Apidologie 40 (2009) 450–463
© INRA/DIB-AGIB/EDP Sciences, 2009
DOI: 10.1051/apido/2009005

Original article

The impacts of an invasive alien plant and its removal on native bees

Caroline Marijke NIENHUIS, Anke Christiane DIETZSCH, Jane Catherine STOUT*

Botany Department, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland

Received 25 April 2008 – Revised 20 November 2008 – Accepted 2 December 2008

Abstract – Although the alien *Impatiens glandulifera* successfully invades riparian habitats and is visited by native insects, knowledge of its impact on native bees is limited. We assessed pollinator abundance in field sites where *I. glandulifera* was absent, present or had been experimentally removed. We measured insect visitation to flowers of potted native plants and to *I. glandulifera*. *Bombus* spp. comprised the highest proportion of visitors in invaded sites, whereas solitary bees made up the highest proportion in sites where *I. glandulifera* was removed. More bees, especially medium- and long-tongued *Bombus* spp. (*B. pascuorum* and *B. hortorum*), foraged on *I. glandulifera* than the native plant species (possibly because the alien was more abundant). We detected no impact of invasion on standardised pollinator abundance, *B. pascuorum* abundance, nor functional insect diversity, which may be due to variable climatic conditions. We suggest that future studies focus on impacts on rare or specialised pollinator taxa.

***Bombus* / *Impatiens glandulifera* / nectar secretion rate / nectar sugar concentration / Syrphidae**

1. INTRODUCTION

Invasive species are regarded as one of the greatest threats to global biodiversity (Vitousek et al., 1997; Sala et al., 2000) as they disrupt the composition and functioning of local ecosystems (Chapin et al., 2000; Richardson et al., 2000; Levine et al., 2003) and pose serious economic and health problems (Davis, 2003). Although direct (e.g. smothering) and indirect (competition for nutrients and water) negative effects of invasive alien plants on native plant communities have been reported (Levine et al., 2003 and references therein), little is known about their direct (and indirect) effects on native pollinators (Traveset and Richardson, 2006; Bjerknes et al., 2007; Goodell, 2008).

Since they must form mutualistic interactions with pollinators already present in the ecosystem in order to establish and invade (Richardson et al., 2000; Parker and Haubensak, 2002; Stout et al., 2006), entomophilous alien plants depend greatly on native pollinators for reproduction and population growth (Parker, 1997). They are more likely to be successful invaders if served by a range of generalist pollinators rather than a single specialised taxon (Richardson et al., 2000; Memmott and Waser, 2002; Johnson and Steiner, 2000; but see Morales and Aizen, 2006). Hence alien plants have the potential to directly and indirectly impact individuals, populations and communities of native generalist pollinators.

Some alien plants, particularly those that produce an abundance of large brightly-coloured flowers with extended flowering seasons, are very attractive to native pollinators (Ghazoul, 2002; Memmott and Waser, 2002). For example, *Impatiens glandulifera* (Balsaminaceae), *Mimosa pigra* (Leguminosae) and *Rhododendron ponticum* (Ericaceae) are regularly visited by native pollinators in the

---

Corresponding author: C.M. Nienhuis, nienhuic@tcd.ie

* Manuscript editor: Jacqueline Pierre

communities they invade (Starý and Tkalců, 1998; Chittka and Schürkens, 2001; Schürkens and Chittka, 2001; Moragues and Traveset, 2005; Stout et al., 2006; Lopezaraiza-Mikel et al., 2007). However, the nectar and pollen provided by these plants may be inappropriate for some native pollinators morphologically (pollinators may not be able to access rewards from flowers), physiologically (they may be nutritionally poor, or even contain toxins (Barker, 1978)) and phenologically (there may be temporal mis-matches between reward supply and pollinator demand). Alternatively, these plants may provide valuable resources for native pollinators, which are in decline globally (Biesmeijer et al., 2006).

If alien plant invasion causes a change in the native plant community by altering the spatial distribution of floral resources (Ghazoul, 2002) or even displacing important native plant species (Rathcke, 1983), invasive alien plants have the potential to indirectly impact both generalist and specialist taxa who utilise these native plants. It is likely that specialist species are those most at threat (see also Biesmeijer et al., 2006).

Impatiens glandulifera Royle (Balsaminaceae) is the tallest annual herb in Europe and is regarded as extremely invasive (Beerling and Perrins, 1993; Hulme and Bremner, 2006). Since its introduction from the Himalayas as a garden plant at the beginning of the 19th century (Beerling and Perrins, 1993), *I. glandulifera* has established, invaded and spread rapidly in riparian habitats across Europe (Perrins et al., 1993; Pyšek and Prach, 1995; Hulme and Bremner, 2006). Their frequent disturbance regimes (i.e. flooding) make riparian habitats ideal sites for *I. glandulifera* to invade as propagules carried by water establish easily (Pyšek and Prach, 1993; Maskell et al., 2006). Riparian habitats are one of the most diverse ecosystems worldwide (Naiman and Décamps, 1997), providing vital resources for native insects (Starý and Tkalců, 1998). *I. glandulifera* has been reported to interfere with such native communities by competing for (Prowse and Goodridge, 2000; Chittka and Schürkens, 2001) and facilitating (Lopezaraiza-Mikel et al., 2007) pollinator visitation to the native flora but may benefit native pollinators by supplying important nectar and pollen resources (Showler, 1989; Starý and Tkalců, 1998).

I. glandulifera is considered invasive in Ireland where it was first recorded in 1906 and since then has spread extensively (Reynolds, 2002). Despite much research being conducted on *I. glandulifera* in continental Europe (Könies and Glavač, 1979; Starý and Tkalců, 1998; Titze, 2000; Chittka and Schürkens, 2001; Hejda and Pyšek, 2006) and the UK (Lopezaraiza-Mikel et al., 2007), no study known to us in Ireland or elsewhere has quantified the impacts of *I. glandulifera* and its removal on native pollinators in a controlled manipulative field experiment. We tested the following hypotheses:

1. Insect abundance and functional diversity, and *Bombus* spp. abundance and diversity, vary between sites invaded by *I. glandulifera* compared with non-invaded sites and sites with *I. glandulifera* removed.
2. Bees preferentially visit alien (*I. glandulifera*) plants.
3. Nectar secretion rate and nectar sugar concentration differ between native and alien (*I. glandulifera*) plants and are correlated with insect visitation.

2. METHODS

2.1. Study site

This study was conducted along the River Liffey, Co. Dublin (outside the conurbation of Dublin), Ireland, between 17th July and 2nd August 2006. *I. glandulifera* is distributed patchily along the river, with dense patches occurring where the bank gradient is gradual and disturbed.

