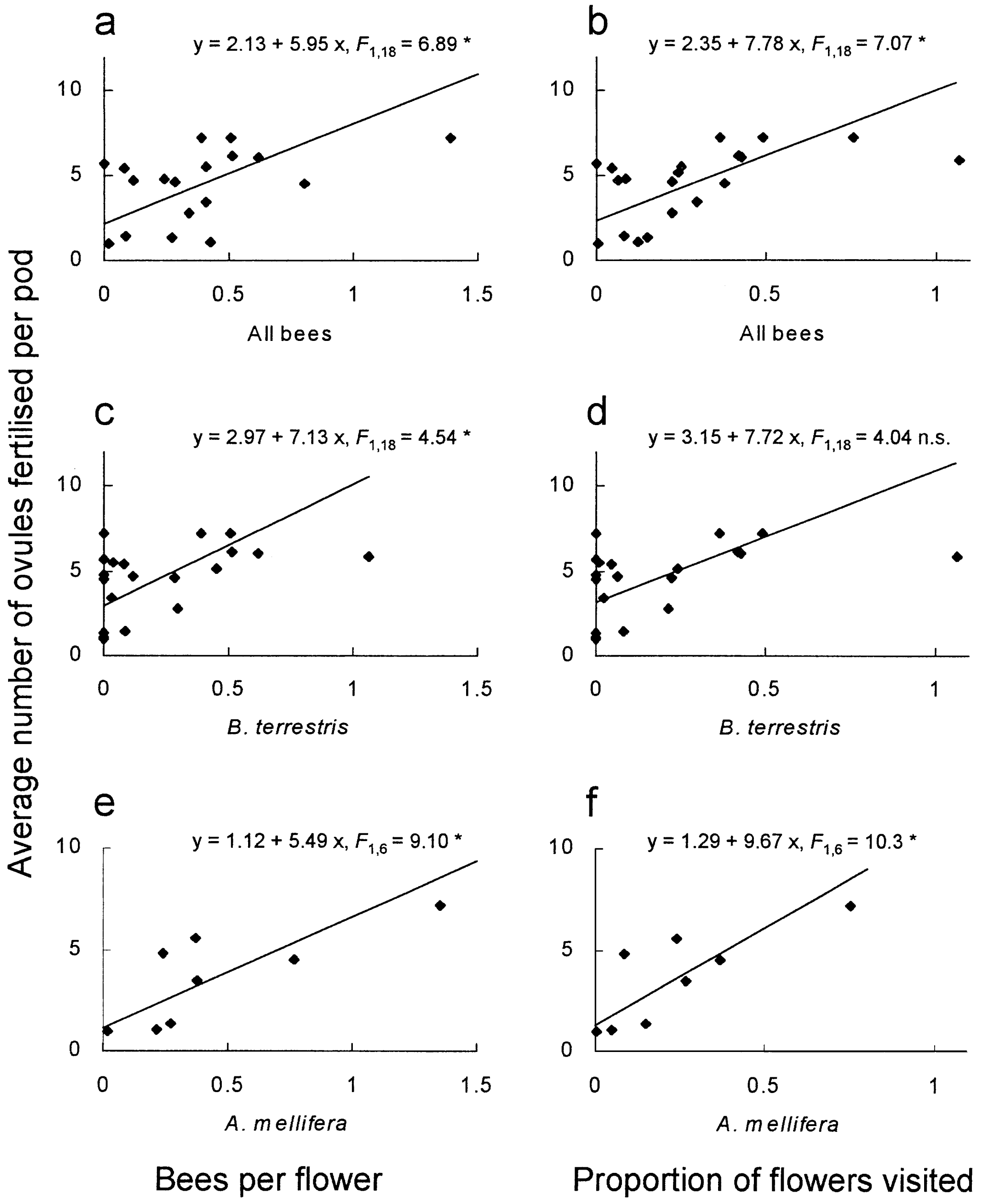

Fig. 4. Relationships between bee visitation rates (bees per flower and proportion of flowers visited) and the average number of ovules fertilised per pod at each site. Graphs a, b, c and d include all sites; e and f only include sites where *Bombus terrestris* was absent. $*P<0.05$.

trend worthy of further investigation. Native bee visitation was too low to assess their impact on pollination. Prolonged observations of pollinator behaviour and glasshouse/cage experiments may be necessary to establish whether *B. terrestris* is a more effective pollinator than *A. mellifera*, and whether the native bees play a role in the pollination of *L. arboreus*.

