

Pollination ecology and seed production of *Rhododendron ponticum* in native and exotic habitats

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Abstract. Alien plants may be reproductively limited in exotic habitats because of a lack of mutualistic pollinators. However, if plants are adequately served by generalist pollinators, successful reproduction, naturalisation and expansion into exotic habitats may occur. *Rhododendron ponticum* is very successful, ecologically damaging invasive plant in Britain and Ireland, but is in decline in its native Iberian habitat. It spreads locally by sending out lateral branches, but for longer distance dispersal it relies on sexually produced seeds. Little is known about *R. ponticum*'s pollination ecology and breeding biology in invaded habitats. We examined the flower-visiting communities and maternal reproductive success of *R. ponticum* in native populations in southern Spain and in exotic ones in Ireland. *R. ponticum* flowers are visited by various generalist (polylectic) pollinator species in both native and exotic habitats. Although different species visited flowers in Ireland and Spain, the flower visitation rate was not significantly different. Insects foraging on *R. ponticum* in Spain carried less *R. ponticum* pollen than their Irish counterparts, and carried fewer pollen types. Fruit production per inflorescence varied greatly within all populations but was significantly correlated with visitation at the population level. Nectar was significantly depleted by insects in some exotic populations, suggesting that this invasive species is providing a floral resource for native insects in some parts of Ireland. The generality of the pollination system may be factor contributing to *R. ponticum*'s success in exotic habitats.

Introduction

Invasive species are recognised as one of the key threats to native biodiversity. Invasions are increasing in frequency and general models are urgently required to predict and manage their impacts. Although many plant species are artificially introduced into non-native habitats, only a fraction of species become invasive (Mack et al. 2000; Richardson et al. 2000). An exotic plant can only become established and invade a new habitat if the physical characteristics are suitable, and if symbiotic micro-organisms, mutualistic pollinators and seed dispersers are present (Richardson et al. 2000; Mooney and Cleland 2001). Despite pollination being crucial to plant reproduction and hence invasion, the role of pollination mutualists in facilitating or constraining invasions has

received little attention (Parker and Haubensak 2002). In order to out-breed, animal-pollinated exotic plants to invade a new habitat, either mutualistic pollinators must be introduced simultaneously (or subsequently), or plants must rely on resident native pollinator species or other methods of reproduction (Valentine 1978; Parker 1997; Richardson et al. 2000; Barthell et al. 2001; Parker and Haubensak 2002; Stout et al. 2002). Specialised pollination mutualisms (where a plant relies on a single species of pollinator) are rare in nature (Schemske 1983; Waser et al. 1996; Pellmyr 2002), although there are notable exceptions (for example see Riley 1892; Barth 1991; Fleming and Holland 1998; Weiblen 2002). If a species does require specialist pollinators, reproductive success may be constrained by a lack of specific pollinators in an exotic habitat (Hopkins 1914; Stout et al. 2002). However, most exotic plants are well served by native, generalist pollinators, particularly when they originate from within the same continent (Valentine 1978) and generalisation in the pollination system is likely in an invading weedy species (Baker 1965).

Although generalist flower visitors may be able to pollinate exotic species, variation in levels of pollinator visitation may promote or inhibit invasive plant spread in an exotic habitat. Low levels of pollinator visitation have been shown to cause pollen limitation in a range of systems (Bierzychudek 1981; Zimmerman and Aide 1989; Burd 1994; Ehrlén and Eriksson 1995; Parker 1997; Thomson 2001; but see Tepedino et al. 1999). For exotic plants, pollinator limitation may result from the plant occurring in small or low density populations which do not attract enough pollinators, or from exotic plants not being able to compete with native ones for pollinator attention (Levin and Anderson 1970; Rathcke 1983; Fritz and Nilsson 1994; Goverde et al. 2002). Alternatively, low numbers of suitable generalist pollinator species may limit pollination success. However, if generalist species can legitimately pollinate introduced plants and these pollinators are abundant, exotic species may be reproductively successful and spread rapidly (Parker 1997; Richardson et al. 2000).

Rhododendron ponticum (Ericaceae) is extensively naturalised throughout the British Isles. It is native to the Black Sea coast, Lebanon and the Iberian peninsula (Cross 1975; Chamberlain 1982; Castroviejo et al. 1993). The pollen record shows that *Rhododendron ponticum* grew in central southern Europe and in Ireland during Pleistocene interglacials (Rotherham 2002). In the current interglacial, the species was artificially introduced into Britain in AD1763, and to Ireland later the same century, as an ornamental species, to provide cover for game and as a wind-break (Brown 1953; Cross 1975; Rotherham 2001). Molecular analysis of chloroplast and ribosomal DNA suggests that naturalised *R. ponticum* populations in the British Isles are descended from Iberian ancestors and that introgression with North American species (*R. catawbiense* and *R. maximum*) has occurred (Milne and Abbott 2000).

In much of its native range, natural stands of *R. ponticum* tend to be small and confined to moist, upland areas (Colak et al. 1998; Rotherham 2001). It is recognised as a 'Red Data Book' species in Bulgaria and is listed as an 'extinction risk species' in southern Spain (Colak et al. 1998; Blanca et al. 1999;

Ojeda et al. 2000). In north-eastern Turkey, however, *R. ponticum* can be an abundant and destructive weed in managed forests (Rotherham 2001) and in Britain and Ireland, it is invasive and severely ecologically damaging (Brown 1953; Rotherham 2001). Plants not only shade out native seedlings, but also secrete allelopathic acids which may inhibit the growth of competitors (Rotherham and Read 1988). Tissues contain acetylandromedol (formerly called andromedotoxin, a grayanotoxin), which is highly toxic if ingested by herbivores and there are few natural enemies of *R. ponticum* in British Isles (Cross 1975; Judd and Rotherham 1992; Yela and Lawton 1997). These toxins have also been found in honey produced from the nectar of *R. ponticum* (Onat et al. 1991; von Malottki and Wiechmann 1996).