Nine sites (of approximately 50 m × 15 m and at least 800 m apart) were selected along the river, three where *I. glandulifera* was absent and the remaining sites were randomly assigned to two treatments: *I. glandulifera* present (mean ± S.E. inflorescences per site = 320 ± 109) and *I. glandulifera* removed (mean ± S.E. inflorescences removed per site = 358 ± 318). *I. glandulifera* was removed by cutting inflorescences and buds from plants already in flower, at least two days before observations began and floral removal continued throughout the observational period to ensure the absence of alien flowers.

2.2. Floral abundance and diversity

After *I. glandulifera* removal, floral abundance and floral diversity was assessed in each site by walking a 60 m transect and recording the number of plant species and the total number of inflorescences per plant species within twelve 2 m^2 quadrats (at 5 m intervals). For each site, floral diversity was calculated using the Shannon diversity index (*H*) (Southwood and Henderson, 2000);

$$H = -\Sigma p_i \log_e p_i, \text{ where}$$

p_i = proportion of total number of inflorescences present of species *i*.

One-factor Analysis of Variance (ANOVA) was used to establish whether floral diversity differed between treatments.

2.3. Insect abundance and diversity

To quantify insect abundance and activity we observed insect visitation rates to native plants. In order to standardise native plant abundance and density, we introduced 18 native plants in pots, six individuals of each of three native species (*Epilobium hirsutum* (Onagraceae), *Filipendula ulmaria* (Rosaceae) and *Stachys palustris* (Lamiaceae)) into each site. These species were chosen because they are widespread in the section where the experiment was conducted along the River Liffey, flower simultaneously with *I. glandulifera*, are frequently visited by insects (Fussell and Corbet, 1992; Comba et al., 1999) and have been used in previous studies (Chittka and Schürkens, 2001; Lopezaraiza-Mikel, 2006). In invaded sites, plants were placed directly next to *I. glandulifera* patches. A small proportion (<10%) of potted plants failed to flower and therefore plants in flower were cut from naturally established stands located outside the sites and placed into water-filled bottles in order to maintain the number of flowering plants in the standard artificial native plant communities. Where necessary, plants were substituted at least one day before observations commenced. Each site was visited once, between 8.00 to 18.00 hrs, on each of three separate days during the period between 17th July and 25th July 2006. On each visit, a total of six plants (two of each of the three native species) were observed for 10 minutes. In addition three randomly selected *I. glandulifera* patches were observed for 10 minutes in each of the invaded sites. All insects visiting flowers for nectar and/or pollen were identified to family (Andrenidae, Apidae and Syrphidae) and social bees to species (*Bombus* spp. and *Apis mellifera*). Andrenids and syrphids were difficult to identify to species on the wing, and we did not want to capture individuals (because we did not want to affect either their behaviour or their populations). The total number of inflorescences per plant species per patch was recorded after observations. Standardised insect abundance was calculated as the number of insects per inflorescence per hour (number of insects arriving at a patch in 10 min / number of inflorescences in patch × 6). In addition, temperature (°C), cloud cover (%) and wind force (Beaufort scale) were recorded during each observation session.

Although insect visitation does not provide a direct measure of insect abundance, other methods such as pan traps were considered too destructive to the insect community. Transect walks were not employed because of variation in native plant communities among sites.

Total standardised insect abundance (analysed separately for all insects, all bees including *Bombus* spp., syrphids and *Bombus* spp.) on native and alien inflorescences were compared among treatments and sites using a balanced two-factor nested Analysis of Covariance (ANCOVA) ('site' as random factor nested within 'treatment' as fixed factor) with temperature, cloud cover and wind force as covariates. Cloud cover (proportional data) and wind force (count data) data were arcsine and square root transformed respectively. ANCOVAs were also performed on non-normal data as analysis of variance is robust to non-normality (Underwood, 1997). Levene's test was used to test for heterogeneity of variances and if necessary data were $\log_{10}$ (x+1) transformed (syrphid and total insect abundance). When transformations were unable to reduce heterogeneity of variances, non-parametric analysis (Mood's Median test) was employed. In addition, we investigated whether insect abundance differed between *I. glandulifera* and the three native plant species in invaded sites, using one-factor ANOVA and a Dunnett's *post-hoc* test. A *post-hoc* power analysis was conducted using total standardised insect abundance.

Because of difficulties in identifying some insects to species (see above), insects were assigned to five functional groups (andrenids, syrphids, long- and medium-tongued *Bombus* spp.

(*B. hortorum* and *B. pascuorum*), short-tongued *Bombus* spp. (*B. pratorum* and *B. terrestris*) and *A. mellifera*. Insect diversity for each site was estimated using the Shannon diversity index (H) (as above).

To test for differences in insect diversity among treatments, data were analysed with one-factor ANOVA as above.

2.4. *Bombus* spp. abundance and diversity

To estimate bumblebee abundance in, and utilisation of, all nine sites, we conducted mark-recapture studies between 26th July and 2nd August 2006, during the removal period after observations on native plants had taken place. *B. pascuorum* was selected as study species because it was the most commonly observed insect visitor in these sites. Each site was visited twice. On the first visit, all *B. pascuorum* individuals encountered during a 1.5 hour period were captured, their thorax marked with red permanent marker and released. Observations on freely foraging bumblebees from colonies kept in captivity have shown that marks on the thorax are clearly visible for up to five days (A. Dietzsch, unpubl. data.). Studies of the foraging range of *B. pascuorum* suggest that the same individuals are unlikely to occur at multiple sites when they are > 800 m apart (Darvill et al., 2004; Knight et al., 2005). Twenty-four hours later, sites were revisited and all bumblebees encountered were caught and the number of marked and unmarked individuals recorded. The number of *B. pascuorum* per site was estimated according to the Lincoln-Peterson formula (N) (Southwood and Henderson, 2000);

$N = (n_1 \times n_2) / m_2$, where

n_1 = total number of *B. pascuorum* caught and marked in first sample,

n_2 = total number of *B. pascuorum* caught in second sample,

m_2 = number of marked *B. pascuorum* recovered in second sample.

To estimate *Bombus* spp. diversity in each site, we used the number of individuals for each *Bombus* spp. (*B. hortorum*, *B. pascuorum*, *B. pratorum* and *B. terrestris*) visiting native and alien patches recorded during observations. For each treatment *Bombus* spp. diversity was estimated using the Shannon diversity index (H) (as above).

To determine whether *Bombus* spp. numbers and diversity differed between treatments, data were analysed using one-factor ANOVA as above.

2.5. Nectar resources

Immediately after observations of insect visitation, nectar standing crop was determined at each site in 10 randomly selected flowers of all plant species that had been visited by bumblebees, using 1 and 5 μL micropipettes (Hirschmann Laborgeräte GmbH & Co.KG, Eberstadt, Germany). In addition, nectar secretion rate (per 24 hours) and sugar concentrations for each study plant species visited by bumblebees were determined at each site by randomly bagging ten flowers per species with bridal veil material to exclude insect visitors. A hand-held refractometer (Ceti-Digit-080, Medline Scientific Ltd, Oxfordshire, UK) was used to measure sugar concentration. We excluded *F. ulmaria* from nectar measurements because flowers were too small to extract any measurable nectar quantities, even after bagging.