Previous studies have found negative relationships between bee visitation and the proportion of seeds aborted after fertilisation (e.g. Stanghellini et al., 1997). The absence of any such relationship here suggests that some factor other than the number of pollinator visits is responsible for determining whether seeds mature. In *L. arboreus* plants in California, inbreeding depression results in a higher proportion of aborted zygotes in selfed than outcrossed pods (Kittelson and Maron, 2000). Alternatively, limitations in environmental resources may induce seed abortion (Burd, 1994). In *L. arboreus* in Tasmania, pollen or pollinator limitation may restrict the proportion of ovules fertilised in a flower (and the total number of zygotes produced in a pod) but inbreeding depression or resource limitation may limit the number of seeds that mature (Stephenson, 1981; Zimmerman and Aide, 1989).

The production of a large number of seeds is thought to be important in invasive species dynamics (Lonsdale,

Table 2
Proportion of under-developed seeds per pod (y) regressed against bee visitation rates (x)

	Regression equation	$F_{1,18}$	P
Bees per flower			
All bees	$y = 0.22 + 0.25x$	0.92	ns[a]
B. terrestris	$y = 0.26 + 0.30x$	3.53	ns
A. mellifera	$y = 0.28 + 0.26x$	0.17	ns
Proportion of flowers visited			
All bees	$y = 0.24 + 0.33x$	1.65	ns
B. terrestris	$y = 0.27 + 0.33x$	2.93	ns
A. mellifera	$y = 0.29 + 0.46x$	0.23	ns

[a] ns, not significant.

1993; Peterson and Prasad, 1998; Clements et al., 2001), especially in species such as *L. arboreus* which rely on sexual reproduction. However, an increase in seed production may only be important if seed abundance is a limiting factor affecting population dynamics. In populations where seed banks already contain many seeds, an increase in the number of seeds produced may not actually affect population size or the spread of the species. Other factors, such as dispersal mechanisms, germination success and resource availability, may influence *L. arboreus* population size and range. These have not been investigated in the current study, but are interesting areas for future research.

Contrary to many previous studies (for example Klinkhamer et al., 1989; Robertson and Macnair, 1995; Stout, 2000), we found no evidence to support the hypothesis that pollinator attraction varies with the population size of *L. arboreus*. This may be because individual *L. arboreus* plants hold many racemes and as few as three plants still represent an attractive resource to foragers. Similarly, there was no effect of plant number on the proportion of flowers setting seed, the average number of ovules fertilised or the proportion of seeds aborted post-fertilisation. Previous authors have found that outcrossing and inbreeding is often affected by plant population size. Pollinators tend to visit a smaller proportion of the available flowers in large patches, and in-breeding rates tend to be increased in smaller populations (Geber, 1985; de Jong et al., 1992; Klinkhamer and de Jong, 1993; Stout, 2000). Inbreeding rates were not measured here, but if inbreeding was increased in the smaller populations of *L. arboreus*, this did not result in a reduction in seed production or an increase in seed abortion at these sites.

The majority of exotic weeds in Tasmania originate from Europe where bumblebees are native (Rozefelds et al., 1999). Many rely on bumblebees for pollination, and the spread of *B. terrestris* through Tasmania could increase seed production in these species. Other introduced, nitrogen-fixing Fabaceae, such as *Cytisus scoparius* L., which is pollinated primarily by bumblebees, may be of particular concern (Bossard, 1991; Parker, 1997; Bellingham, 1998; Peterson and Prasad, 1998; Stout, 2000). Alternatively, variable reproductive systems and simple pollination mechanisms may reduce the impact of additional *B. terrestris* pollination (Huryn and Moller, 1995; Huryn, 1997).

In Tasmania, *B. terrestris* may be competitively excluding *A. mellifera* from *L. arboreus*, *C. scoparius* and other species (e.g. *Digitalis purpurea* L., Scrophulariaceae). *A. mellifera* only forages from these species in large numbers when *B. terrestris* is absent. Since *B. terrestris* visits a wide range of both native and introduced plant species, there are also fears that they could compete with and displace native Tasmanian pollinators (including birds) (Hingston and McQuillan, 1999). Furthermore, *B. terrestris* may also affect native plants directly: *B. terrestris* individuals are larger than native bees in Tasmania, and may not be effective pollinators of some native plants (Huryn, 1997; Gross and Mackay, 1998).

In summary, invasions by non-native flora and fauna are of global concern, and in Australia, in particular, habitats are increasingly threatened by exotic plant and animal species. This study highlights concerns about the increased seed production mediated by exotic bee pollination of *L. arboreus* in Tasmania. The recent establishment of *B. terrestris*, in addition to the already established*A. mellifera*, not only poses the threat of increased pollination of weed species, but may also have negative impacts on native pollinators and plant species. Generalisations about the effects of exotic bees on Tasmanian ecosystems should not be made from a limited number of studies, however, and further research is required.

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