Successful spread in Ireland is thought to occur as a result of effective seedling recruitment (Cross 1981). Seeds are produced sexually (rather than apomictically) and zoophilous pollination by a range of insects is presumed (Cross 1975). Experiments indicate that outcrossing greatly improves seed set (J.C. Stout, unpublished data). Mejías et al. (2002) found more than 13 species of insect visiting *R. ponticum* flowers in native populations in southern Spain, with large bees (*Bombus terrestris* and *Xylocopa violacea*) making up 65% of all flower visits. Given the different climatic conditions in native (Mediterranean) and exotic (temperate) habitats, plus differences in the insect fauna of these two areas, there are likely to be different pollination regimes in these places. Whilst flowers are probably visited by generalist, opportunistic foragers on the islands of Britain and Ireland, we may expect fewer species to visit flowers. This is partly because of a generally depauperate insect fauna in the British Isles compared with continental Europe, but also because *R. ponticum* is a relatively recently introduced exotic species which has not co-evolved with native pollinators. We may also expect a lower rate of visitation in exotic habitats, possibly due to native insects favouring native flower species with which they have co-evolved. Exotic plant species that produce profuse volumes of nectar do attract native pollinators (Stary and Tkalcu 1998; Chittka and Schurkens 2001; Ghazoul 2002), but we do not know how nectar production by exotic *R. ponticum* affects pollinator visitation. In addition, we do not know how variation in visitation rates affects sexual reproductive success in this species.

In this study, we compare the pollination ecology and seed set of *R. ponticum* in exotic (temperate) and native (Mediterranean) habitats. Specifically, we tested the following hypotheses:

1. The diversity of flower visitors is greater in native habitats.
2. Visitation rates per flower are higher in native habitats.
3. Flower visitors in exotic habitats are more generalist i.e. they visit more flower species during a single foraging bout.
4. Insect visitation reduces nectar standing crop, and hence nectar levels vary with visitation rates in both native and exotic habitats.
5. Maternal reproductive success (seed and fruit production) is reduced in exotic habitats due to pollinator limitation.

Methods

Study sites

Eight populations of *R. ponticum* were studied in Spain and Ireland. In Spain, two populations (approximately 3.5 km apart) within the Parque Natural Los Alcornocales (~5 km inland from the Strait of Gibraltar) were studied from 20 to 28 April 2002 (Table 1, Figure 1). In Ireland, two populations in each of Killarney National park (Co. Kerry), Connemara (Co. Galway), and Co. Dublin were studied from 16 May to 20 June 2002 (Table 1, Figure 1).

Identity and abundance of flower visitors

In each population, four randomly selected patches of *R. ponticum* flowers (with a mean of 82.5 flowers per patch) were observed for 10 min each, at each of three periods during the day (9.30–10.30, 12.30–13.30, and 15.30–16.30) on each of at least three days. All insects visiting flowers for nectar and/or pollen and the number of flowers and inflorescences visited by each individual were recorded.

Table 1. Populations used in this study, their size in terms of the number of flowering plants in the population, their position, elevation (Elev. in m above sea level), surrounding habitat type and the dates on which timed observations were carried out.

Location	Population	Size	Position	Elev (m)	Habitat type	Date
Los Alcornocales, Spain	El Palancar	18	36°04'56"N 05°32'36"W	483	Stream valley, steep SSW facing slope	21, 23, 25 April
	Las Corzas	27	36°06'39"N 05°31'42"W	490	Stream valley, steep SE facing slope	22, 26, 27 April
Co. Dublin, Ireland	Howth Head	~150	53°22'36"N 06°04'12"W	130	Stream valley, gentle NE facing slope	16 May, 03, 04, 06, 17, 19 June
	Glencullen	~150	53°13'48"N 06°16'20"W	335	Steep NE facing slope	05, 18, 20 June
Killarney National Park, Ireland	Gortderraree	> 1000	51°59'17"N 09°33'29"W	0	Flat area on edge of woodland	29, 31 May, 11 June
	Gortracussane	> 1000	52°00'20"N 09°32'24"W	36	Flat area on edge of heathland	30 May, 10, 12 June
Connemara, Ireland	Recess	~100	53°28'00"N 09°44'20"W	16	Flat, lakeside habitat	25, 27 May, 14 June
	Kylemore	> 1000	53°33'42"N 09°51'58"W	19	Steep S facing slope	26, 28 May, 13 June

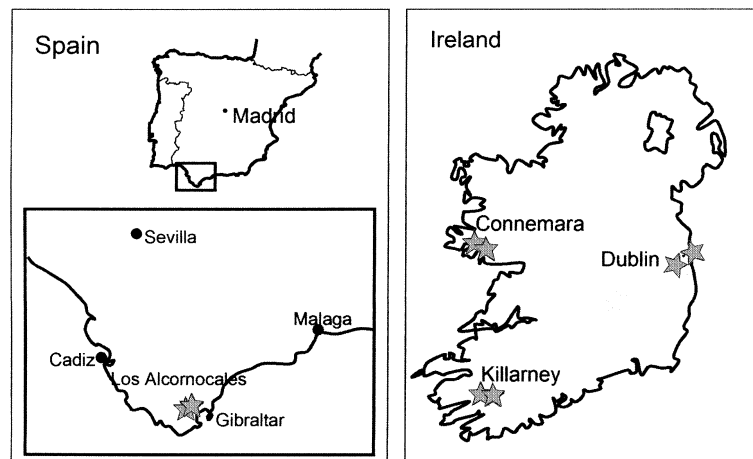


Figure 1. Location of *Rhododendron ponticum* populations in Spain and Ireland that were used in this study (grey stars). Named cities are marked with filled circles.

Two measures of visitation rate were calculated: the number of insects per flower per hour (number of insects arriving at patch in 10 min \div number of flowers in patch \times 6) and the number of visits per flower per hour (number of flower visited in patch in 10 min \div number of flowers in patch \times 6). In order to assess multivariate patterns in the structure of flower visitor communities, Bray-Curtis dissimilarity matrices were constructed using the identity and visitation rates of flower-visitors for each time period on each day. Samples with no visitors were excluded from this analysis. Non-metric multi-dimensional scaling (nMDS) plots were constructed using the PRIMER package of statistical software (*Plymouth Routines in Multivariate Ecological Research*, Plymouth Marine Laboratory, Plymouth, UK) to visualise patterns of community structure. Hypothesis of difference among communities were tested using Non-parametric multivariate analysis of variance (NP-MANOVA) (Anderson 2001), with the factors location and population (nested within location). The PRIMER routine SIMPER (Similarity of Percentages) was used to identify which species were important in discriminating among samples from the different populations.