The relationship between nectar standing crop and insect abundance was investigated using correlations. Pearson's product moment correlation was utilised for all data related to *I. glandulifera* (parametric) and Spearman's rank correlation was employed for data related to *E. hirsutum* and *S. palustris* (non-parametric). One-factor ANOVAs were used to examine whether nectar sugar concentrations and secretion rates differed between *I. glandulifera* and the native plant species. Data for nectar secretion rates were $\log_{10}(x)$ transformed to reduce heterogeneity of variance. Dunnett's *post-hoc* tests were utilised to compare sugar concentrations and secretion rates between the three species.

MINITAB 13 (Minitab, 2000) was used for all statistical analyses.

3. RESULTS

3.1. Floral abundance and diversity

The co-flowering vegetation in the sites contained a species rich assemblage of native plants and included *Calystegia sepium* (Convolvulaceae), *Chamaenerion angustifolium* (Onagraceae), *Cirsium palustre* (Asteraceae), *Epilobium hirsutum* (Onagraceae), *Eupatorium cannabinum* (Asteraceae), *Filipendula ulmaria* (Rosaceae), *Rubus fruticosus* agg (Rosaceae), *Scrophularia aquatica* (Scrophulariaceae), *Senecio jacobaea* (Asteraceae), and *Stachys palustris* (Lamiaceae). Neither floral

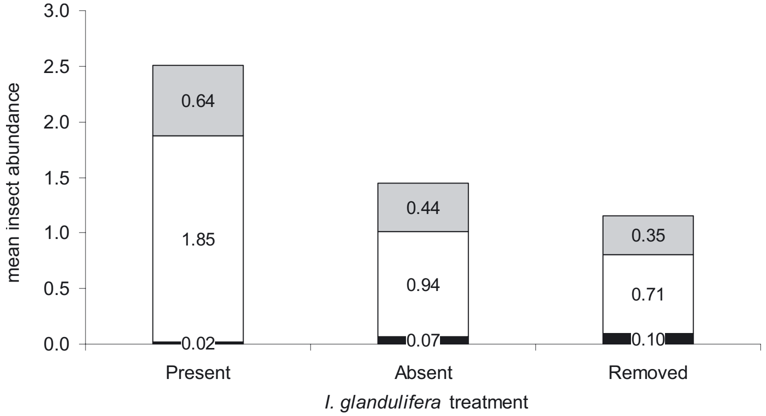

Figure 1. Mean insect abundance (standardised as insects per inflorescence per hour) on native inflorescences made by *Bombus* spp., other Hymenoptera and Syrphidae in sites where *I. glandulifera* was present, absent and had been experimentally removed. *Bombus* spp. (grey bars), Syrphidae (open bars), and other Hymenoptera (closed bars).

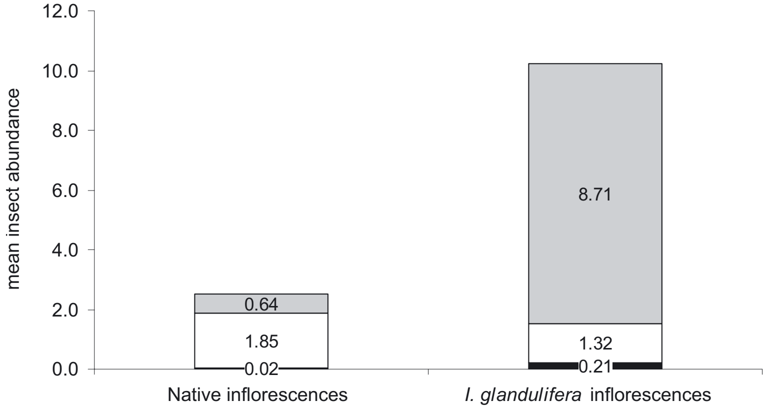

Figure 2. Mean insect abundance (standardised as insects per inflorescence per hour) on native versus *I. glandulifera* inflorescences made by *Bombus* spp., other Hymenoptera and Syrphidae in sites where *I. glandulifera* was present. *Bombus* spp. (grey bars), Syrphidae (open bars), and other Hymenoptera (closed bars).

abundance ($F_{2,8}$ = 0.86, $P > 0.05$) nor floral diversity (H ranging from 0.96 to 1.70; $F_{2,8}$ = 0.61, $P > 0.05$) differed significantly among treatments, probably due to high variation among sites within treatments.

3.2. Insect diversity

In 360 observation minutes, a total of 263 individual insects were observed visiting native potted plants (138 Hymenoptera and 125 Diptera). Sites containing *I. glandulifera* attracted more flower visitors (12.75 individuals per inflorescence per hour) than non-invaded sites (*I. glandulifera* absent = 1.45 individuals per inflorescence per hour; *I. glandulifera* removed = 1.16 individuals per inflorescence per hour). Both *Bombus* spp. and syrphids seemed to be more abundant on native inflorescences in invaded compared to non-invaded sites (Fig. 1), with *Bombus* spp. being especially abundant on *I. glandulifera* inflorescences in sites where the alien was present (Fig. 2). However, syrphids made up higher proportions of flower visitors in sites

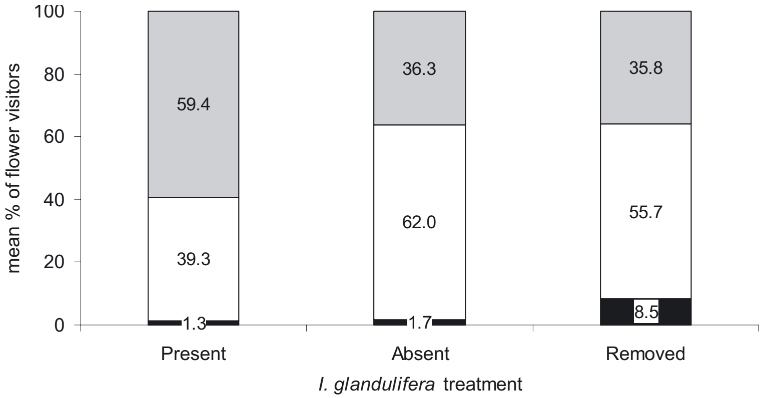

Figure 3. Mean percentage of flower visitors to native and alien inflorescences made by *Bombus* spp., other Hymenoptera and Syrphidae in sites where *I. glandulifera* was present, absent and had been experimentally removed. *Bombus* spp. (grey bars), Syrphidae (open bars), other Hymenoptera (closed bars).

