

Generalist foraging of pollinators: diet expansion at high density

Colin Fontaine^{1,2*†}, Carine L. Collin^{1†‡} and Isabelle Dajoz¹

¹BioEmCo – UMR 7618, Ecole Normale Supérieure, 46 rue d'Ulm, F-75230 Paris cedex 05, France; and ²NERC, Center for Population Biology, Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK

Summary

1. Plant–pollinator interactions are crucial for the reproduction of most angiosperms. When faced with perturbations, plant–pollinator networks might be robust mainly due to the presence of highly generalist species. Perturbations can, in turn, affect how pollinators exploit their food sources and therefore their degree of generalization.

2. In particular, generalization of pollinators might vary with forager density. At high densities floral resources available in plant communities would be more rapidly depleted than at low densities. According to optimal foraging theory (OFT), this decrease in resources should lead to an increase in diet breadth.

3. We investigated the impact of pollinator density on diet breadth of *Bombus terrestris*. We recorded the individual foraging behaviour of bumblebees from eight colonies. They foraged in presence of either one or several conspecifics on experimental plant communities composed of five plant species. Diet breadth was calculated as the number of plant species visited, as well as by the Levins index. We analyzed the effect of forager density on diet breadth at both the individual and the colony levels.

4. We found that forager density affected degree of generalization at individual and colony levels. A more competitive environment increased individual generalization, as predicted by OFT, and decreased the variability in generalization across colonies. Moreover, we found that bumblebee size was positively related to the amplitude of diet breadth change.

5. *Synthesis*. Our study sheds light on an additional level of complexity of plant–pollinator systems, showing that pollinator diet breadth is a flexible trait which results from behavioural adaptation to resource availability. More generally, changes in foraging insects' diet via competition for resources are likely to ensue from anthropogenic ecosystem disturbance and to impact upon the functioning of plant–pollinator networks.

Key-words: *Bombus terrestris*, bumblebees, diet breadth, generalization, intraspecific competition, Levins index, optimal foraging, plant communities, plant–pollinator interactions, pollination

Introduction

While the idea of specialized interactions between plants and their pollinators is still widespread, it is now commonly recognized that the degree of generalization between plants and pollinators is greater than once thought (Waser *et al.* 1996). Recent theoretical studies have predicted that generalist species form the backbones of pollination webs, retarding the extinction of specialized species when webs are perturbed (Memmott *et al.* 2004, 2007; Fortuna & Bascompte 2006). Given the paucity of information on the effect of species

extinctions, for example, on pollinator diet breadth, these theoretical studies have made the simplifying assumption that the degree of pollinator generalization was fixed. However, the degree of generalization of pollinator species is itself likely to vary in response to perturbations. Furthermore, such variation in diet breadth has been shown to impact the stability and functioning of food webs (Kondoh 2003). A deeper understanding of generalist species' foraging behaviour and variation in their degree of generalization may thus provide important new insights into the functioning of plant–pollinator communities.

Pollinators play a key role in communities, and their decline is leading to a crisis that is affecting both native and cultivated plant species (Kearns *et al.* 1998; Ghazoul 2005; Steffan-Dewenter *et al.* 2005; Biesmeijer *et al.* 2006; Fontaine *et al.* 2006).

*Correspondence author. E-mail: c.fontaine@imperial.ac.uk

†These two authors contributed equally to the work.

‡Present address: E-mail: cl.collin@gmail.com.

Studies conducted on anthropogenic disturbance of pollination systems indicate that habitat fragmentation leads to a reduction in both diversity and abundance of the pollinating fauna (Rathcke & Jules 1993; Murcia 1996; Aizen & Feinsinger 2003). Importantly, this decrease in pollinator abundance affects not only rare or specialized species, but also generalized and originally abundant species (Kremen *et al.* 2002; Kremen *et al.* 2004). Such variation in pollinator population densities may translate into modifications of competitive interactions both between and within species. Competition can in turn impact foraging behaviour and preferences (e.g. in bumblebees; Brian 1957; Morse 1977) and thus diet composition, or diet breadth, leading to variation in the degree of generalization exhibited by pollinators. An increase, or a decrease, in diet breadth is predicted by optimal foraging theory (OFT) as the amount of resources available decreases, or increases, respectively (Emlen 1966; MacArthur & Pianka 1966). So, when resources are rare, e.g. because of competition, the range of food items taken might theoretically increase (Schoener 1971).