Total visitation rates were also analysed using a four-factor nested ANOVA (factors: location, population nested within location, time, and date nested within population within location) ($n = 4$). Variances (for this and subsequent ANOVAs) were tested for heterogeneity using Cochran's test and data were transformed wherever necessary. When transformations failed to reduce heterogeneity of variances, analyses were carried out on untransformed data. Large, balanced ANOVAs are robust to breaches of this assumption, but significant results were treated with caution (Box 1953; Underwood 1981). Significant terms were analysed using *post hoc* Student–Newman–Keuls (SNK) tests to determine which means differed from one-another.

Temperature, cloud cover and wind force were measured during each observation period and their relationship with insect visitation rates tested using Pearson's product moment correlation.

Pollen loads of flower visitors

To assess whether the most common flower visitors pick up *R. ponticum* pollen (and hence have the potential to disperse this pollen) and to estimate the number of flower species included in an individual's foraging bout, 70 insects of the most abundant species foraging on *Rhododendron ponticum* flowers were collected at the end of the period of observations (37 from Ireland: 26 *Bombus* spp. (5 *B. jonellus*, 9 *B. lucorum/magnus*, 11 *B. monticola*, 1 *B. pratorum*), 5 *Andrena lapponica* and 6 Syrphids (3 *Eristalis tenax* and 3 *Seriocomyia silentis*); and 33 from Spain: 4 *Bombus terrestris*, 6 *Eucera* spp., 8 small bees (*Lasioglossum*, *Andrena* and *Melitta* spp.), 4 *Xylocopa violaceae*, 6 *Bombylius major* and 5 *Oxythya funesta*). Individuals were collected whilst foraging, stored in individual plastic collection tubes and killed by freezing. In the lab, distilled water was added to the collection tube to cover the insect. Tubes were then shaken on an electronic table-top shaker for 1 h. Insects were removed from collection tubes, held with forceps and rinsed over a clean centrifuge tube. The contents of the collection tubes were drained into the centrifuge tube, and the collection tube was rinsed to minimise pollen loss. Tubes were then centrifuged at 4000 rpm for 10 min. The supernatant was decanted off, and the pollen pellet was air-dried. Pollen pellets were resuspended in 0.5 ml absolute alcohol and mixed thoroughly. Ten 5 μ l sub-samples were taken from each sample and examined under a light microscope (at 100 \times and 400 \times). Pollen grains were identified to morpho-types and the total number of each type of pollen was counted for each sub-sample.

We estimated the total number of pollen grains carried by an individual insect by calculating the mean number in the 10 sub-samples and multiplying this by 100. Obviously, some pollen grains will have been lost or overlooked in this process, but since the same technique was used for all individuals, we believe that comparisons made among individuals are valid. We compared the total number of pollen grains, number of pollen types, number of *R. ponticum* pollen tetrads (Ericaceous pollen forms tetrads consisting of 4 cells – in this analysis each tetrad was counted as a single pollen grain) and proportion of *R. ponticum* pollen among insect species within Ireland and Spain and between the two countries using non-parametric analysis (Mann–Whitney *U* and Kruskal–Wallis tests).

Nectar production

We measured nectar volumes each time observations of flower visitation were made. Nectar standing crop was measured using 1 and 5 μ l micropipettes

(Drummond 'Microcaps', Drummond Scientific Co, USA) in 16 randomly selected flowers immediately after observations were made of pollinator visitation (i.e. at three times during the day on each day of observation). In addition, six randomly selected inflorescences were protected from insect visitation in each population with bridal veil material. Two or three days later, nectar volumes were measured in 16 randomly selected flowers from the six protected inflorescences. The volume of standing crops of nectar were analysed using a four-factor nested ANOVA (factors: location, population nested within location, date nested within population within location, and time, plus interactions) ($n = 16$). Data from only two of the three days were used for each population because rain filled flowers with water in three populations on the third day. Similarly, the volume of nectar from protected flowers were analysed using a two-factor (location and population nested within location) nested ANOVA ($n = 16$). To determine whether nectar was being depleted at the population level, nectar volumes of protected flowers were compared with standing crop volumes in each population using t -tests (F -tests were first carried out to determine if variances were significantly different and then, depending on the outcome of the F -tests, t -tests assuming equal or unequal variances were carried out). Visitation rates were inversely transformed and correlated with average nectar standing crop volumes for each observation period.

Seed and fruit production

From 31st January to 6th February 2003, when fruits were fully mature, five inflorescences from five plants in each of the six populations in Ireland were collected. Fruits were removed from petioles, weighed and measured, and stored in separate paper bags for 4–6 days until they burst and seeds were released. 73 randomly selected fruits were re-weighed and measured and the number of seeds contained in these fruits were counted. Dry fruit weight and length correlated closely with seed number (Pearson's product moment correlation: weight $r = 0.945$, $t_{71} = 24.44$, $p < 0.001$; length $r = 0.815$, $t_{71} = 11.85$, $p < 0.001$) and so simple linear regression equations were calculated to predict seed number from fruit size. Fruit weight was most closely correlated with seed number and so was used to estimate seed number in all the remaining fruits collected (number of seeds = $[2484.2 \times \text{fruit weight}] - 74.113$, $R^2 = 0.894$), except in cases when fruits had burst in the field and some seeds may have been lost. In the latter cases, fruit length was used to predict seed number (number of seeds = $[40.805 \times \text{fruit length}] - 313.03$, $R^2 = 0.664$). Fruits were not collected from populations in Spain due to earlier than expected ripening and fruit burst, and because *R. ponticum* is an endangered species in Spain. The number of fruits per inflorescence were counted in all populations, in Ireland and in Spain. The number of fruits per inflorescence and average number of seeds per fruit were calculated for each inflorescence,

and analysed using 3-factor nested ANOVA (factors: location, population nested within location and plant nested within population within location) ($n = 5$). The relationship between average pollinator visitation rates and the average number of fruits and seeds per population was tested using Spearman's rank correlation.

Results

Identity and abundance of flower visitors

During a total of 48 h of observations, 982 insects from four insect orders were observed visiting 4053 *R. ponticum* flowers. The majority of flower visitors in all populations were Hymenoptera and Diptera (Figure 2). In Los Alcornocales, the main flower visitors were bees from several genera (*Bombus terrestris*, *Xylocopa violaceae*, *Eucera longicornis*, *Lassioglossum*, *Andrena* and *Melitta* spp., Hymenoptera; Apoidea) and bee flies (*Bombylius major*, Diptera; Bombyliidae), whilst in the Irish populations, we found mainly bumblebees (*Bombus* spp., Hymenoptera; Apidae) and hoverflies (Diptera; Syrphidae). More species of insect were observed visiting flowers in Los Alcornocales and Co. Dublin than in Killarney and Connemara (Species richness: El Palancar 23; Las Corzas 19; Howth Head 20; Glencullen 24; Gortderraree 7; Gortracussane 8; Recess 6; Kylemore 11), but the diversity of visitors per flower did not follow the same pattern (Shannon Diversity H' : El Palancar 2.35; Las Corzas 1.92; Howth Head 1.92; Glencullen 1.94; Gortderraree 1.35; Gortracussane 1.44; Recess 1.51; Kylemore 2.03).