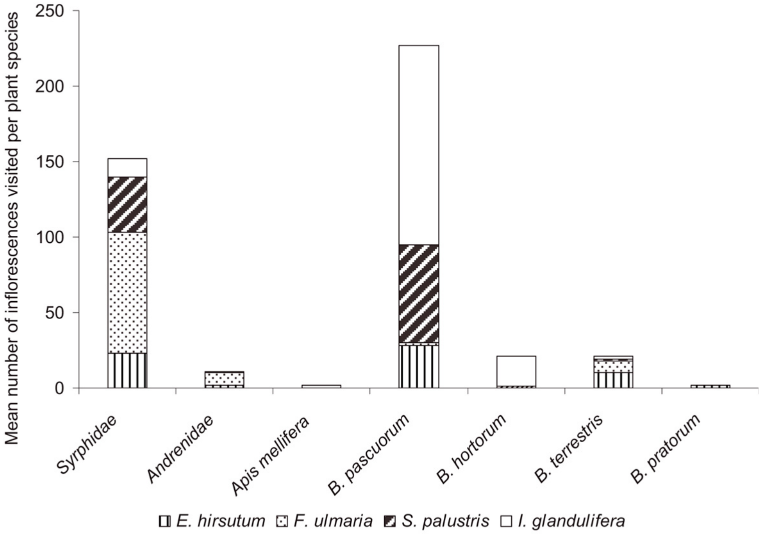

Figure 4. Mean number of native and alien inflorescences visited by each insect taxa.

without *I. glandulifera* whereas *Bombus* spp. comprised a higher proportion in invaded sites (Fig. 3). Other bees only constituted a minority of visitors, including *Andrena* spp. (seven visitors) and *A. mellifera* (one visitor), and made up a higher proportion of visitors when *I. glandulifera* was removed (Fig. 3). *Bombus* spp. visitors included medium-tongued *B. pascuorum* (112 visitors), long-tongued *B. hortorum* (10 visitors), short-tongued *B. terrestris* (eight visitors) and short-tongued *B. pratorum* (one visitor).

The different plant species attracted different pollinator groups: syrphids more frequently visited *F. ulmaria*, thereafter *S. palustris*, *E. hirsutum* and, rarely, *I. glandulifera*. In contrast, bees primarily visited *I. glandulifera* followed by *S. palustris*, *E. hirsutum* and, rarely, *F. ulmaria*, except andrenids which mainly visited *F. ulmaria* (Fig. 4). *B. pascuorum* was the most frequent *Bombus* spp. recorded and many of this species' visits were to *I. glandulifera*. *B. hortorum* chiefly visited *I. glandulifera*

Table I. Insect abundance on native plants [N], and on native versus alien plants in invaded sites [N vs. A], standardised as insects per inflorescence per hour, compared among treatments [T] and sites (nested within treatments S[T]) using parametric tests (ANCOVA F and ANOVA F) and non-parametric tests (Mood's Median X^2). "Bee" = all bees including *Bombus* spp. Covariates include temperature (TP), cloud cover (CC) and wind force (WF). ns = non-significant results, *$P < 0.05$, **$P < 0.001$.

		Total insect	Bee	*Bombus* spp.	Syrphids
N	T	$F_{2,26} = 0.19$ ns	$F_{2,26} = 0.69$ ns	$F_{2,26} = 1.07$ ns	$F_{2,26} = 0.48$ ns
	S(T)	$F_{6,26} = 4.61$ ns	$F_{6,26} = 1.15$ ns	$F_{6,26} = 1.09$ ns	$F_{6,26} = 2.26$ ns
	TP	$F_{1,26} = 7.09$ *	$F_{1,26} = 0.25$ ns	$F_{1,26} = 0.33$ ns	$F_{1,26} = 1.67$ ns
	CC	$F_{1,26} = 12.80$ *	$F_{1,26} = 1.68$ ns	$F_{1,26} = 3.09$ ns	$F_{1,26} = 0.63$ ns
	WF	$F_{1,26} = 1.16$ ns	$F_{1,26} = 0.16$ ns	$F_{1,26} = 0.21$ ns	$F_{1,26} = 0.45$ ns
N vs. A		$F_{1,17} = 16.01$ *	$X^2_1 = 18$ **	$X^2_1 = 18$ **	$F_{1,17} = 0.29$ ns

inflorescences, whereas *B. terrestris* visited native plants more often. *Bombus* spp. visited all plants primarily for nectar, except for *F. ulmaria* where *Bombus* spp. collected pollen only (they were not observed to extend their probosces for nectar collection).

The functional diversity of insects (H ranging from 0.54 to 1.08) did not vary among treatments ($F_{2,8} = 0.42$; $P = 0.676$).

3.3. Insect abundance

Analysis of standardised insect abundance on native plants revealed no significant differences among treatments with only total insect abundance varying between sites (Tab. I). During observations there was a mean (± S.E.) temperature of 23.1 ± 2.9 °C and mean (± S.E.) cloud cover of 49 ± 40%. Total insect abundance was influenced negatively by cloud cover and temperature whereas bee, *Bombus* spp. and syrphid abundances remained unaffected by the environmental variables (Tab. I). Abundance, if visitors to both native and alien plants are considered, differed between sites within treatments ($F_{6,26} = 3.94$, $P < 0.05$) but not between the three treatments ($F_{2,26} = 0.40$, $P > 0.05$). There was no significant difference in the number of bees and the number of syrphids recorded visiting native plants overall ($F_{1,53} = 3.84$, $P > 0.05$). In sites where *I. glandulifera* was present, significantly more insects (except syrphids) were observed on alien *I. glandulifera* than on native plants (Tab. I) and significantly more bees were observed visiting *I. glandulifera* than syrphids ($F_{1,17} = 24.37$, $P < 0.001$). In these sites, insect abundance was significantly higher on *I. glandulifera* than native *E. hirsutum* and *S. palustris* ($F_{3,35} = 6.02$, $P < 0.05$; Dunnett's *post-hoc* test $P < 0.05$), but there were no differences between *I. glandulifera* and *F. ulmaria* (Dunnett's *post-hoc* test $P > 0.05$).

We detected low power ($\alpha = 0.065$) for the analysis on total insect abundance (three sites per treatment), and increasing the number of sites per treatment by a factor of ten (N = 30) did not increase power greatly ($\alpha = 0.319$).