The role of competition on pollinators' diet composition has received considerable theoretical and empirical attention; however, most studies focused on the effect of interspecific competition (e.g. Morse 1977; Inouye 1978; Walther-Hellwig *et al.* 2006). Intraspecific changes in densities have been found to influence diet breadth at both individual and population levels (e.g. Bigger & Fox 1997; Bolnick *et al.* 2003). However, to our knowledge, only Heinrich (1979) experimentally studied the impact of intraspecific competition on individual pollinators' diets. To better understand how competition and individual variation might play a role in species generalization, we tested for an effect of conspecific foragers on both individual and colony diet breadth in a generalist pollinator. We quantified diet breadth of the common bumblebee *Bombus terrestris* foraging under contrasting densities. In order to obtain complete data on individual diets, we recorded the behaviour of bees foraging on experimental plant communities with natural flowers in a flight room. We specifically addressed the following question: does an increase in density of foraging conspecifics lead to an increase in diet breadth, as predicted by OFT? We also tested whether changes in individual diets affect diet breadth at the colony level. Our findings are

discussed in the context of optimal foraging predictions and in relation to the potential impact of generalist pollinators' behaviour on the functioning of pollination systems.

Methods

To test for an effect of forager density on the diet breadth of individual bees, we designed an experiment under controlled conditions with captive *Bombus terrestris* L. (Hymenoptera: Apidae; commercial breeder SARL GTICO, France). Bumblebees, individually marked with coloured numbered tags (Thomas Apiculture, France), were monitored while foraging on experimental plant communities under two contrasting density treatments: low with only two pollinator individuals foraging together, and high with more than six active individuals. The experimental units of our design were composed of a plant community associated with two unrelated bumblebee colonies that were used in succession. A total of four experimental units were set up, that is, four plant communities, each associated to two colonies ($n = 8$ colonies). Each density treatment was randomly assigned to two experimental units. Bumblebees from a given colony always foraged at the same density on the same plant community. Over the course of the experiment, bees were maintained in their hives; they had daily access to a sucrose solution (at the end of the day) and were supplemented with pollen approximately for every 5 days, in an attempt to maintain their vitality without satiating the individuals.

PLANT SPECIES AND COMMUNITIES

We chose five hermaphroditic plant species differing in size and architecture. These species produced flowers with contrasting features to make them easily distinguishable by bees (Table 1). It has been shown that pollinators are more selective when flower types differ in multiple traits (Gegeer & Laverly 2005). The species were: *Anagallis arvensis* L., *Erodium cicutarium* (L.) Bechere and Thell, *Galeopsis segetum* Necker, *Medicago sativa* L. and *Mimulus guttatus* DC.; hereafter named after their genus. Among these, *Erodium*, *Medicago* and *Mimulus* are visited by bumblebees in natural populations (Robertson 1929; Fontaine *et al.* 2006). Natural visitors are not well described for *Galeopsis*, but bees visit its tubular flowers and pollen falls on their back while they reach for nectar (C. L. Collin & C. Fontaine, personal observation). We also included *Anagallis*, though it is a predominantly selfing species (Gibbs & Talavera 2001), to offer the choice of another open morphology (see Table 1). Seeds purchased at Herbiseed (UK) were germinated in Petri dishes. Seedlings were

Table 1. Plant and floral traits for the plant species used in the experimental communities

Species	Plant height	Flower colour	Flower width (mm)	Flower depth (mm)	Nectar volume (μL)	Percentage of sugars (%)	Reward(s)
<i>Anagallis arvensis</i>	short	orange	8.9 ± 0.1	n/a	–	–	pollen
<i>Erodium cicutarium</i>	short	lilac	12.8 ± 0.3	n/a	–	–	pollen
<i>Medicago sativa</i>	medium	purple	4.3 ± 0.1	7.0 ± 0.1	0.14 ± 0.03	> 50	nectar + pollen
<i>Galeopsis segetum</i>	tall	white	16.1 ± 0.2	23.2 ± 0.3	0.93 ± 0.13	35.2 ± 1.40	nectar + pollen
<i>Mimulus guttatus</i>	medium	yellow	24.6 ± 0.5	18.0 ± 0.3	0.03 ± 0.01	29.6 ± 6.1	nectar + pollen

