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Pollinator webs, plant communities and the conservation of rare plants: arable weeds as a case study

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Summary

1. Little is known about the pollinators of rare plants, which is cause for concern given that pollination is essential for the long-term survival of most plant species. The aim of this study was to determine the probable pollinators of three species of rare arable weed: red hemp-nettle *Galeopsis angustifolia*, small-flowered catchfly *Silene gallica* and spreading hedge-parsley *Torilis arvensis*. Species of arable weed are among those suffering the greatest declines in the UK.

2. Five field sites were chosen, two of which were sampled in 2 years. Visitation and pollen transport webs were constructed for the entire plant–pollinator community at each site. Visitation webs described the frequency with which each insect species visited each plant species. Pollen transport webs quantified which insect species transported the pollen of which plant species.

3. A wide range of insect species visited the three plant species. A pollinator importance index was calculated that combined information on both the relative abundance of each insect carrying the pollen of the rare plant and its pollen fidelity. Using this method *Galeopsis angustifolia* was most likely to be pollinated by *Bombus pascuorum* at one site and *Sphaerophoria scripta* at another. *Silene gallica* was also likely be pollinated by *Sphaerophoria scripta*.

4. The pollinator fauna of the three plant species varied considerably across their geographical range, but less from one year to the next.

5. *Synthesis and applications*. All three species of rare plant were linked to other plant species in the community by shared pollinators. In many cases these other plant species constituted the primary food sources for the shared pollinators. Therefore, the long-term survival of rare plant populations is likely to depend on the more common plant species in the community. We recommend that management of the rare plants studied here should also include the protection and management of populations of some of the more common plant species in their respective communities.

Key-words: conservation management, *Galeopsis angustifolia*, networks, pollination, *Silene gallica*, *Torilis arvensis*

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Introduction

Currently, 12·5% of the world's vascular plant species are facing extinction (Wilcock & Neiland 2002). This situation is reflected in the UK, where 40% of the flora is considered to be at risk (Marren 1999) and 66 of the approximately 2951 plant species (Preston, Pearman & Dines 2002) are listed in the government's Biodiversity Action Plan (Anonymous 1994). Farmland probably holds more rare and endangered plant species than any other habitat in the UK, and species of arable weed, i.e. plants associated with crop fields, are among those suffering the greatest declines (Rich & Woodruff 1996). Most arable weeds have declined since the 19th century, and losses accelerated towards the end of the 20th century with increasing intensification of agricultural

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methods (Robinson & Sutherland 2002; Wilson & King 2003).

While data on the distribution and abundance of rare plant species do exist, there is a paucity of information concerning the interactions between these and other species in the community. Given that 67% of flowering plants rely on animal pollinators for reproduction (Kearns & Inouye 1997), their fitness will be seriously compromised if this interaction is threatened. While pollination constitutes a critical 'free service' in all natural terrestrial ecosystems and in many agro-ecosystems (Costanza *et al*. 1997), it is under increasing pressure from human activities. Anthropogenic threats include the introduction of alien plants (Chittka & Schürkens 2001), habitat fragmentation (Aizen & Feinsinger 1994) and agricultural intensification (Kearns, Inouye & Waser 1998). Little is known about the pollinators of rare plants and, tellingly, one of the best books on British rare plants (Marren 1999) fails to address this issue.

Plants of temperate regions tend to have a generalized pollinator fauna (Aizen & Feinsinger 1994; Bond 1994; Memmott 1999; Dicks 2002; Olesen & Jordano 2002; Memmott, Waser & Price 2004). These pollinators tend to be generalists themselves, feeding on and/or pollinating a range of different plant species (Waser *et al*. 1996). It follows that rare plant populations will probably be linked to other plant species in a community via shared pollinators. These other, more common, plant species almost certainly constitute the primary food sources for these shared pollinators. Therefore, the long-term survival of rare plant populations may depend on these other plant species in the community.

Not all insects that visit flowers act as pollinators and not all pollinators are equally good at pollinating a given plant species (Stebbins 1970). The primary factors affecting an insect's effectiveness or efficiency as a pollinator can be divided into 'quality' and 'quantity' components (Waser & Price 1983). The quality component refers to the amount of compatible pollen transferred on each visit, and quantity can be reflected by measuring the frequency with which the insect species visits the flowers (Mayfield, Waser & Price 2001). The quantitative balance between removal and delivery of pollen is another factor that may affect a pollinator's effectiveness, although there are methodological problems associated with such studies (Thomson & Goodell 2001).

The aim of the work presented here was to determine which pollinators and plants may be critical for the survival of three arable weed species, red hemp-nettle *Galeopsis angustifolia* Hoffm. (Lamiaceae), small-flowered catchfly *Silene gallica* L. (Caryophyllaceae) and spreading hedge-parsley *Torilis arvensis* Link. (Apaiceae). All three are listed as priority species in the UK Biodiversity Action Plan. We used a plant–pollinator web approach (Jordano 1987; Memmott 1999; Dicks, Corbet & Pywell 2002) to present quantitative visitation data for these three plant species at five field sites (one site for *Silene gallica* and two sites for *Torilis arvensis* and *Galeopsis angustifolia*) and pollen transport data at three sites. A measure combining insect quality and quantity aspects in terms of pollination was then used to assess the pollinator importance (PI) of visiting insect species for the pollination of the rare plants. We also compared data across sites and from 2 years of sampling to outline the spatial and temporal variation in these systems. This information was used to provide recommendations for the conservation of the three arable weeds. Our methods could provide a model for the study of the pollination requirements of rare plants in general.

Methods

PLANT SPECIES

Galeopsis angustifolia is found mostly on calcareous soils but also on shingle and coastal sands in the south-east of England and limestone scree elsewhere (Wilson & King 2003). It was once a common cornfield weed in some areas but is now in severe and rapid decline (Preston, Pearman & Dines 2002) following the shift from spring- to winter-sown crops. A late-flowering annual, *Galeopsis angustifolia* often fails to set seed within winter-sown crops because of their early harvest (Preston, Pearman & Dines 2002).