3.4. *Bombus* spp. abundance and diversity

The mean total number (± S.E.) of *B. pascuorum* individuals caught and marked in first sample (n_1) and subsequently caught in second sample (n_2), and the mean number (± S.E.) of marked *B. pascuorum* individuals recovered in second sample (m_2) for each treatment were: *I. glandulifera* absent: 15.3 ± 7.4, 18.7 ± 5.8 and 6.3 ± 2.3, *I. glandulifera* removed: 7.0 ± 2.6, 10.0 ± 4.0 and 3.3 ± 1.8, *I. glandulifera* present: 41.7 ± 11.3, 42.0 ± 10.7 and 31.7 ± 9.4, respectively. Overall, mean values of N (estimates of abundance according to the Lincoln-Peterson formula, calculated per site and averaged per treatment) suggested that there were fewer *B. pascuorum* individuals in sites where *I. glandulifera* was removed (Fig. 5), although this difference was not significant (N ranging from 0 to 76; $F_{2,8} = 2.11$, $P > 0.05$). There were no significant differences in *Bombus* species diversity

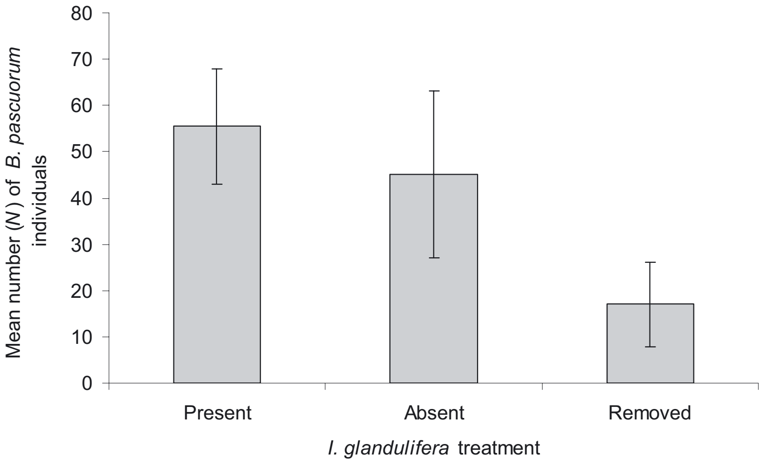

Figure 5. Mean value of N (estimated using the Lincoln-Peterson formula) for *B. pascuorum* individuals in sites where *I. glandulifera* was present, absent and had been experimentally removed.

Table II. Nectar standing crop (μL), nectar secretion rate (μL/24 hrs) and nectar sugar concentration (%) of native (*Epilobium hirsutum* and *Stachys palustris*) and alien (*Impatiens glandulifera*) plant species (mean ± S.E.).

Plant species	Nectar standing crop	Nectar secretion rate	Nectar sugar concentration
E. hirsutum	0.054 ± 0.007	0.502 ± 0.072	47.1 ± 1.4
S. palustris	0.011 ± 0.003	0.167 ± 0.049	47.1 ± 1.1
I. glandulifera	0.043 ± 0.016	10.619 ± 2.176	53.9 ± 2.2

among treatments (*H* ranging from 0.00 to 0.95; $F_{2,8} = 0.13$, $P > 0.05$).

3.5. Nectar resources

When flowers were bagged to prevent insect visitation, nectar was found in native *E. hirsutum* and *S. palustris* species and alien *I. glandulifera*. Mean nectar standing crop was low in all plant species (Tab. II). No significant correlation was found between insect abundance and nectar standing crop in *E. hirsutum* ($r = 0.263$, $P > 0.05$), *S. palustris* ($r = 0.073$, $P > 0.05$) or *I. glandulifera* ($r = -0.564$, $P > 0.05$).

Mean nectar secretion rate was significantly larger in *I. glandulifera* than in *E. hirsutum* and *S. palustris* ($F_{2,20} = 24.51$, $P < 0.001$; Dunnett's *post-hoc* test $P < 0.05$ for both comparisons; Tab. II). Mean sugar concentration was higher in *I. glandulifera* compared with both *E. hirsutum* and *S. palustris* ($F_{2,20} = 4.36$, $P < 0.05$; Dunnett's *post-hoc* test $P < 0.05$ for both comparisons; Tab. II).

4. DISCUSSION

Knowledge on the impacts of invasive alien plants on native pollinators is limited and our study is among the first to explicitly address this topic. We observed that the presence and/or removal of *I. glandulifera* did not seem to affect insect abundance or diversity although in invaded sites the alien attracted large numbers of bees, especially generalist *Bombus* spp. which could be due to its highly rewarding nectar resources. Here, we discuss the implications of our findings for native pollinators, in particular bees, and make suggestions for further study.

4.1. Insect diversity

The large, brightly-coloured flowers of *I. glandulifera* have been previously shown to attract a range of generalist insects (Fussell and Corbet, 1992; Titze, 2000; Lopezaraiza-Mikel et al., 2007). We found no differences in insect functional diversity among invaded and non-invaded sites suggesting that *I. glandulifera* does not reduce diversity at the site level. However, we did not identify solitary bees and syrphids to species, and grouping may mean we missed changes in some rare and/or specialist taxa. *Bombus* spp. were the most common visitors to *I. glandulifera*, whilst syrphids visited native plants more often. This supports similar findings from the UK (Lopezaraiza-Mikel et al., 2007). This is unsurprising considering the differences in floral morphology between two of the native plants (*F. ulmaria* and *E. hirsutum* have radially symmetrical flowers) and *I. glandulifera* (zygomorphic flowers) and may explain *Bombus* spp. preference for the alien, as bees favour the latter shape (Proctor et al., 1996). *I. glandulifera* could be less attractive to syrphids because they are too small to access nectar in the spur located at the posterior of the lower sepal (Titze, 2000).

Bombus flower preferences varied among species, which may be explained by tongue length and corolla depths (Inouye, 1980; Prýs-Jones and Corbet, 1991; Comba et al., 1999): medium- and long-tongued *Bombus* spp. (*B. pascuorum* and *B. hortorum*) favoured the deep *I. glandulifera* flowers and short-tongued *Bombus* spp. (*B. terrestris* and *B. pratorum*) the more shallow native flowers. Short-tongued *Bombus* spp. might not be able to extract nectar from *I. glandulifera*, or it may take them longer, reducing their energetic gain (Harder, 1983). *I. glandulifera* may therefore be providing a nectar resource mainly for longer-tongued *Bombus* spp. Additionally, even though pollen is readily accessible to visiting insects, no visitors (both bees and syrphids) were observed actively collecting pollen during the experimental period.