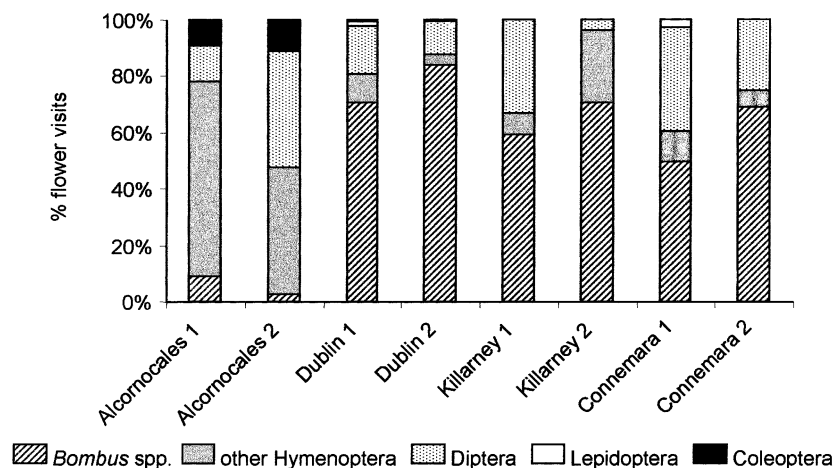


Figure 2. Percentage of flower visits made by the different insect taxa.

Differences in the identity and abundance of flower visitors are visualised using n-MDS plots, where Spanish samples group separately from Irish ones (Figure 3). Low stress values indicate that these are good two-dimensional

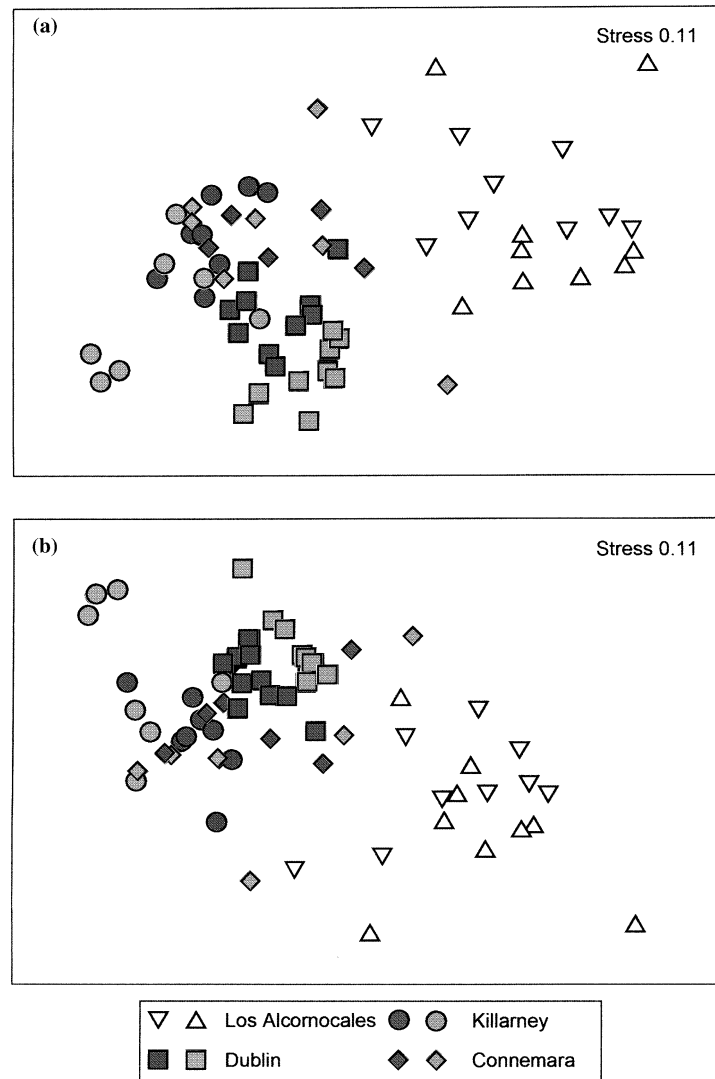


Figure 3. n-MDS plots based on Bray-Curtis dissimilarity matrices of (a) abundance and identity of individuals attracted per flower per hour, and (b) abundance and identity of visitors making flower visits per flower per hour. Each point represents a time period on a specific observation day. The more similar observations are, in terms of the abundance and identity of flower visitors, the closer together they appear on the plot. Low stress values indicate that these are good two-dimensional representations of the multivariate data (Clarke 1993).

representations of the multivariate data (Clarke 1993). Multivariate analyses revealed significant differences in the communities of flower visitors according to location and population (insects per flower per hour: location $F_{3,4} = 3.799$, $p = 0.001$, population $F_{4,64} = 2.441$, $p = 0.001$; flower visits per flower per hour: location $F_{3,4} = 3.057$, $p = 0.001$, population $F_{4,64} = 2.794$, $p = 0.001$). Pairwise *post hoc* tests revealed significant differences in the structure of flower visitor communities, in terms of number of individuals per flower per hour, among all locations except Killarney and Connemara, and among the two Los Alcornocales and the two Co. Dublin populations but not among the two populations within the other two locations. Post-hoc tests of flower visits per flower per hour revealed similar patterns, and in addition, there were significant differences in flower visitor communities among the two populations in Killarney. SIMPER indicated that the dissimilarities between countries were chiefly attributable to the presence of solitary bee species (*Eucera*, *Lasioglossum*, *Andrena* and *Melitta* spp.), *Bombus terrestris* and *Bombylius major* in Spain, and the relatively high abundance of *Bombus lucorum*, *B. pratorum*, *B. monticola* and *B. hortorum* in Ireland.