Silene gallica is a winter annual found on arable land and on waste ground and sandy shores (Anonymous 1998). By 1930 it had been lost from many inland sites and has since declined further as a result of agricultural intensification, particularly increased use of herbicides and fertilizers (Preston, Pearman & Dines 2002). The species' vulnerability to harsh winters is also thought to be a factor in its decline (Anonymous 1998).

Torilis arvensis is an annual plant most frequently found on heavy calcareous soils, almost exclusively in autumn-sown cereal crops (Anonymous 1998). It has seen one of the most dramatic declines in recent years of any arable weed, possibly because of its inability to compete in dense crop swards (Preston, Pearman & Dines 2002) and because it produces fruit late in the summer, which is destroyed by early harvesting dates or ploughing of stubbles (Wilson & King 2003). Additionally, the destruction of field edges is threatening its habitat.

FIELD SITES

Galeopsis angustifolia site 1 (GA1) was on privately owned farmland near Chedworth, Gloucestershire, UK (national grid reference SP 039131). The study area was a disused airfield now used to grow cereal crops, and *Galeopsis angustifolia* is found growing between cracks in the tarmac of the old runway that crosses the cereal field. *Galeopsis angustifolia* site 2 (GA2) was part of a wildlife reserve in Snettisham, Norfolk, UK (TF 649304) belonging to the Royal Society for the Protection of Birds. The *Galeopsis angustifolia* at the site is associated with areas of open shingle with only a very sparse cover of other vegetation. The site was approximately 100 m from the edge of the tidal flats.

The single *Silene gallica* study site (SG) was north-east of Aylsham, Norfolk, UK (TG 247286). The population of *Silene gallica* occurs on the south-facing slope of a disused railway cutting. The vegetation comprises dry, slightly calcareous grassland on a light, free-draining soil. The *Silene gallica* plants are largely restricted to areas of spoil and disturbance associated with rabbit burrows.

Torilis arvensis site 1 (TA1) was on privately owned farmland near Bath, Somerset, UK (ST 674654). The *Torilis arvensis* grows in a cereal field, mainly in the 6-m margins left around the edges of the crop in accordance with the UK Countryside Stewardship Scheme. *Torilis arvensis* site 2 (TA2) was at the edge of one of three cereal fields with Site of Special Scientific Interest (SSSI) status near Langport, Somerset, UK (ST 338225), which have been owned and managed as a reserve by the Somerset Wildlife Trust since 1992.

SAMPLING

At each site, the study population and its associated vegetation type were identified and defined as the study plot. Establishing boundaries was a relatively simple procedure because of clear demarcation from neighbouring vegetation. Plot dimensions varied as a result of natural variation in the area covered by the target species and its associated vegetation (Table 1). Where study species grew at the edges of cereal fields (GA1, TA1 and TA2), the plot width was restricted to 6 m, the maximum width of the field margins. However, as shown in Table 1, all plots were approximately equal in area.

A stratified random sampling procedure was used for sampling plant–pollinator interactions in each plot. The longest edge of the plot was divided into quarters, from each of which a transect line was extended perpendicularly. The position of each transect was allocated at random within its quarter. Each transect was further divided into quarters. Within each quarter, a 1-m^2 quadrat was randomly placed and sampled. Each sampling occasion in a plot thus involved the sampling of 16 quadrats.

Floral abundance

On each sampling occasion the floral units per plant species within each quadrat were counted. A floral unit was defined as an individual flower or collection of flowers that an insect of approximately 0·5 cm could walk within or fly between (Saville 1993). Plant naming authorities are listed in Stace (1997).

Insect visitation

All five sites were sampled for plant–pollinator interactions in 2002. In 2003, sites GA2 and SG were sampled for comparison, although time constraints led to a sampling effort of 50% of the 2002 level. Sampling commenced when the study species started flowering (June being the earliest) and continued weekly until flowering ended (Table 1) or the site was harvested (end of September being the latest).

Sampling of quadrats involved catching all insects that visited flowers during a 15-min period. Sampling only took place during warm, dry weather and some of the variation in quadrat numbers was because of rainfall preventing sampling. All insect visitors to flowers were sampled, i.e. no a priori decisions were made about probable pollinators. Insects were caught either using a net or directly captured into a glass vial containing ethyl acetate lined with a small paper bag. This lining prevented insect contact with the sides of the glass vial, thereby allowing the vial to be reused for subsequent catches with a low risk of pollen contamination. The anaesthetized insects were then transferred in their bags to a larger killing container and subsequently removed from the bag and frozen until processed in the laboratory. Insects were identified by either G. W. Hopkins or by taxonomists at the National Museum of Wales, Cardiff, UK. Insect naming authorities are listed in the Royal Entomological Society *Handbooks for the Identification of British Insects* (Royal Entomological Society 1978).

Pollen transport

In the laboratory, each insect was systematically dabbed with a *c.* 27 mm^3 section of gelatine-fuchsin (Dafni 1992) to sample and stain its pollen. Pollen storage areas such as pollen baskets on bumblebees were

Table 1. Plot sizes and phenology of the target plant species at each site

Species	Site	Plot dimensions (m)	Plot area (m^2)	Number of quadrats (2002)	Flowering begins	Flowering ends
Galeopsis angustifolia	GA1	200 × 6	1200	172	19/07/02	03/09/02*
Galeopsis angustifolia	GA2	40 × 30	1200	192	08/07/02	27/09/02
Silene gallica	SG	50 × 25	1250	176	08/07/02	19/09/02
Torilis arvensis	TA1	200 × 6	1200	240	15/07/02	05/09/02
Torilis arvensis	TA2	200 × 6	1200	120	10/07/02	07/08/02†

**Galeopsis angustifolia* died of mildew at this point.
†The site was harvested on this date, so data collection ceased at this point.

avoided as these contain pollen unlikely to be available for pollination. The gel was then placed on a slide, heated to melting point and covered with a cover slip. Forceps used throughout the sampling were thoroughly cleaned of pollen between insects. Pollen was sampled only in 2002.

Pollen analysis was conducted for three sites: GA1, GA2 and SG. A reference collection of pollen for each site was used to identify and quantify the pollen removed from the insects sampled. Pollen identification was undertaken blind, i.e. with no information concerning the insect from which the pollen was collected.