Note: Flower diameter (*Anagallis*, *Erodium*) or width at entrance of the tube as well as flower depth (*Galeopsis*, *Medicago*, *Mimulus*) were measured with a digital caliper. Nectar was extracted into 5 μL microcapillaries and nectar volume determined from the portion of the capillary filled. Total percent of sugars was measured using Bellingham & Stanley Ltd. (Tunbridge Wells, UK) hand refractometer adapted to small volumes. Means \pm SE are presented for 24 flowers (but for nectar measurements in *Mimulus*: $n = 40$ for volume and $n = 4$ for percentage of sugars). *Anagallis* and *Erodium* bear open flowers with easy access and contained no measurable amounts of nectar. Floral characteristics under our growing conditions were determined at peak flowering by randomly sampling one flower per plant. A qualitative assessment of the reward(s) offered by each species is indicated; pollen amount per flower was not quantified.

transplanted into individual pots and grown under artificial lighting (Metal Halide and then Sodium lighting; photoperiod of 16 : 8 h light : dark). Each individual plant was randomly assigned to a plant community in one of the four experimental units. Each plant community was composed of six plants per species ($n = 30$ plants), haphazardly and evenly placed among the 50 nodes of a 20×20 cm grid drawn on a 1×2 m platform in a flight room. The five plant species were all present throughout the experiment, although they exhibited different flowering phenologies. Floral densities were calculated from the number of floral units per species, where floral unit is defined as the number of open flowers for *Anagallis*, *Erodium* and *Mimulus*, the number of whorls for *Galeopsis*, and the number of inflorescences for *Medicago*. We chose to record floral densities and foraging behaviour (see below) at this level because bumblebees had to fly between floral units, which allowed taking data at a similar level of precision for species with different morphologies. Each plant community was used only once per day, thus ensuring that only fresh *Anagallis* and *Erodium* flowers, which have floral life spans of *c.* 1 day, were exposed to bumblebees. *Galeopsis*, *Medicago*, and *Mimulus* likely presented a mixture of fresh and old flowers; the old flowers had time to be replenished with nectar from day to day.

POLLINATOR OBSERVATIONS

To allow bees to adjust to the experimental system, each colony was trained for a several hours prior to observations on a plant community similar to those used for the experiment. From 19 June to 7 July 2005, we observed all four experimental units daily, but in a different order each day, to avoid temporal patterns and to obtain nearly homogeneous sample sizes among colonies. Over the course of the experiment, an average of eight bees (range 5–13) was observed per colony and each experimental unit had 16–18 monitored individuals ($n = 66$ total). The individual codes of bumblebees introduced into the array were noted, and we only recorded the foraging behaviour of two focal bees not previously followed, whatever their size. Two observers followed one bumblebee each and recorded its foraging behaviour with The OBSERVER software (v.2.01; Noldus Information Technology). Pre-programmed keys on keyboards allowed visitation sequences, that is, ordered lists of visits to floral units, to be recorded.

In the low-density treatment there were only two bumblebees foraging at a time. We recorded their foraging behaviour whether or not they were both actively foraging at the same time. In the high-density treatment, the foraging behaviour of two focal bumblebees was recorded if at least five other individuals were actively foraging throughout the entire sequence. Up to 12 bumblebees may have been present simultaneously in the array at high density. In order to achieve a sufficient activity in the high-density treatment, bumblebees were occasionally stimulated from a distance with a stick. Observation sessions lasted an average of 54 min (range 20–106; total observation time 59 h) and ended when both focal bumblebees had stopped foraging.

DIET BREADTH AND STATISTICAL ANALYSES

Diet breadth calculation

A simple way to measure bumblebees' diet breadth is to score the number of plant species they visit, that is, probe at least once during a foraging bout, which can vary from 1 to 5 in our design. The diet breadth was also quantified using the Levins index (1968) that accounts for this number of species visited (richness) as well as the relative frequencies at which these species are visited (evenness).

This index is $1/\sum p_i^2$, where p_i is the proportion of visits to the i th plant species. In this study, this index could range from 1 to 5, that is, from extreme specialization to maximum possible generalization via even visitation of all available plant species. Compared to a richness measure, the Levins index downplays the importance of rarely visited hosts, and is best used to compare the diets of insects foraging within the same community (Cane & Sipes 2006; and references therein). The two diet breadth estimates were calculated at both the level of individual ($n = 66$) and the level of colonies ($n = 8$), by pooling the data of all foragers within a colony.