Univariate analysis of both measures of visitation rates revealed significant variation according to the date that observations were carried out (Table 2). Visits per flower per hour also varied between populations within locations, and the number of individuals per flower per hour showed significant variation according to the interaction between time of day and population (Table 2). SNK tests revealed that there was a significant peak in the number of

Table 2. Univariate ANOVA of visitation rates according to location [L], population (nested within location) [P(L)], time of day [T] and date (nested within population within location) [D(P(L))].

Visitation rate	Source of variation	F	df	p
Individuals per flower per hour	L × T	0.57	6,8	0.743
	T × P(L)	3.28	8,32	0.008**
	T × D(P(L))	0.78	32,201	0.792
	L	4.21	3,4	0.099
	P(L)	No test		
	T	1.86	2,6	0.235
	D(P(L))	15.68	16,32	< 0.0001***
Flower visits per flower per hour	L × T	0.83	6,8	0.581
	T × P(L)	1.58	8,32	0.169
	T × D(P(L))	1.25	32,201	0.179
	L	5.10	3,4	0.0747
	P(L)	3.67	4,16	0.0264*
	T	0.6	2,6	0.581
	D(P(L))	8.14	16,32	< 0.0001***

Variances were significantly heterogeneous for both individuals per flower per hour (Cochran's $C = 0.2786$, $p < 0.01$) and flower visits per flower per hour (Cochran's $C = 0.1469$, $p < 0.01$), but transformation failed to decrease heterogeneity and so analyses were carried out on untransformed data. No test was possible for Population because there was no suitable denominator. Significant terms are marked with asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

individuals per flower per hour during the middle of the day in Las Corzas. Furthermore, within Los Alcornocales and Co. Dublin, there was variation in the visitation rates between populations, regardless of time of day.

Temperatures during observation periods were higher on average in Spain compared with Ireland (mean \pm SE: Los Alcornocales 20.3 ± 0.47 °C, Co. Dublin 17.3 ± 0.24 °C, Killarney 14.5 ± 0.17 °C, Connemara 13 ± 0.19 °C). Visitation rates were positively related to temperature and negatively related to percentage of cloud cover and wind force (Table 3).

Pollen loads of flower visitors

Pollen loads were extremely variable among individual insects. Total estimated pollen loads ranged from 40 grains (on a, *Bombylius major*) to 292,960 (on an *Andrena lapponica* (mean = 13,029.86, SE = 4,362.17). There were no significant differences between the total estimated pollen loads on different insect types from within Ireland or Spain, but there were significant differences between insects from the two countries: Irish insects carried greater total pollen loads than Spanish ones (mean \pm SE Ireland: $18,121 \pm 8,260$, Spain: $7,321 \pm 3,1,86$; Table 4). Bumblebees carried less *R. ponticum* pollen than other Irish insects, but there was no difference in the number of *R. ponticum* grains carried by different species of Spanish insects. Again, there was a significant difference between the two countries: Irish insects carried more *R. ponticum* pollen than Spanish ones (mean \pm SE Ireland: 321.6 ± 83.9 , Spain: 104.2 ± 44.3 ; Table 4). In terms of the proportion of *R. ponticum* pollen in the pollen loads, the only significant difference was, again, between insects from the two countries: Irish insects carried a higher proportion of *R. ponticum* pollen than Spanish ones (mean \pm SE Ireland: 61.0 ± 0.50 , Spain: 30.7 ± 5.84 ; Table 4). Finally, there was a significant difference in the number of pollen types carried by different species of insects from Spain (bees carried more types than *Oxythrea funesta* (chafers), which carried more types than *Bombylius major* (bee flies)). Spanish insects carried significantly fewer pollen types than Irish ones (mean \pm SE Ireland: 6.03 ± 0.50 , Spain: 4.45 ± 0.42 ; Table 4).

Table 3. Relationship between visitations rates (in terms of the number of individuals per flower per hour and the number of flowers visited per flower per hour) and climatic factors (temperature, cloud cover and wind force) ($n = 278$).

	Individuals per flower per hour			Flower visits per flower per hour		
	<i>r</i>	<i>t</i>	<i>p</i>	<i>r</i>	<i>t</i>	<i>p</i>
Temperature	0.719	17.18	***	0.568	11.45	***
Cloud cover	-0.544	10.77	***	-0.391	7.06	***
Wind force	-0.486	9.24	***	-0.398	7.21	***

r, Pearson's product moment correlation coefficient; *t*, Student's *t* test statistic; *** $p < 0.001$.

Table 4. Non-parametric tests (Mann–Whitney U or Kruskal–Wallis, depending on the number of samples) for differences in total estimated pollen loads (Total pollen), the number of pollen types carried, the number of *Rhododendron ponticum* tetrads carried (No. Rp tetrads) and the proportion of *R. ponticum* pollen in the pollen load (Prop Rp tetrads).

	Ireland		Spain		Ireland versus Spain	
	Bees	Btw taxa	Bees	Btw taxa	Bees	Btw taxa
Total pollen	$U_{26,5} = 40$, ns	$U_{31,6} = 71$, ns	$K_3 = 0.997$, ns	$K_2 = 4.633$, ns	$U_{37,33} = 404.5$,*	
No. pollen types	$U_{26,5} = 25$,*	$K_2 = 7.82$,*	$K_3 = 4.87$, ns	$K_2 = 2.17$, ns	$U_{37,33} = 311$,*	
No. Rp tetrads	$U_{26,5} = 49.5$, ns	$U_{31,6} = 54$, ns	$K_3 = 4.23$, ns	$K_2 = 0.105$, ns	$U_{37,33} = 339$,*	
Prop Rp tetrads	$U_{26,5} = 64$, ns	$U_{31,6} = 45$, ns	$K_3 = 4.17$, ns	$K_2 = 6.51$,*	$U_{37,33} = 410.5$,*	

Tests were made between bee species within Ireland or Spain (Bees), and then between all insect taxa (Btw taxa) (with bees pooled if there were no significant differences between bee species). Finally, pollen loads from Irish and Spanish insects were compared regardless of species identity. ns: non-significant results, * $p < 0.05$.

Nectar production

Analysis of nectar standing crop volumes showed significant variation according to location, time of day, day of observation and according to the interaction between time of day and day of observation (Table 5). Killarney and Connemara nectar standing crop volumes were higher than Los Alcornocales and Co. Dublin (Figure 4). Nectar standing crop was higher in the morning in El Palancar and in Gortderraree, and differed between days in Gortracussane, Recess and Kylemore. In the other populations, nectar volumes varied at different times of day on different days, with no distinct

Table 5. Univariate ANOVA of standing crop nectar volumes according to location [L] and population (nested within location) [P(L)], time of day [T] and date [D(P(L))] (nested within population within location).