Some of the more closely related plant species could not be differentiated, while other pollen species were placed into 'type' groups for classification. For example, at GA1 the *Epilobium* species *Epilobium hirsutum*, *Epilobium parviflorum* and *Epilobium tetragonum* are known collectively as the *Epilobium* type group. Pollen from the target rare plants was always identified to species.

ANALYSIS

Visitation and pollen transport webs for each site were drawn using software written in Mathematica™. The pollen transport data were used to determine whether an insect was a potential pollinator or not, i.e. insects not transporting any pollen could not be pollinators. Pollen transport data were also used to calculate PI, a measure of the importance of a particular insect species in pollinating a particular plant species (Schemske & Horvitz 1984). This combined both quality and quantity components (*sensu* Waser & Price (1983) of each pollinator's performance. We used a modified version of the methods of Dicks (2002) following Lindsey (1984) and Primack & Silander (1975) to calculate PI (equation 1). Given that we were dealing with numerous unique plant–pollinator interactions, we used the proportion of the insect's pollen load compatible with the rare plant in question as a measure of pollinator quality, as used by Ne'eman, Dafni & Potts (1999), and not the amount of pollen deposited per visit. To demonstrate the calculation, the PI of the bumblebee *Bombus hortorum* (Hymenoptera: Apidae) for *Galeopsis angustifolia* would be calculated as follows:

$$\text{PI} = (\text{relative abundance of pollinator}) \times (\text{pollen fidelity}) \qquad \text{eqn 1}$$

where relative abundance of pollinator is the proportion of all insects carrying *Galeopsis angustifolia* pollen grains that are of the species *Bombus hortorum* and pollen fidelity is the mean proportion of individual *Bombus hortorum* pollen loads that originate from the rare plant species. Thus, at GA1, three out of 20 individuals carrying *Galeopsis angustifolia* pollen were *Bombus hortorum*, giving the species a relative abundance of 0·15. The three individuals' pollen loads contained proportions of *Galeopsis angustifolia* grains of 0·80, 1·00 and 0·61, resulting in the pollen fidelity value of 0·80 (the mean of the three values).

This calculation takes into account the two main factors considered to affect the importance of an insect for pollination of a given plant species. Some visitors may be effective at one of the components, but ineffective at or disadvantageous for the other (Fishbein & Venable 1996). For example, an insect could be an important pollinator of *Galeopsis angustifolia* by carrying only *Galeopsis angustifolia* pollen grains, despite visiting relatively infrequently. Alternatively, a frequent visitor may be of little value as a pollinator if it carried few *Galeopsis angustifolia* pollen grains and many grains from other species.

For all quantitative analyses only insects identified to species level were used; these constituted the vast majority of insects collected. For all analyses using pollen data, only insects carrying five or more grains of any one pollen species were considered to be carriers of that pollen species. PI values were only calculated for insect species where the total number of individuals carrying pollen exceeded two.

Temporal and spatial analysis

Temporal comparisons were between data from 2002–2003 at SG and GA2, and spatial comparisons between GA1 and GA2 and between TA1 and TA2 in 2002. The comparisons were made using both the full data sets and data sets standardized (by random removal of quadrats) so that the 2002 and 2003 data sets had the same sampling effort.

Results

Visitation webs were constructed for all sites; pollen transport webs were constructed and pollinator importance values calculated for insects visiting the rare plants at sites GA1, GA2 and SG. All the visitation and pollen transport webs are drawn to the same scale. Note that in the visitation webs all interactions are shown, not just those involving insects identified to species, consequently Fig. 1a actually shows 25 insects visiting *Galeopsis angustifolia* (rather than 22 as stated in the text). Figures 1–4 show the web outlines only, and full species details are printed in the supplementary material (see Fig. S1a–h).

POLLINATION OF *GALEOPSIS ANGUSTIFOLIA* AT SITE GA1

Despite being nationally scarce, *Galeopsis angustifolia* was the most abundant and generalized plant species in the plot. Twenty-two insect species (51% of all species) visited *Galeopsis angustifolia*, and 10% of all visits in the plot were to *Galeopsis angustifolia*, making it the second most frequently visited plant species. While *Galeopsis angustifolia* was visited by many insect species (Fig. 1a), the common carder bee *Bombus pascuorum*