4.2. Insect abundance

Our results suggest that the presence of *I. glandulifera* did not affect insect abundance, when measured as visitation to native co-flowering plant species. This finding contrasts with Lopezaraiza-Mikel et al. (2007) who observed a higher insect abundance in sites containing *I. glandulifera*. There may be several explanations for this. Firstly, our data were collected as visitation rates, whereas Lopezaraiza-Mikel et al. (2007) measured insect abundance using transect methods. Secondly, our study was conducted during a short time period when all potted native species and *I. glandulifera* were co-flowering and may not reflect the situation at other times of the year. Thirdly, we only had three sites per treatment and high within-treatment variation among plots, which may have reflected variable climatic conditions, since insect abundance decreased with increased cloud cover and temperature. We were unable to completely standardise climatic conditions due to logistical (number of observers) and temporal constraints (flowering period of plants). Indeed, small scale variability in weather is a standard source of variation in field experiments of this sort. Power analysis suggested that increasing the number of sites per treatment may not enhance experimental power and would simultaneously increase the spatial scale of the experiment, and may introduce further variation among sites. Fourthly, invaded sites attracted a higher proportion of bees, and most of these bees (principally *B. pascuorum*) preferentially visited the alien. Therefore, the abundance of insects, as recorded as visitation to native plants, did not vary since native plants still attracted other visitors (such as short-tongued *Bombus* spp. and syrphids) which tended not to visit *I. glandulifera*. Lastly, in our sites, isolated *I. glandulifera* patches did not occupy extensive areas of the river bank common elsewhere in Europe (Beerling and Perrins, 1993; Pyšek and Prach, 1995), and left enough space for the persistence of native plants, which represented an attractive resource to insects, particularly those less able to, or efficient at, exploiting *I. glandulifera*.

4.3. *Bombus* spp. abundance and diversity

Contrary to our hypothesis, invaded sites did not attract a greater abundance of

B. pascuorum or diversity of *Bombus* spp. compared with non-invaded sites. Study sites contained a diverse native flora, which did not vary significantly among sites, with many valuable forage plants including *Epilobium hirsutum*, *Rubus fruticosus* agg and *Cirsium* spp. that provide forage resources for a variety of *Bombus* species (Fussell and Corbet, 1992). We can assume that the abundance of shorter-tongued *Bombus* species (e.g. *B. terrestris*) may not be influenced greatly by *I. glandulifera* as they did not utilise the alien frequently. However, if the invasion by *I. glandulifera* becomes more widespread, causing a loss of the native flora, we might see quite different results (c.f. Lopezaraiza-Mikel et al., 2007).

Although we only sampled during a short time period, with its prolonged flowering season (June to October), *I. glandulifera* may support the survival and reproduction of *B. pascuorum* colonies which persist until late October, when flowering native plants become scarce (Sowig, 1989; Starý and Tkalců, 1998) and queens build up fat bodies in preparation for hibernation (Prýs-Jones and Corbet, 1991). Then again, *I. glandulifera* provides no resources to initial queens emerging in spring and could be displacing important early flowering resources (Lopezaraiza-Mikel et al., 2007). *I. glandulifera* is probably less valuable to early emerging and short-tongued species with short colony cycles, such as *B. pratorum*. The impact of alien plants on the entire *Bombus* colony cycle and on *Bombus* populations and colony sizes merits further investigation and studies addressing this are currently being undertaken in Ireland (Dietzsch and Stout, in prep.).

I. glandulifera is common in disturbed habitats, which support more widespread generalist *Bombus* spp. such as *B. terrestris* and *B. pascuorum*. As a result, *I. glandulifera* might be a vital forage resource for and may be supporting increased populations of common generalist medium- and long-tongued *Bombus* spp., which have been recognised as important for conservation (Fitzpatrick et al., 2007), especially in built-up areas of Ireland. However, the possible spread of *I. glandulifera* into rare habitats and the consequent displacement of native plants may have severe implications on the survival of threatened bee species in Ireland.

4.4. Nectar resources

We observed no relationship between nectar standing crop and insect abundance. Standing crop was low in all study plants. This has been reported elsewhere (Comba et al., 1999) and may be due to low nectar secretion rates of native plants, *Bombus* spp. efficiently depleting resources and/or high ambient temperatures (up to 28.5 °C in the shade) causing water to evaporate more quickly.

I. glandulifera produced significantly more nectar (20 and 81 times respectively) that was higher in sugar concentration compared to both *E. hirsutum* and *S. palustris*. However, native species were rooted in pots whilst *I. glandulifera* plants were naturally rooted in the soil, which may bias these results. Nevertheless, similarly low nectar secretion rates and sugar concentrations have been measured for naturally established plants of both *E. hirsutum* (0.489 ± 0.074 μL and 13.7 ± 1.5% respectively) and *S. palustris* (1.162 ± 0.222 μL and 36.0 ± 2.6% respectively) (Nienhuis and Stout, in prep.). *Bombus* spp. prefer nectar-rich flowers (Heinrich, 1976; Corbet et al., 1984) with high sugar concentrations (Corbet et al., 1979) and they require energetically high rewards to maintain colonies (Comba et al., 1999; Titze, 2000; Morales and Aizen, 2006). It is unclear however, whether the quality of *I. glandulifera* nectar and pollen is nutritionally adequate for *Bombus* spp. and their colonies and current research is addressing this issue (Nienhuis and Stout, in prep.).

4.5. *I. glandulifera* removal

Our study implies that *I. glandulifera* flower removal had no effect on insect abundance nor did it impact *B. pascuorum* numbers and *Bombus* spp. diversity. In contrast, Lopezaraiza-Mikel et al. (2007) found significant reductions in both species richness and insect abundance when the alien was removed compared to when it was present. Alien flower removal might not have severely impacted insect abundance in our study sites because insects feeding on *I. glandulifera* switched to native plants instead. This is unlikely however, as the alien attracted mainly large bees (*Bombus* spp.) and other insects are therefore not likely to be impacted greatly. In addition, alien flower removal might not have impacted insect abundance in our study sites severely because the alien formed small patches compared to Lopezaraiza-Mikel et al.'s (2007) sites that were all heavily invaded and where *I. glandulifera* was the dominant plant. This suggests that pollinators were not deterred from returning to sites and were able to locate alternative forage resources rapidly after alien removal. Other studies also suggest that localised control of alien plants does not impact pollinator activity (Aigner, 2004) and species diversity is quick to recover following removal (Hejda and Pyšek, 2006). These findings imply that removing small patches of *I. glandulifera* flowers in order to prevent the alien from setting seed might be feasible for conservation purposes on a local scale. However, further research is needed to investigate what impacts removing monospecific and widespread stands on a regional scale has on pollinators with different life history strategies relying solely on *I. glandulifera*, on specialised and rare pollinator taxa and the native plant community supporting such pollinators.

5. CONCLUSIONS

Medium- and long-tongued *Bombus* spp. are utilising the sugar-rich nectar of *I. glandulifera*. However, it is unclear whether *Bombus* spp. are actively employing *I. glandulifera* pollen for colony maintenance and whether the pollen is nutritionally adequate. Although localised *I. glandulifera* flower removal does not seem to affect insect abundance, our study highlights the need for further experimental long-term studies focusing on pollinator population responses to the spread and consequent removal of *I. glandulifera*, especially on a regional scale.

ACKNOWLEDGEMENTS

We thank Caroline Byrne for assistance in the field, and Karl Duffy for helpful discussions. We are grateful to Dave Goulson, Karl Duffy and two anonymous referees for comments on the manuscript. This study was funded by the Irish Government (Department for the Environment and Local Government) via an Environmental Protection Agency Postgraduate Studentship (2005-PHD5-B-17) provided under the Environmental Research Technological Development and Innovation (ERTDI) Programme as part of the National Development Plan 2000–2006, which was awarded to JCS and supported the PhD of CMN.