Statistical models

To examine differences in diet breadth as a function of the density of foragers, we performed repeated measures mixed-model ANCOVAs (nlme package, R v.2.5.1) of individual diet breadths. Individual bumblebees were treated as repeated measures of their colony in order to avoid pseudo-replication. Fixed main effects of the full models were Density treatment, and four covariates, Bumblebee size, flower abundance, flower diversity (see below for description) and length of foraging bouts; all second and third order interactions were included. The full models were then reduced using backward simplifications (p. 327; Crawley 2007). We used a similar model to test if the length of foraging bouts (in number of floral units visited) differed between density treatments. The minimum model retained after backward simplifications was the null model, indicating that there was no significant difference in length of foraging bouts between density treatments (mean \pm SE = 115 ± 9 visits).

Covariates description

In addition to the Length of foraging bouts, we included three covariates thought to influence foraging behaviour: Bumblebee size, flower abundance and flower diversity. First, the individual size of bumblebees can influence their choice of flowers (Harder 1985). We used thorax width (in mm) as a measure of Bumblebee size; it was highly correlated with wing cell length and mouthpart length ($r > 0.7$ and $P < 0.0001$ for all, $n = 24$). Since we did not choose bees based on their size, the two individuals followed per observation session were of different or similar size depending on the session; however the mean size of observed bees did not significantly differ between the eight colonies (one-way ANOVA, $F_{(7,58)} = 0.21$, $P = 0.14$). Second, we included Flower abundance on the array as the sum of floral units for the three main species (range 194–491). This covariate is an estimation of the abundance of resources that could have influenced bumblebees' behaviour. Third, we used the Levins index to calculate the diversity of floral units present in the plant community for each observation session. High values of floral diversity thus meant that the number of open floral units was evenly distributed among the plant species.

We tested for an effect of density treatment on colony diet breadth using *t*-tests, and the homogeneity of variance was further investigated with a Levene test. All analyses were performed in R v.2.5.1.

Results

All the plant species in the experimental communities were visited, although the visitation rates were not even across species and were likely influenced by the level of reward (Table 1). The two species with open flowers and low reward were rarely visited (total number of visits observed: *Anagallis* 2, and *Erodium* 43), whereas the three with the high rewards were

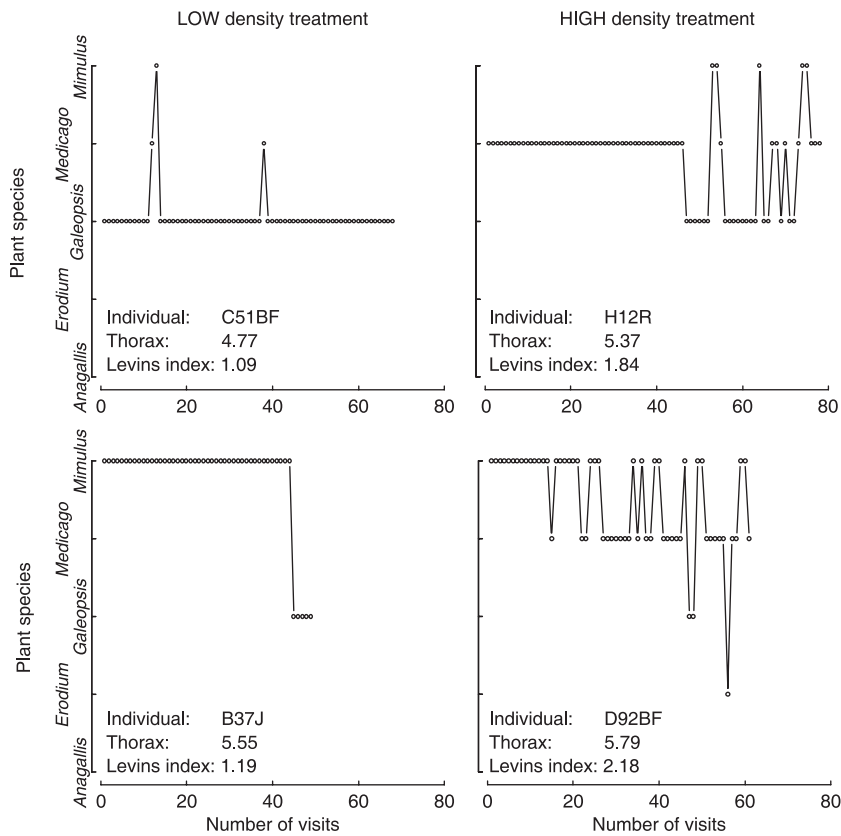


Fig. 1. Examples of foraging bouts at two pollinator densities. The two upper panels are for small bumblebees and the two lower are for large individuals. Each dot represents a visit to a plant and movements between plant species are indicated by lines. The individual codes correspond to the colony name followed by the number and colour of the individual's tag. The thorax width and the individual Levins index are also shown.