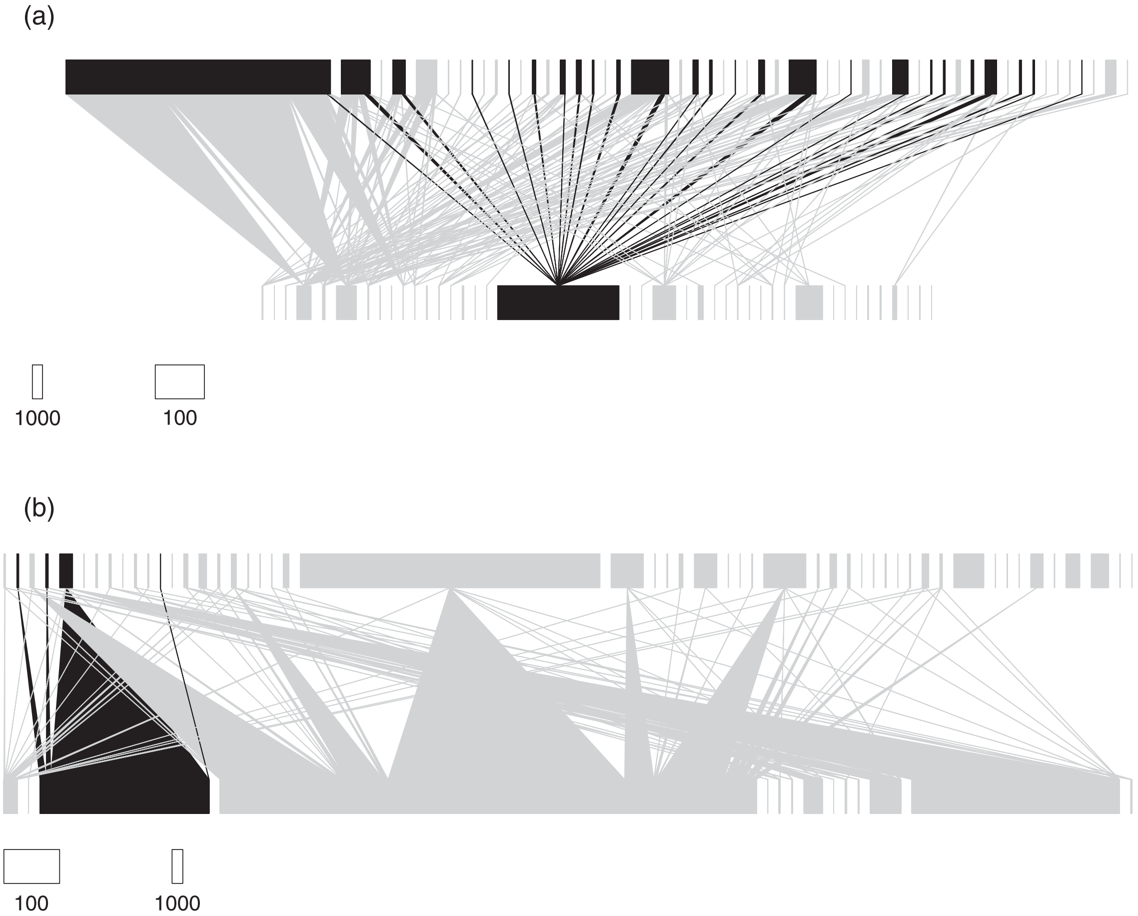

Fig. 1. (a) Visitation web for *Galeopsis angustifolia* at GA1. Each species of plant and insect is represented by a rectangle: the lower line represents flower abundance; the upper line represents insect abundance. The widths of the rectangles are proportional to their abundance at the field site, and the size of the lines connecting them represents the recorded frequency of the interaction. The target plant and the species it interacts with are shown in black. The scale bar represents number of floral units (1000) and number of insects (100). (b) Pollen transport web for *Galeopsis angustifolia* at GA1. The lower line represents pollen abundance; the upper line represents insect abundance. The scale bar represents the number of pollen grains (1000) and the number of insects (100). For full visitation and pollen transport webs showing the identity of the plants and insects see the online supplementary information.

Table 2. PI values for the pollen-carrying species of the target rare plants at GA1, GA2 and SA. A higher value indicates a greater assumed importance in terms of pollinator services to the plant

Plant species (site)	Insect species	Relative abundance	Pollen fidelity	PI	*n* (number of individuals caught)
Galeopsis angustifolia (GA1)	*Bombus hortorum*	0·15	0·80	0·12	3
	Bombus lucorum	0·10	0·58	0·06	3
	Bombus pascuorum	0·70	0·47	0·33	17
Galeopsis angustifolia (GA2)	*Episyrphus balteatus*	0·50	0·04	0·02	20
	Platycheirus albimanus	0·25	0·17	0·04	6
	Sphaerophoria scripta	0·25	0·31	0·08	3
Silene gallica (SG)	*Episyrphus balteatus*	0·12	0·15	0·02	14
	Sphaerophoria scripta	0·31	0·34	0·11	20

(Hymenoptera: Apidae) was responsible for the vast majority of pollen transport (Fig. 1b) and hence was the most important pollinator of *Galeopsis angustifolia* at GA1 (Table 2). *Bombus pascuorum* comprised 70% of individuals carrying *Galeopsis angustifolia* pollen, and carried 94% of all *Galeopsis angustifolia* pollen. The only plant apart from *Galeopsis angustifolia* that *Bombus pascuorum* visited with any frequency was *Odontites vernus* (Scrophulariaceae), to which it made 18% of its visits. Pollen data showed that *Bombus pascuorum* carried 11 different types of pollen, indicating that it also fed on these plant species. However, 98% of the pollen carried was either *Veronica* type (55%) or *Galeopsis angustifolia* (43%). *Odontites vernus* was the

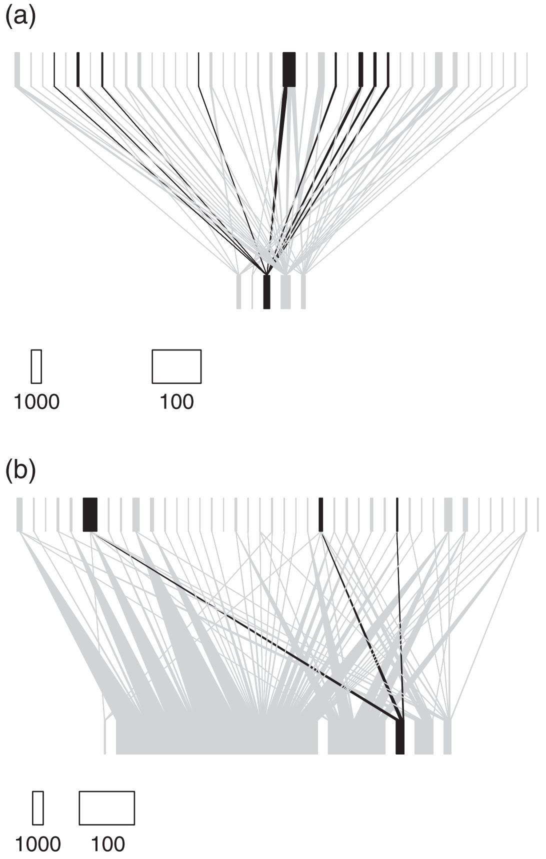

Fig. 2. (a) Visitation web and (b) pollen transport web for *Galeopsis angustifolia* at GA2. For further information see legend to Fig. 1.

only member of the *Veronica* type group to be visited by *Bombus pascuorum* at this site, indicating that *Odontites vernus* and *Galeopsis angustifolia* are the main food source for *Bombus pascuorum* at this site.