Impacts de l'introduction puis de l'élimination d'une plante invasive étrangère sur les abeilles indigènes.

***Bombus* / *Impatiens glandulifera* / plante invasive / plante introduite / secrétion nectarifère / concentration en sucres / nectar / pollinisateur / diversité écologique / abondance écologique**

Zusammenfassung – Die Auswirkungen der Einschleppung und der anschließenden Beseitigung einer Neophyte auf einheimische Bienen. Die Kenntnis über die Auswirkungen von Neophyten auf die einheimischen bestäubenden Insekten ist äußerst gering. Einige invasive Pflanzen haben auffällige florale Kennzeichen, eine hohe Nektarsekretion und sind daher attraktiv für einheimische Insekten. Eine dieser Arten ist *Impatiens glandulifera*, die sich erfolgreich in Flussauen von ganz Europa verbreitet hat und deren Effekte auf die einheimische Flora recht gut untersucht sind. Wir wissen allerdings wenig über direkte oder indirekte Auswirkungen von *I. glandulifera* auf einheimische Bestäuber. Wir erfassten die Abundanz von Bestäubern in Untersuchungsgebieten, in denen *I. glandulifera* vorkam bzw. nicht vorkam und in Gebieten, in denen *I. glandulifera* experimentell entfernt wurde. An jedem Standort legten wir nach einem standardisierten Muster Pflanzengesellschaften aus drei einheimischen Arten an und erfassten die Insektenbesuche an diesen Pflanzen. Zusätzlich erfassten wir die Besuche an *I. glandulifera* und führten Experimente zur Wiederfindung markierter *Bombus pascuorum* durch, um die Nutzung der Standorte durch Hummeln zu beurteilen. Die Anwesenheit und/oder die Entfernung von *I. glandulifera* hatte weder auf die standardisierte Abundanz von Insekten noch auf die funktionelle Insektendiversität einen signifikanten Einfluss (Tab. I), was eventuell auf die unterschiedlichen klimatischen Bedingungen zurück zu führen ist. Allerdings scheinen

Bombus spp. den höchsten Anteil an Besuchen an Standorten mit Neophyten zu haben während Solitärbienen den höchsten Anteil an Standorten ausmachten, an denen *I. glandulifera* entfernt wurde (Abb. 3). Darüber hinaus waren *Bombus* spp. an den entsprechenden Standorten besonders häufig an Blütenständen von *I. glandulifera* zu finden, wobei mittel- und langrüsselige Hummeln (*Bombus pascuorum* und *B. hortorum*) die Neophyte bevorzugt besuchten (Fig. 4). Allerdings lockten Standorte mit *I. glandulifera* nicht mehr *B. pascuorum* an als Neophyten-freie Standorte (Abb. 5) und auch die Diversität von *Bombus* spp. unterschied sich nicht zwischen "befallenen" und "nicht befallenen" Standorten. Trotzdem macht die hohe Produktion von zuckerreichem Nektar (Tab. II) *I. glandulifera* zu einer äußerst attraktiven Nektarquelle für die einheimischen mittel- und langrüsselige Hummeln in Irland. So mögen die Generalisten unter den Hummelarten, die eine wichtige Bedeutung für die Bestäubung haben, durch *I. glandulifera* als alternative Trachtquelle letztendlich sogar unterstützt werden. Andererseits werden bereits gefährdete Bestäuber durch Neophyten eventuell zusätzlich bedroht, da einheimische Pflanzen verdrängt werden. Unsere Ergebnisse lassen darauf schließen, dass die Entfernung von kleinen Ansammlungen von *I. glandulifera*-Pflanzen für örtlich begrenzte Naturschutzmaßnahmen Sinn macht. Es ist aber unklar, welche Auswirkungen die Entfernung von *I. glandulifera* an größeren Monokultur-Standorten für Hummeln und diejenigen Bestäuber hat, die diese Balsaminenart als alleinige Trachtquelle nutzen. In Langzeitstudien sollte daher untersucht werden, wie Bestäuberpopulationen auf die Verbreitung und auf die konsequente Entfernung von *I. glandulifera* reagieren.

***Bombus* / *Impatiens glandulifera* / Nektar-Sekretionsrate / Nektar-Zuckerkonzentration / Syrphidae**

REFERENCES

Aigner P.A. (2004) Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*, Biol. Conserv. 116, 27–34.

Barker R.J. (1978) Poisoning by plants, in: Morse R.A. (Ed.), Honey bee pests, predators, and diseases, Cornell University Press, London, pp. 275–296.

Beerling D.J., Perrins J.M. (1993) *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.), J. Ecol. 81, 367–382.

Biesmeijer J.C., Roberts S.P.M., Reemer M., Ohlemueller R., Edwards M., Peeters T., Schaffers A.P., Potts S.G., Kleukers R., Thomas C.D., Settele J., Kunin W.E. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands, Science 313, 351–354.

Bjerknes A.L., Totland Ø., Hegland S., Nielsen A. (2007) Do alien plant invasions really affect pollination success in native plant species? Biol. Conserv. 138, 1–12.

Chapin F.S., Zavaleta E.S., Eviner V.T., Naylor R.L., Vitousek P.M., Reynolds H.L., Hooper D.U., Lavorel S., Sala O.E., Hobbie S.E., Mack M.C., Diaz S. (2000) Consequences of changing biodiversity, Nature 405, 234–242.

Chittka L., Schürkens S. (2001) Successful invasion of a floral market, Nature 411, 653.

Comba L., Corbet S.A., Hunt L., Warren B. (1999) Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens, Ann. Bot. 83, 369–383.

Corbet S.A., Kerstlake C.J.C., Brown D., Morland N.E. (1984) Can bees select nectar-rich flowers in a patch? J. Apic. Res. 23, 234–242.

Corbet S.A., Unwin D.M., Prys-Jones O.E. (1979) Humidity, nectar and insect visits to flowers, with special reference to *Crataegus*, *Tilia* and *Echium*, Ecol. Entomol. 4, 9–22.

Darvill B., Knight M.E., Goulson D. (2004) Use of genetic markers to quantify bumblebee foraging range and nest density, Oikos 107, 471–478.

Davis M.A. (2003) Biotic globalization: Does competition from introduced species threaten biodiversity?, BioScience 53, 481–489.

Fitzpatrick U., Murray T.E., Paxton R.J., Breen J., Cotton D., Santorum V., Brown M.J.F. (2007) Rarity and decline in bumblebees – a test of causes and correlates in the Irish fauna, Biol. Conserv. 136, 185–194.