Table 2. Minimum models for bumblebees' diet breadth (number of plant species used, as well as Levin index) under two density treatments

Source	Number of plant species visited			Levins index		
	d.f. _(n,d)	<i>F</i>	<i>P</i>	d.f. _(n,d)	<i>F</i>	<i>P</i>
Density treatment	1,6	8.73	0.026	1,6	11.77	0.014
Bumblebee size	n/a	n/a	n/a	1,54	11.2	0.001
Density × Bee size	n/a	n/a	n/a	1,54	9.88	0.003
Flower abundance	n/a	n/a	n/a	1,54	13.73	0.0005
Flower diversity	1,56	11.26	0.001	n/a	n/a	n/a
Bout length	1,56	5.86	0.019	1,54	4.68	0.035

In the low-density treatment there were two bumblebees foraging, whereas under High density, there were at least six foraging. Thorax width was included as a covariate to take into account the bumblebee size. Two factors describing experimental plant communities were used as covariates: the total number of floral units (flower abundance), and flower diversity. The length of foraging bouts was also included as a covariate because of the sensitivity of Levins index to the number of visits recorded. We indicate as n/a the effects that were excluded following model simplification (p. 327; Crawley 2007). The covariance structure imposed by the effect 'Individual bee' repeated within colonies was significant ($P < 0.0001$).

frequently visited (3017, 2736 and 2632 visits for *Galeopsis*, *Medicago* and *Mimulus*, respectively). Despite this disparity, all bumblebees did not forage on all rewarding species and instead visited those differently depending on the density treatment (see examples of foraging bouts on Fig. 1).

THE EFFECT OF BEE DENSITY ON INDIVIDUAL DIET BREADTH

- At the individual level, the diet of bumblebees was significantly influenced by the density of conspecifics foraging simultaneously (Table 2). On average, bumblebees visited

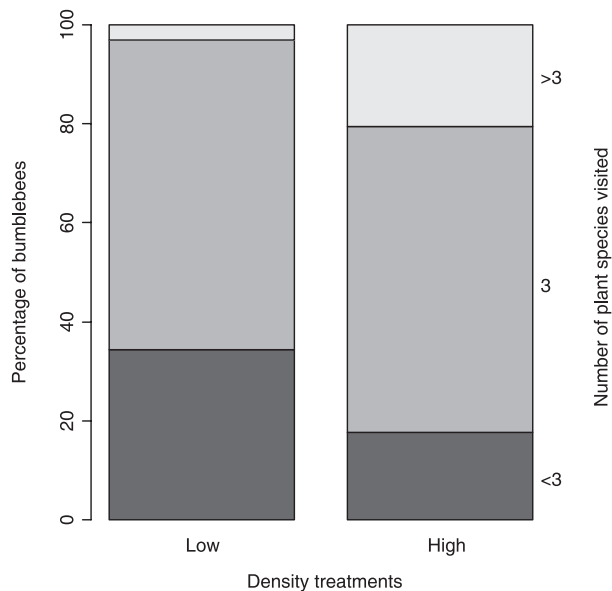
more plant species under the high-density treatment than under the low treatment (Table 3). Most bees visited at least three plant species (Fig. 2), including the three most rewarding. The percentage of bees that visited fewer than three species was smaller at high than at low density whereas it was the opposite for bees that visited more than three species (Fig. 2).

Using the Levins index, we also found that bumblebee diet breadth was greater under high than under low densities (Tables 2 and 3). Furthermore, we found that bumblebee size had a different impact on the diet breadth calculated using the Levins index depending on the density at which bees foraged (significant interaction between Density treatment and

Table 3. Diet breadth at the colony and individual level under two density treatments