POLLINATION OF *GALEOPSIS ANGUSTIFOLIA* AT SITE GA2

Nine insect species (23% of all species) visited *Galeopsis angustifolia* at site GA2 (Fig. 2a). However, only four individuals (3% of all insects analysed) belonging to three insect species, *Episyrphus balteatus* (Diptera: Syrphidae), *Platycheirus albimanus* (Diptera: Syrphidae) and *Sphaerophoria scripta* (Diptera: Syrphidae), carried *Galeopsis angustifolia*'s pollen (Fig. 2b). PI values (Table 2) indicated that *Sphaerophoria scripta* was by far the most effective pollinator of *Galeopsis angustifolia* at this site. This was because, despite *Episyrphus balteatus* carrying 46% of all *Galeopsis angustifolia* pollen in the plot, *Platycheirus albimanus* 43% and *Sphaerophoria scripta* only 11%, *Sphaerophoria scripta* had a pollen fidelity value eight times and 1·8 times greater than *Episyrphus balteatus* and *Platycheirus albimanus*, respectively. *Sphaerophoria scripta* was caught visiting only *Galeopsis angustifolia* at GA2, but was found to also carry pollen from a subgroup of the Asteraceae, probably from *Senecio jacobaea* and/or *Senecio viscosus*, both relatively abundant species at the site.

POLLINATION OF *SILENE GALLICA* AT SITE SG

Nine species (10% of all species in the plot) visited *Silene gallica* (Fig. 3a). Of all visits made, 17% were to *Silene gallica*. The most abundant visitors to *Silene gallica* were *Sphaerophoria scripta* (50% of all visitors) and *Episyrphus balteatus* (14%). No other species made up more than 9% of visitors.

Eleven species (38% of all insect species) were found carrying pollen of *Silene gallica* (Fig. 3b). Forty-two per cent of individuals carrying *Silene gallica* pollen were *Sphaerophoria scripta* and 12% were *Episyrphus balteatus*. Other than *Platycheirus albimanus* (8%), no other species made up more than 8% of individuals carrying pollen of *Silene gallica*. *Platycheirus albimanus* carried the largest quantity of *Silene gallica* pollen (33%) in the plot. *Sphaerophoria scripta* carried 23%, and *Pollenia pediculata* (Diptera: Calliphoridae) and *Rhagonycha fulva* (Coleoptera: Cantharidae) each carried 9%. Overall insect numbers were low and there were only two individuals of *Platycheirus albimanus* carrying pollen, so PI indices were calculated for *Sphaerophoria scripta* and *Episyrphus balteatus* only. These suggested that *Sphaerophoria scripta* was twice as important as *Episyrphus balteatus* for pollination of *Silene gallica* (Table 2). The visitation and pollen transport data showed that the plant species visited most frequently by *Sphaerophoria scripta*, after *Silene gallica*, was *Hypericum pulchrum* (Clusiaceae), and that it also visited four other species, *Achillea millefolium* (Asteraceae), *Brassica napus* (Brassicaceae), *Heracleum sphondylium* (Apiaceae) and *Senecio jacobaea* (Asteraceae).

POLLINATION OF *TORILIS ARVENSIS* AT SITE TA1

Torilis arvensis was the most abundant and generalized plant species in the plot, being visited by 25 (40%) insect species, and 15% of all visits to flowers were to *Torilis arvensis*. *Chloromyia formosa* (Diptera: Stratiomyidae) appeared to visit only *Torilis arvensis*, on which it was caught nine times. The most abundant insects on *Torilis arvensis*, however, were hoverflies (Diptera: Syrphidae) (22%). Eighteen species were identified, with the number of individuals per species caught ranging from one (*Cheilosia pagana*, *Metasyrphus luniger* and *Syrphus torvus*) to 19 (*Sphaerophoria scripta*). Syrphids visited 27 out of the 35 plant species at the site. The plant species most frequently visited by syrphids were *Sinapis arvensis* (Brassicaceae), 18% of visits, and *Epilobium tetragonum* (Onagraceae), 13%.

POLLINATION OF *TORILIS ARVENSIS* AT SITE TA2

Three species of insect visiting *Torilis arvensis* were identified, *Scathophaga stercoraria* (Diptera: Scathophagidae), *Metasyrphus luniger* (Diptera: Syrphidae) and *Meligethes nigrescens* (Coleoptera: Nitidulidae). Each

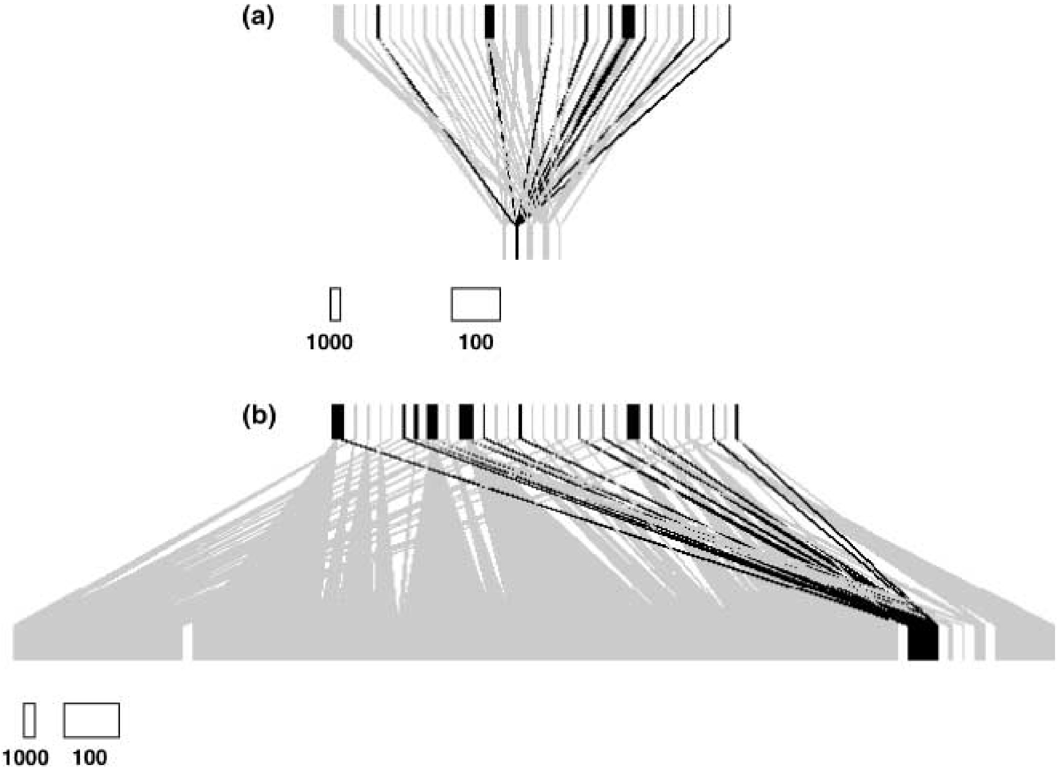

Fig. 3. (a) Visitation web and (b) pollen transport web for *Silene gallica* at SG. For further information see legend to Fig. 1.