	<i>F</i>	df	<i>p</i>
L × T	2.06	6,8	0.170
T × P(L)	0.44	8,16	0.881
T × D(P(L))	3.70	16,720	<0.001***
L	25.24	3,4	0.005**
P(L)	0.26	4,8	0.896
T	9.30	2,6	0.015*
D(P(L))	9.29	8,16	<0.001***

Variances were significantly heterogeneous and so data were transformed using $\ln(X+1)$ to reduce heterogeneity (Cochran's $C = 0.0606$, $p > 0.05$). Significant factors are marked with asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

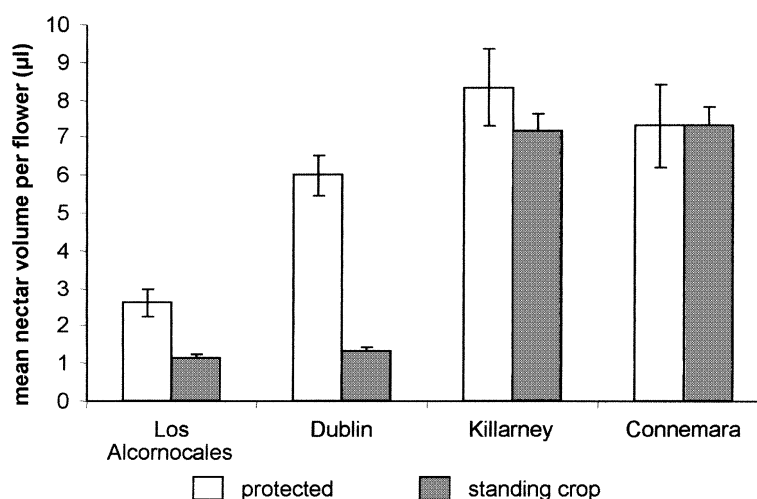


Figure 4. Mean nectar volume per flower ($\mu\text{l} \pm \text{SE}$) according to whether flowers were protected from insect visitation (open bars) or not (standing crop – shaded bars).

patterns. The nectar volume per flower in inflorescences protected from insect visitation varied significantly among locations ($F_{3,4} = 11.6$, $p = 0.019$) but not between populations within locations ($F_{4,120} = 0.79$, $p = 0.532$). SNK tests revealed that protected flowers from Ireland contained significantly higher nectar volumes than protected flowers from Spain ($p < 0.05$; Figure 4). Nectar levels were significantly lower in open compared with protected flowers in Los Alconocales and Co. Dublin (assuming unequal variances: Los Alconocales: $t_{35} = 3.97$, $p < 0.0001$; Co. Dublin: $t_{34} = 8.47$, $p < 0.0001$), but not in Killarney and Connemara (assuming equal variances: Killarney: $t_{222} = 0.921$, $p = 0.358$; Connemara: $t_{222} = 0.005$, $p = 0.996$). Nectar standing crop volumes were inversely correlated with insect visitation rates (1/individuals per flower per hour: $r = 0.753$, $t_{63} = 9.07$, $p < 0.001$; 1/flower visits per flower per hour: $r = 0.607$, $t_{63} = 6.06$, $p < 0.001$).

Seed and fruit production

In Ireland, an average of 191.77 (SE = 11.58) seeds were produced per flower, and 8.83 (SE = 0.74) fruits per inflorescence. In Spain, an average of 10.82 (SE = 0.86) fruits were produced per inflorescence. There were no significant differences in average seed production per fruit between location or populations in Ireland (location: $F_{2,3} = 0.34$, $p = 0.734$; population: $F_{3,24} = 2.42$, $p = 0.091$), but significant variation was found among plants within populations ($F_{24,120} = 10.95$, $p < 0.0001$). Similarly, the average number of fruits per inflorescence varied significantly among plants within populations ($F_{32,160} = 10.38$, $p < 0.0001$), but not between locations or populations (location: $F_{3,4} = 5.21$, $p = 0.072$; population: $F_{4,32} = 2.03$, $p = 0.114$). There was no significant relationship between visitation rates and average number of seeds per fruit (individuals per flower per hour: $r_s = 0.6$, $n = 6$, $p > 0.05$; flower visits per flower per hour: $r_s = 0.657$, $n = 6$, $p > 0.05$), but the number of fruits per inflorescence were correlated with visitation rates (individuals per flower per hour: $r_s = 0.857$, $n = 8$, $p < 0.02$; flower visits per flower per hour: $r_s = 0.881$, $n = 8$, $p < 0.02$) (Figure 5).

Discussion

Species richness and abundance of flower visitors

Long-lived plants, capable of vegetative reproduction, such as *R. ponticum*, may be expected to evolve specialised pollination mutualisms (Bond 1994; Waser et al. 1996). However, Mejias et al. (2002) reported a range of species pollinating *R. ponticum* in its native habitat in Spain, and we found that the large floral display of *R. ponticum* attracts many anthophile species in both native Spanish and exotic Irish habitats. There was spatial variation in the