Fussell M., Corbet S.A. (1992) Flower usage by bumblebees – a basis for forage plant management, J. Appl. Ecol. 29, 451–465.

Ghazoul J. (2002) Flowers at the front line of invasion? Ecol. Entomol. 27, 638–640.

Goodell K. (2008) Invasive exotic plant-bee interactions, in: James R.R., Pitts-Singer T.L. (Eds.), Bee pollination in agroecosystems, Oxford University Press, Oxford, pp. 166–183.

Harder L.D. (1983) Flower handling efficiency of bumble bees: morphological aspects of probing time, Oecologia 57, 274–280.

Heinrich B. (1976) The foraging specialization of individual bumblebees, Ecol. Monogr. 46, 105–128.

Hejda M., Pyšek P. (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? Biol. Conserv. 132, 143–152.

Hulme P.E., Bremner E.T. (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal, J. Appl. Ecol. 43, 43–50.

Inouye D.W. (1980) The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees, Oecologia 45, 197–201.

Johnson S.D., Steiner K.E. (2000) Generalization versus specialization in plant pollination systems, Trends Ecol. Evol. 15, 140–143.

Knight M.E., Martin A.P., Bishop S., Osborne J.L., Hale R.J., Sanderson R.A., Goulson D. (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species, Mol. Ecol. 14, 1811–1820.

Könies H., Glavač V. (1979) Über die Konkurrenzfähigkeit des Indischen Springkrautes (*Impatiens glandulifera* ROYLE) am Fuldaufer bei Kassel, Philippia 4, 47–59.

Levine J.M., Vilà M., D'Antonio C.M., Dukes J.S., Grigulis K., Lavorel S. (2003) Mechanisms underlying the impacts of exotic plant invasions, Proc. R. Soc. B-Biol. Sci. 270, 775–781.

Lopezaraiza-Mikel M.E. (2006) The impact of alien species on native pollination systems, PhD thesis, University of Bristol, Bristol.

Lopezaraiza-Mikel M.E., Hayes R.B., Whalley M.R., Memmott J. (2007) The impact of an alien plant on a native plant-pollinator network: an experimental approach, Ecol. Lett. 10, 539–550.

Maskell L.C., Firbank L.G., Thompson K., Bullock J.M., Smart S.M. (2006) Interactions between non-native plant species and the floristic composition of common habitats, J. Ecol. 94, 1052–1060.

Memmott J., Waser N.M. (2002) Integration of alien plants into a native flower-pollinator visitation web, Proc. R. Soc. B-Biol. Sci. 269, 2395–2399.

Minitab (2000) MINITAB$^{\text{TM}}$ Statistical Software for Windows, Release 13.30, State College, PA, USA.

Moragues E., Traveset A. (2005) Effect of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands, Biol. Conserv. 122, 611–619.

Morales C.L., Aizen M.A. (2006) Invasive mutualisms and the structure of plant-pollinator interactions in the temperate forests of north-west Patagonia, Argentina, J. Ecol. 94, 171–180.

Naiman R.J., Décamps H. (1997) The ecology of interfaces: riparian zones, Annu. Rev. Ecol. Syst. 28, 621–658.

Parker I.M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch Broom), an invasive exotic shrub, Ecology 78, 1457–1470.

Parker I.M., Haubensak K.A. (2002) Comparative pollinator limitation of two non-native shrubs: do mutualisms influence invasions? Oecologia 130, 250–258.

Perrins J., Fitter A., Williamson M. (1993) Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles, J. Biogeogr. 20, 33–44.

Proctor M., Yeo P., Lack A. (1996) The natural history of pollination, Timber Press, Portland, Oregon.

Prowse A., Goodridge F. (2000) Pollinator visitation rates of *Impatiens glandulifera* and other native riparian vegetation, Aspect. Appl. Biol. 58, 249–254.

Prýs-Jones O.E., Corbet S.A. (1991) Bumblebees, Richmond Publishing Slough.

Pyšek P., Prach K. (1993) Plant invasions and the role of riparian habitats – a comparison of four species alien to central Europe, J. Biogeogr. 20, 413–420.

Pyšek P., Prach K. (1995) Invasion dynamics of *Impatiens glandulifera* – a century of spreading reconstructed, Biol. Conserv. 74, 41–48.

Rathcke B. (1983) Competition and facilitation among plants for pollinators, in: Real L. (Ed.), Pollination biology, Academic Press, Inc., London, pp. 305–329.

Reynolds S.C.P. (2002) A catalogue of alien plants in Ireland, National Botanic Gardens, Glasnevin, Dublin.

Richardson D.M., Allsopp N., D'Antonio C.M., Milton S.J., Rejmánek M. (2000) Plant invasions – the role of mutualisms, Biol. Rev. 75, 65–93.

Sala O.E., Chapin F.S., Armesto J.J., Berlow E., Bloomfield J., Dirzo R., Huber-Sanwald E., Hünneke L.F., Jackson R.B., Kinzig A., Leemans R., Lodge D.M., Mooney H.A., Österheld M., Poff N.L., Sykes M.T., Walker B.H., Walker M., Wall D.H. (2000) Biodiversity – global biodiversity scenarios for the year 2100, Science 287, 1770–1774.

Schürkens S., Chittka L. (2001) The significance of the invasive crucifer species *Bunias orientalis* (Brassicaceae) as a nectar source for central European insects, Entomol. Gen. 25, 115–120.

Showler K. (1989) The Himalayan balsam in Britain – an undervalued source of nectar, Bee World 70, 130–131.

Southwood T.R.E., Henderson P.A. (2000) Ecological methods, Oxford Blackwell Science, Oxford.

Sowig P. (1989) Effects of flowering plants patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera, Apidae), Oecologia 78, 550–558.

Starý P., Tkalců B. (1998) Bumble-bees (Hym., Bombidae) associated with the expansive touch-me-not, *Impatiens glandulifera* in wetland biocoridors, Anz. Schädl. Schädl. Pflanzenschutz, Umweltschutz 71, 85–87.

Stout J.C., Parnell J.A.N., Arroyo J., Crowe T.P. (2006) Pollination ecology and seed production of

Rhododendron ponticum in native and exotic habitats, Biodivers. Conserv. 15, 755–777.

Titze A. (2000) The efficiency of insect pollination of the neophyte *Impatiens glandulifera* (Balsaminaceae), Nord. J. Bot. 20, 33–42.

Traveset A., Richardson D.M. (2006) Biological invasions as disruptors of plant reproductive mutualisms, Trends Ecol. Evol. 21, 208–216.

Underwood A.J. (1997) Experiments in ecology: their logical design and interpretation using analysis of variance, Cambridge University Press, Cambridge.

Vitousek P.M., D'Antonio C.M., Loope L.L., Rejmánek M., Westbrooks R. (1997) Introduced species: a significant component of human-caused global change, New Zeal. J. Ecol. 21, 1–16.