of these species visited *Torilis arvensis* only once. Other insects caught on *Torilis arvensis* were an Oedemerid beetle and an unidentified ichneumonid (Hymenoptera), which both visited once, and five individuals belonging to the family Syrphidae. In all, only 3% of all visits in the plot were to *Torilis arvensis*, thus potential pollinators of *Torilis arvensis* at this site seemed rare. The syrphids were the most frequent visitors to *Torilis arvensis*, and this family had a broad visitation pattern, visiting 20 out of the 38 plant species (53%). However, 44% of visits by syrphids were to three plant species, *Rubus fruticosus* agg. (Rosaceae), *Lapsana communis* (Asteraceae) and *Medicago lupulina* (Fabaceae).

Most other plant species at TA2 were also relatively specialized in terms of insect visitors, with a mean (median) of 2·68 (1) insect species visiting. This was a very low level of visitation in comparison with the other sites that had similar numbers of plant species (GA2, SG and TA1), which had mean (median) levels of 11·8 (9), 9 (9) and 5·7 (4) visiting insect species per plant species, respectively.

TEMPORAL AND SPATIAL VARIATION

From the full 2002 data set we established, using PI calculations, that *Sphaerophoria scripta* was probably the most important pollinator of *Galeopsis angustifolia* at GA2. While we had no PI data for 2003, *Sphaerophoria scripta* and *Platycheirus albimanus* were two of the four most frequent visitors to *Galeopsis angustifolia* in both years, suggesting that the pollinator fauna of the rare plant species could remain fairly consistent over more than 1 year. These results did not change when we standardized for sample size by randomly removing quadrats from the data.

The putative pollinators of *Silene gallica* also remained the same over time. Three species, all syrphids (*Sphaerophoria scripta*, *Episyrphus balteatus* and *Platycheirus albimanus*), made the majority of visits to *Silene gallica* in both 2002 and 2003 [73% in 2002 and 88% in 2003 (raw data), 81% in 2002 and 87% in 2003 (standardized data)].

Considerable differences were found between the potential pollinators of *Galeopsis angustifolia* at the two sites. Aside from *Platycheirus albimanus*, which was a frequent visitor at both sites, the other visitors were different at the order level. At GA1, 70% of individuals carrying *Galeopsis angustifolia* pollen were *Bombus pascuorum*, 15% were *Bombus hortorum*, 10% were *Bombus lucorum* and 5% were *Epistrophe diaphana* (Diptera: Syrphidae) (Fig. 1b), whereas at GA2 50% of individuals carrying *Galeopsis angustifolia* pollen were *Episyrphus balteatus*, 25% were *Platycheirus albimanus* and 25% were *Sphaerophoria scripta* (Fig. 2b).

Torilis arvensis was visited by 25 insect species at TA1 and only three at TA2, and no single insect species visited *Torilis arvensis* at both sites. Based on qualitative analysis of the data from these five sites, spatial variation seems considerably greater than temporal variation.

Discussion

This study used data on three plant species, at five field sites, to construct visitation and pollen transport webs, which provide a quantitative community-level approach to understanding the pollinator requirements of rare plant species. We found that spatial variation appears to be greater than temporal variation. The implications of this work for the conservation of these species, for rare plants in general and for the study of plant–pollinator communities are discussed below, along with the limitations of our approach.

The interaction-based approach used in this study has provided information about the pollinator requirements of rare plants that would be extremely difficult to gather using other methods. As predicted, the rare plants share pollinators with more common species, making their survival at least in part dependent on those species. This pattern is seen in all five of the communities sampled, despite large differences in plant and insect abundance and diversity between sites (Figs 1–4). Furthermore, our data show that neither the most abundant visitors nor pollen carriers of a rare plant, nor the species carrying the largest quantities of the plant species' pollen, are necessarily its most important pollinators.

In agreement with previous studies on plant–pollinator networks (Bond 1994; Memmott 1999; Dicks 2002; Olesen & Jordano 2002), our results show that *Galeopsis angustifolia*, *Silene gallica* and *Torilis arvensis* are generalists with respect to pollination, and that their visitors also show a relatively high level of generalization. Pollen transport data reveal greater levels of generalization in plant–pollinator communities than suggested by the visitation data alone. For example, *Silene gallica* only had nine observed visitor species but 11 species carried its pollen. Equally, not all visitors carry pollen. For example only four of 22 visitors to *Galeopsis angustifolia* at GA1, and three of nine at GA2, actually carried any *Galeopsis angustifolia* pollen.

The most accurate method for determining which species are the most effective pollinators of each rare plant species would be to conduct bagging experiments (Klein, Steffan-Dewenter & Tscharntke 2003), allowing access by specific insect species, and excluding all others right up to seed set. However, this was not practical at our field sites, as each of the rare plants was visited by numerous insect species (some up to 25 species), making the experimental exclusion of each species impossible. Instead a probabilistic method was used, with limitations such as the necessary assumption that pollen fidelity and relative abundance are equally influential on a pollinator's overall efficiency, and are not influenced by each other.