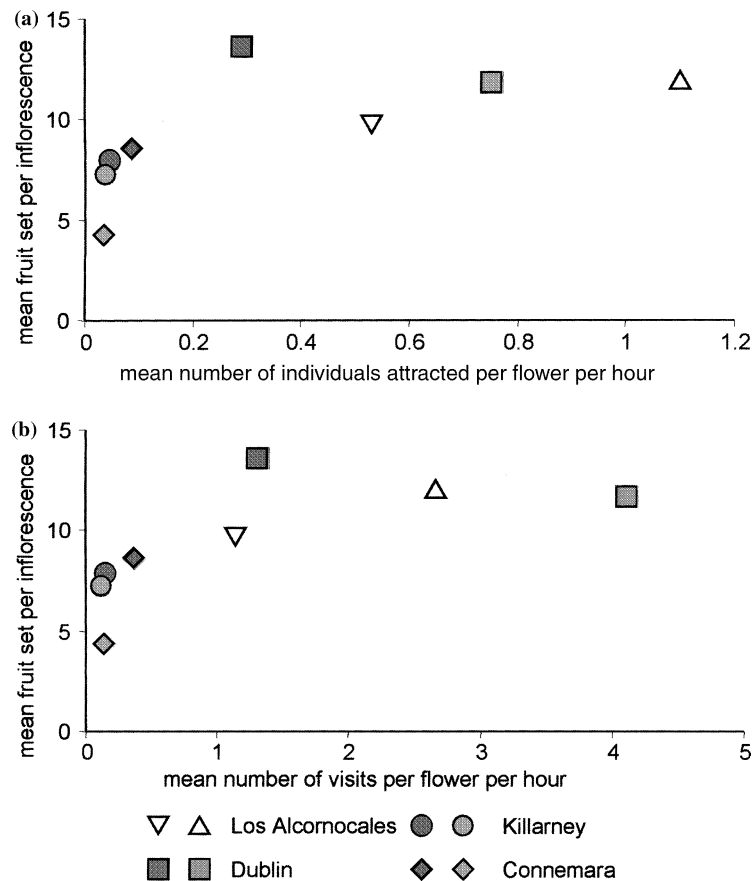


Figure 5. Mean fruit set per inflorescence in each population against visitation rates: (a) mean number of individuals attracted per flower per hour, and (b) mean number of visits per flower per hour.

visitor species assemblage, particularly between native and exotic habitats. Whilst solitary bees dominated visitor assemblages in Spain, bumblebees dominated in Ireland. Most of the solitary bee species that visited flowers in Spain simply do not occur in Ireland, and conversely, bumblebees are better suited to northern temperate climates and so are more abundant in Ireland (Williams 1996). We predicted that the number of insect species visiting *R. ponticum* flowers may be lower in Ireland because of a more depauperate insect fauna on the islands of NW Europe. This did not appear to be the case: we found a total of 27 insect species visiting *R. ponticum* flowers in Spain and 31 species in Ireland. Hymenoptera dominated the flower visiting assemblage, with at least 9 genera of bee visiting flowers in Spain, compared with only 2 genera of bee in Ireland. In Ireland, a more diverse Dipteran community was

observed (10 fly genera were seen in Ireland, compared with 5 in Spain). Since more observations were made in the exotic habitat (18 days of observations in six populations in Ireland; compared with six days in two populations in Spain), the number of species observed may be an artefact of the sampling programme. Hence, our results must be interpreted with caution as this study only provides a sample of the flower visiting community. In addition, it is possible that differences in the number of flowering plants in native and exotic populations affected levels of pollinator attraction, with small Spanish populations failing to attract the full range of potential visitors. Whilst we may have underestimated the number of species visiting flowers in Spain, subsequent casual observations of flower visitors in Ireland have not revealed any further species (J.C. Stout personal observations).

Visitation rates

Significant differences were observed in the specific identity and abundance of flower visiting insect assemblages between native and exotic locations, but no significant differences in visitation rates were observed among locations. Most variation in visitation rates was within and between days, most likely due to temporal variation in weather conditions during the observation periods. On average, visitation rates were higher in Los Alcornocales and Co. Dublin than in Killarney and Connemara (Figure 5) *R. ponticum* populations were smaller and more discrete in the former locations, and much larger in the latter. In larger populations, visit rates per flower might be lower simply because of a superabundance of flowers. Alternatively, insect abundance may have been generally lower in the west of Ireland, possibly due to bad weather during the early part of the year. Differences in insect phenology between the east and west of Ireland could also cause variation in visitation rates. In Co. Dublin, worker, male and queen bumblebees were seen foraging on *R. ponticum*, whilst in the west only queens were seen (observations of different populations in Ireland were interspersed through time- Table 1). This may have implications for pollination efficiency as queens may be more likely to facilitate cross pollination (J.C. Stout unpublished data). Visitation rates to exotic flowering plants have been shown to vary among communities elsewhere (Parker and Haubensak 2001), although to our knowledge, no one has previously compared flower visitation rates among native and exotic locations.

Generality of flower visitors

Analysis of the pollen loads of the most common visitors to *R. ponticum* in both exotic and native habitats indicated that flower visitors were polylectic (visit more than one flower type during a foraging bout). Common flower visitors in Ireland carried more pollen types than those from Spain, but

Spanish flower visitors still carried more than four pollen types on average. Irish flower visitors carried a higher proportion of *R. ponticum* pollen on their bodies than Spanish ones and this may be due to the dominance of *R. ponticum* in the Irish landscapes studied. Exotic populations were far larger than native ones, and in Ireland, alternative forage sources were not abundant. Irish flower visitors may have sampled a wider range of the floral spectrum (and hence carried more pollen types), but collected the majority of their food from *R. ponticum*. Although all of the insect species examined carried *R. ponticum* pollen, we did not examine where on the body pollen was carried, nor did we investigate which insects contacted the stigma of flowers whilst foraging. Hence this preliminary analysis of pollen loads only tells us that a range of insects are potential pollinators. More work in this area is required to determine which insects are actually pollinating flowers.

Nectar

Sugar concentration in *R. ponticum* nectar is approximately 30% in both native and exotic habitats (Mejías et al. 2002; J.C. Stout unpublished data). Although it is thought that acetylmandromedol is present in nectar, this did not seem to have an effect on visitors. However, no honeybees (*Apis mellifera*; Hymenoptera, Apidae) were observed to visit *R. ponticum* flowers in Ireland, possibly because toxic nectar transfers into honey (von Malottki and Wiechmann 1996). There was an inverse relationship between average nectar volume and visitation rates suggesting depletion by insect visitors. Nectar depletion by flower visiting insects was only evident in Los Alcornocales and Co. Dublin, indicating that in the west of Ireland there might be a superabundance of nectar resources relative to the abundance of flower visitors. Standing crops were relatively high, suggesting either that flowers secrete nectar at a rapid rate, or that insects are not emptying flowers that they visit. Insects may either be leaving nectar in flowers because they are collecting pollen, because they can not reach deep enough into the flower corolla to collect nectar, or for some other reason related to their foraging strategy (Hodges and Wolf 1981).

Pollinators access nectar through a channel on the upper petal (Mejías et al. 2002), this channel being relatively deep. Short-tongued visitors may not be able to reach to the bottom of the channel. The depth of the channel would also account for the nectar robbing observed in Spain, where nectar was collected from a small hole in the base of the upper petal, mainly by *B. terrestris* and *Lasioglossum* spp. bees (Inouye 1983). Nectar robbing was never observed in Ireland. One factor that might explain this is that the *B. terrestris* subspecies in Ireland (subsp. *audax*) is morphologically slightly different to the subspecies in Spain (subsp. *terrestris*). Alternatively, larceny may not have been observed in Ireland because *R. ponticum* flowers in Ireland are morphologically slightly different from flowers in Spain, presumably as a result of introgression between *R. ponticum* and *R. catawbiense* and *R. maximum* (Milne and Abbott 2000).