Plants may interact via shared pollinators in negative as well as positive ways. Competition between plant species via pollinators can occur, for example through improper pollen transfer resulting in pollen loss by the

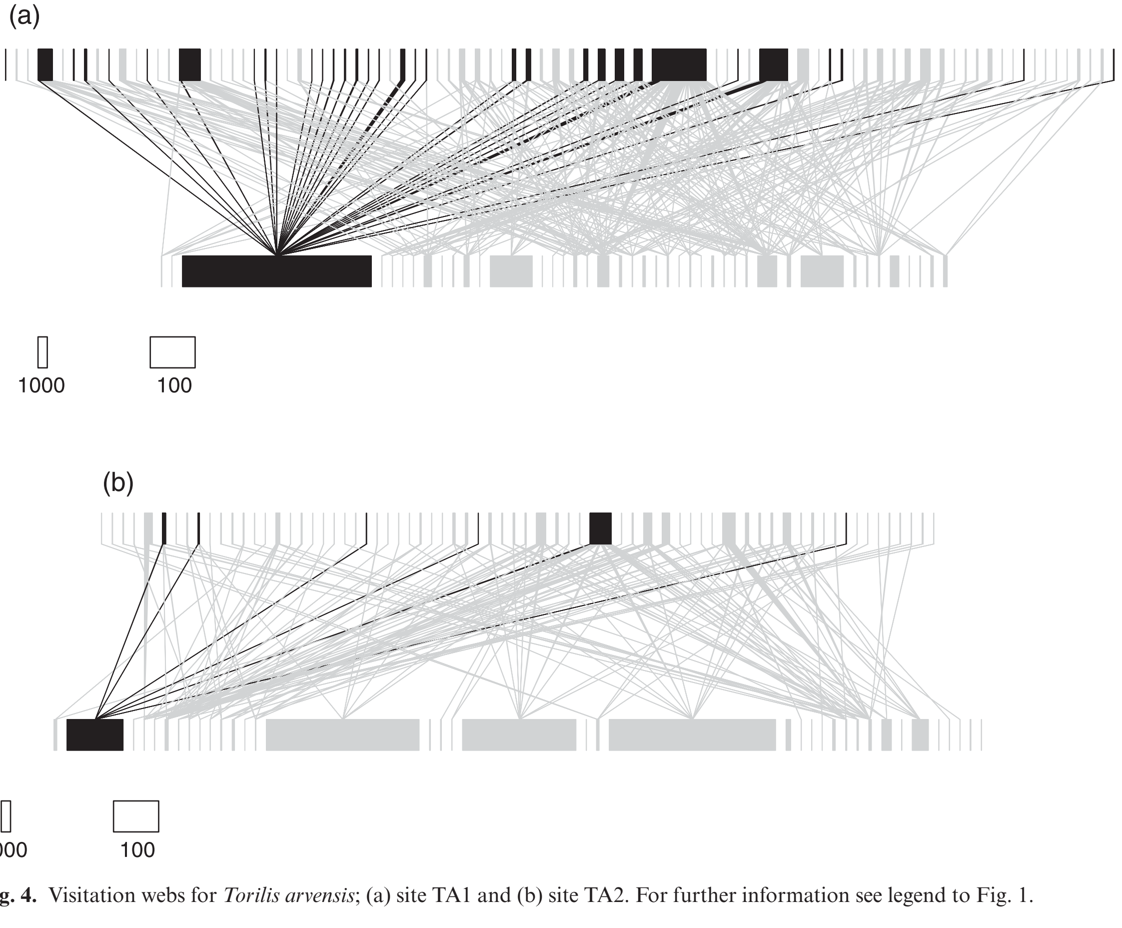

Fig. 4. Visitation webs for *Torilis arvensis*; (a) site TA1 and (b) site TA2. For further information see legend to Fig. 1.

donor and stigma clogging, exploitation, or chemical or physical interference by pollen, all of which can lower seed set in the recipient (Feinsinger 1978; Waser 1978), or simply through competition for pollinator visitation (Rathcke 1983). However, there is evidence to suggest that sequentially flowering species that compete for pollination can simultaneously facilitate each other's pollination by providing the resources necessary for the survival of adequate numbers of pollinators throughout the year, in a form of 'effective mutualism' (Waser & Real 1979), supporting our assumption that the more abundant plant species facilitate the pollination of the rarer plants in their communities. Indeed, seed set may increase even if there is competition for visitation by pollinators (i.e. a reduction in visitation rates), as long as the quality of each visit is high (Rathcke 1983).

Relatively small numbers of insects were used to calculate PI values for some of the insect species (Table 2). This problem was unavoidable because with such large-scale studies there is an inevitable trade-off between the number of sites and species sampled, and the sampling intensity at each site.

Our method effectively shortens the list of potential pollinators and gives us a fair indication of the species pollinating each plant species. It is on this basis that we provide the management recommendations outlined below for the particular study sites as examples of a more general approach to the management of rare plants.

MANAGEMENT RECOMMENDATIONS

Galeopsis angustifolia appears to rely very heavily on *Bombus pascuorum* for pollination at GA1 and therefore this relationship should be considered essential for the maintenance of this population of *Galeopsis angustifolia*. The only other plant used with any frequency by *Bombus pascuorum* at GA1 is *Odontites vernus* (55% of the pollen on *Bombus pascuorum* was probably from this species). The early death by mildew of all *Galeopsis angustifolia* in the plot (Table 1), which thus eliminated the main source of food for *Bombus pascuorum*, emphasizes the importance of maintaining *Odontites vernus* as a resource for *Bombus pascuorum* during periods when *Galeopsis angustifolia* is not in flower. To conserve *Bombus pascuorum* (and thereby *Galeopsis angustifolia*) at this site, *Odontites vernus* should be encouraged and protected as far as practically possible. There are few data on the foraging ranges of bumblebees (Osborne *et al*. 1999), although it is known that some individuals forage over distances of up to 2 km (Walther-Hellwig & Frankl 2000). However, *Bombus pascuorum* appears to prefer resources closer to the nest, if they are available (Kreyer *et al*. 2004), and is thought to stay mainly within 500 m of the nest (Walther-Hellwig & Frankl 2000).

The most important pollinator of *Galeopsis angustifolia* at GA2 is probably the syrphid *Sphaerophoria scripta*. Web data show that *Sphaerophoria scripta* visits and carries pollen of one or both *Senecio* (Asteraceae) species (*Senecio viscosus* and *Senecio jacobaea*) at the site. We recommend therefore that efforts be made to conserve these plant species. *Galeopsis angustifolia* appears to have an extremely low level of pollen transport at GA2. Considering the increased risks of extinction through reduced pollinator visitation for small populations of plants (Spira 2001), the planting of *ex-situ* propagated plants from seeds collected at the site to increase the current population size should be considered in the management of *Galeopsis angustifolia* at this site.

For *Silene gallica*, management plans should incorporate measures to ensure the maintenance of *Sphaerophoria scripta*. *Sphaerophoria scripta* appears to feed on a wide variety of plant species, including *Hypericum pulchrum*, and therefore we suggest that the population of this plant be maintained at this site. Interestingly, no species other than *Sphaerophoria scripta* visits this plant species or carries its pollen at site SG, so it is vital not only for *Silene gallica* but also for *Hypericum pulchrum* that the importance of *Sphaerophoria scripta* as a pollinator at this site is recognized and acted upon.

Chloromyia formosa may be of particular importance in the pollination of *Torilis arvensis* at TA1 because of its apparent specialization on the flowers of this species. If so, *Torilis arvensis* must be maintained in high numbers at this site in order to provide sufficient resources to support an adequate population of *Chloromyia formosa*. *Chloromyia formosa* is specialized for feeding on *Torilis arvensis* according to criteria defined by Reed (1995), who suggested that to be considered specialized for feeding on a particular plant, an insect must be caught more than eight times on the same plant species at the same site. The cut-off point of eight times helps to avoid confusing low abundance with specialization, and we consider it a useful, if slightly arbitrary, measure of specialization.

Some of the other most frequent visitors to *Torilis arvensis* at TA1 also visit *Sinapis arvensis* and *Epilobium tetragonum* frequently, and so these plant species should be considered an important resource for potential pollinators of *Torilis arvensis*. We recommend therefore that *Sinapis arvensis* and *Epilobium tetragonum* be protected and maintained at this site, and planted alongside *Torilis arvensis* at any new sites. However, given the wide range of plants visited by the potential pollinators of *Torilis arvensis*, it would be advisable to manage the site to maintain the diversity of plant species currently present.

At site TA2 *Chloromyia formosa* was caught on *Euphorbia exigua* (Euphorbiaceae) and so is not a true specialist at a national scale. This result emphasizes the value of replicating the study of the pollination of rare plants in geographically separate populations. However, this local specialization of *Chloromyia formosa* on *Torilis arvensis* could be important in terms of pollination, as it could result in high levels of pollen fidelity in calculating PI values for this insect species.

Torilis arvensis was not visited frequently at TA2, and so it is particularly important that the plant species supporting the insect populations are at least maintained, and ideally increased. The seemingly low visitation rate at this site is probably partly the result of the reduced sampling effort at this site (which was the result of the harvesting of the crop; Table 1), but even allowing for this, insect abundance at this site seems low. The potential pollinators of *Torilis arvensis* at TA2 utilize a wide range of plant species, and it is therefore recommended that this site is managed for as diverse an assemblage of plant species as possible, preferably containing *Lapsana communis*, *Rubus fruticosus* agg. and *Medicago lupulina*, as these are the three most generalized plant species and therefore provide resources for potential pollinators of many of the plant species at the site.

Our limited data suggest that the pollinator fauna of rare plants can vary considerably across their geographical range, while showing far less variation at a given site from 1 year to the next. While the small number of field sites studied for the rare plant species limits the extent to which generalized statements can be made regarding their pollinator fauna, given the substantial spatial variation found in these systems it is clear that measures aimed at conservation of the pollinators of these plants should be tailored to each community in which they are found rather than based on assumptions of their similarity between sites.

CONCLUSIONS

The data we present on the plants and pollinators at each field site are not exhaustive surveys of the species present, nor are they intended to be; rather, they are quantitative samples of the community context in which the interactions between rare plants and their pollinators take place. This approach has allowed us to identify the probable key pollinators of rare plant species, and to make specific recommendations for management of the plant–pollinator communities in which they are found. Interestingly, our three arable sites (GA1, TA1 and TA2) had higher numbers of both plants and insects (both species and abundance) than the two non-arable sites (GA2 and SG). This can be seen clearly by comparing the size of the visitation webs (Figs 1–4), which are drawn to the same scale, showing that agro-ecosystems can be important for the conservation of biodiversity.

Our results and management recommendations can play a vital part in protecting rare plant species, but we are also aware that the management of arable land for conservation can conflict with the growing of crops. For example, at site TA2 managers have found it hard to maintain the diversity of arable plants without sacrificing the success of their cereal crop (Marren 1999). There is hope, however, for the continued growth of arable weeds on some of Britain's farms, as a result of new agri-environment schemes (DEFRA 2005) that provide subsidies to farmers for employing environmentally beneficial practices such as wide, unsprayed field margins, beetle banks and less intensive hedgerow management. Indeed, arable plants are increasingly recognized as essential for maintaining farmland biodiversity (Altieri 1999; Marshall *et al*. 2003). The seeds of arable insect-pollinated species such as *Stellaria media* (Caryophyllaceae) and *Sinapis arvensis* (Brassicaceae) form a major part of the diet of most farmland bird species (Marshall *et al*. 2003), many of which are currently in decline (Siriwardena *et al*. 1998; Stephens *et al*. 2003; Butler, Bradbury & Whittingham 2005). *Galeopsis* spp. are also a component of farmland bird diets (Marshall *et al*. 2003). In turn, the insects that feed on arable plants, both herbivores and flower feeders, provide an important food source for the chicks of many of these bird species (Wilson *et al*. 1999). In addition, certain arable plants play an important role in maintaining complexes of beneficial insects, which provide invaluable services to farmers in limiting insect pest populations (Altieri 1999). The financial incentives of government agri-environment schemes, and the growing awareness among farmers of the ecosystem services that arable plants can provide, are important steps towards their protection. However, it is essential that we target each species' specific ecological needs if we are to manage them effectively (Fox 2004). If future agricultural policies are devised with this in mind, using information on vital ecological interactions such as pollination, it may yet be possible for rare arable plants to flourish in the British countryside once again.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Appendix S1.

Fig. S1. Visitation webs for sites GA1, GA2, SG, TA1 and TA2. Pollen transport webs for sites GA1, GA2 and SG.