One of these differences is in the size of the channel on the upper petal: in Irish populations, the channel was wider and shallower than in Spanish ones (J.C. Stout personal observations). This may have precluded the need for insects to rob flowers in Ireland

Seed and fruit production

R. ponticum flowers are self-compatible but seed and fruit production is reduced with pollinator exclusion (Mejías et al. 2002) and significantly improved by outcrossing (J.C. Stout unpublished data). This suggests that flowers set seeds only as a result of facilitated selfing and outcrossing, with insects mediating pollen transfer. On average, levels of seed production were reasonably high in all populations. Although there was no significant difference in average fruit set among geographic locations, we found fruit set was positively correlated with visitation rates at the population level. Although other factors, such as resource limitation, may limit fruit set (Zimmerman and Aide 1989), our results indicate that there may be pollinator limitation in some populations in the west of Ireland. Indeed, insects were rarely seen to visit flowers here. Despite this, populations of *R. ponticum* in Killarney and Connemara are still spreading (Cross 1982). Any reduction in fruit set in any one inflorescence as a result of pollination limitation is offset by the presence of millions of inflorescences. Paradoxically, there were high levels of insect visitation and seed set in native populations in Los Alcornocales, and yet populations are in decline. It is probable that moisture deficits are limiting population recruitment in Spain (Mejías et al. 2002), whilst environmental conditions appear to be ideal for *R. ponticum* in the west of Ireland (Cross 1975). In Co. Dublin, high seed and fruit production may well be facilitating spread in suitable habitats (Doogue et al. 1998).

Pollinator limitation can occur in sparsely distributed exotic plants because floral displays are too small to attract pollinators or because of competition for pollinators with native plants (Rathcke 1983). In the case of *R. ponticum* in Ireland, floral displays can be huge and so low visitation rates may be due to low relative pollinator density compared with relative flower density, or due to a lack of appropriate pollinators in these areas (either because of a lower insect diversity and abundance, or recent declines in pollinator species). Little is known of the pollinator fauna of Ireland, but most of the species observed visiting flowers in Co. Dublin are found in Killarney and Connemara. Seed set per fruit was not correlated with visitation rates, suggesting that there may not be pollen limitation once flowers are visited and a single insect visit may be enough to fertilise all the ovules in a flower (particularly given the high pollen loads found on insects in this study). Experiments are underway to determine whether this is the case and to assess the relative success of geitonogamy (within-plant pollen transfer) and xenogamy (cross fertilisation) in Irish *R. ponticum* plants.

Pollinators or visitors?

Despite a wide range of insect species visiting flowers, only a small fraction of the visitor assemblage may act as effective pollinators (Wilson and Thomson 1991; Johnson and Steiner 2000). Effective pollinators need to pick up pollen from anthers, and they also need to deposit it on a receptive stigma. *R. ponticum* flowers are relatively large and we would expect a large insect to be the primary pollinator. Bees such as *Xylocopa violacea* in Spain and *Bombus* spp. in Ireland are probably the most common legitimate pollinators, although rare visits by large insects such as *Macroglossum stellatarum* (hawk moths; Lepidoptera: Sphingidae) in Ireland and *Scolia quadripunctata* (mammoth wasps; Hymenoptera: Scoliidae) in Spain may also facilitate effective pollination. Small insects and/or specialist pollen feeders may not contact both of the necessary reproductive structures or may not carry pollen on suitable parts of their bodies (although they may facilitate within-flower self-pollination). In addition, we cannot rule out the possibility that specialised pollinators do exist in native habitats and were not seen in this study; or that specialists once occurred, but with the decline in *R. ponticum* in these areas, these species have declined or even disappeared. However, specialised flower visitors have not previously been recorded visiting *R. ponticum* (Mejías et al. 2002), and generalist pollination systems are common within the Mediterranean region, and in the *Rhododendron* genus (Herrera 1989; Ng and Corlett 2000; Thompson 2001). A survey of the flower visitors of *R. ponticum* in north-eastern Turkey, where it is not in decline, may reveal specialist pollinators.

Conclusions

Many successful invasive flowering plants produce an abundance of flowers which are visited by a range of pollinators and secrete profuse volumes of nectar (Titze 2000; Ghazoul 2002). *Rhododendron ponticum* is a good example of this. This study of the flower visiting communities of *R. ponticum* in both native and exotic habitats suggests a generalised system, with many insect species potentially facilitating pollen transfer, with none of these species relying exclusively on *R. ponticum*. Generalisation may be one reason for *R. ponticum*'s success as an invasive species. Indeed, generalist pollinators have been shown to visit invasive plant species in several systems (Parker 1997; Stary and Tkalcu 1998; Titze 2000; Brown and Mitchell 2001; Chittka and Schurkens 2001; Stout et al. 2002). To our knowledge, no previous studies have examined the flower-visiting assemblage of a species in its native and exotic habitat. Although we observed high levels of spatial and temporal variation in flower visitation, due, in part, to varying weather conditions, *R. ponticum* received similar overall levels of pollinator visitation in Ireland and in Spain, and set a comparable number of seeds per fruit. There is lower fruit production in the west of Ireland, but this does not appear to be constraining

invasion. Many species of native insect collect nectar and/or pollen from *R.ponticum* in Ireland, and so the species may be providing an important floral resource, particularly when native flowers are not in bloom (for example, as is *Impatiens glandulifera* for *Bombus* spp. In the Czech Republic, Stary and Tkalcu 1998). However, invasive *R.ponticum* may outcompete native plants and may be partly responsible for the decline in native flowers in the first place (Cross 1982). It may also have adverse impacts on native pollinator communities as well, for example through honey poisoning. The precise nature of interactions between *R.ponticum* and the communities of native plants and pollinators in the habitat it is invading are not well understood. The same is true of many invasive plants and further research on their pollination ecology is needed to enable better understanding of current invasions and to predict the likely occurrence and consequences of future invasions. Generalism is common in plant-pollinator systems, and may represent a key element of plant invasion that has previously been overlooked.

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