	Number of plant species visited		Levins index	
	Colony	Individual (mean \pm SE)	Colony	Individual (mean \pm SE)
High density				
Colony A	4	2.75 \pm 0.16	2.14	1.38 \pm 0.05
Colony H	5	3.00 \pm 0.19	2.46	1.75 \pm 0.19
Colony E	4	3.15 \pm 0.15	2.52	1.77 \pm 0.13
Colony D	4	3.20 \pm 0.49	2.12	1.87 \pm 0.21
Mean \pm SE	4.25 \pm 0.25	3.03 \pm 0.11	2.31 \pm 0.21	1.68 \pm 0.08
Low density				
Colony B	3	2.25 \pm 0.16	1.13	1.14 \pm 0.06
Colony C	3	2.66 \pm 0.21	2.43	1.70 \pm 0.23
Colony G	3	2.89 \pm 0.11	1.54	1.55 \pm 0.01
Colony I	4	2.89 \pm 0.20	2.62	1.66 \pm 0.11
Mean \pm SE	3.25 \pm 0.25	2.68 \pm 0.09	1.93 \pm 0.71	1.51 \pm 0.07

Colony level values were obtained by pooling all the visits of all the bumblebees from a given hive. Individual level values represent the mean diet breadth of all bumblebees from a given colony. Means \pm 1SE are also provided for each density treatment. Sample sizes for both diet breadth estimates were $n = 8$ colonies and $n = 66$ bees (34 and 32 for high and low-density treatments, respectively).

**Fig. 2.** Percentage of bumblebees that visited three plant species, and more and fewer than three plant species at two pollinator densities.

Bumblebee size, Table 2). Diet breadth increased with bumblebee size when bees foraged at high density but decreased with size in the low-density treatment (slope values of 0.63, $P = 0.015$, and -0.43 , $P = 0.0008$, respectively; Fig. 3). To investigate which bee size category was more sensitive to density treatment, we calculated the change in diet breadth for the 50% smallest and the 50% largest bumblebees. Between low and high density, large bumblebees showed a 23% increase in diet breadth whereas small bumblebees experienced a 4% decrease. Figure 1 illustrates examples of foraging bouts at high and low pollinator densities for small and large bumble bees.

The floral diversity, and hence the diversity of resources offered by plant species in the communities, had a positive effect on the number of plant species visited (slope of 0.65;

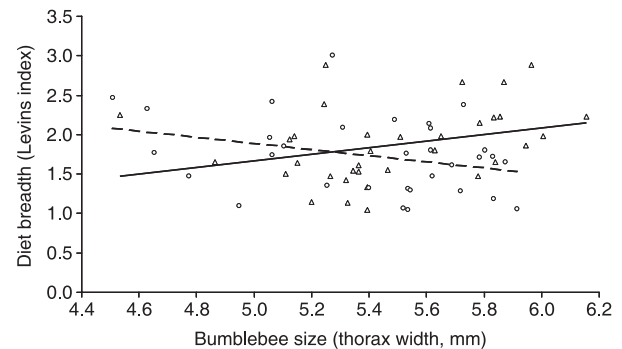
**Fig. 3.** Diet breadth of bumblebees foraging at two densities. Diet breadth was calculated using the Levins index for individual bumblebees that differed in size. Under the low-density treatment, two individuals foraged together (circles, broken line), and at high density at least six bees foraged at the same time (triangles, solid line).

Table 2). The amount of available resources, quantified by the abundance of flowers across species, led to a significant decrease in diet breadth (Levins index only, slope of -0.003 ; Table 2). Finally, foraging bout length had significant effects on diet breadth (Table 2). Longer foraging bouts led to an increase in the number of plant species visited by bumblebees (slope of 0.002), but also to a decrease in Levins index values (slope of -0.001).

THE EFFECT OF BEE DENSITY ON COLONY DIET BREADTH

At the colony level, pollinator density treatment had a significant effect on the number of plant species visited by bumblebees, with a greater number of species visited under the high-density treatment ($t = 2.83$, $P = 0.03$, $n = 8$; Table 3). However, when we take into account the relative visitation frequencies of the plant species using the Levins index, density treatments had no significant effect on mean diet breadth of colonies (Welch t -test for unequal variances: $t = 1.02$, $P = 0.34$, $n = 8$; Table 3), but did significantly affect the

variances across colonies. The variance was much greater at Low- than at high-density (Levene test for homogeneity of variances: $F_{(1,6)} = 9.79$, $P = 0.02$). The higher variability of colony diet breadth at low-density was due to the fact that foragers of two out of the four colonies were mainly specialized on one plant species (*Mimulus*), resulting in a very low colony Levins index equal to the mean individual index (colonies B and G in Table 3).

Discussion

Our results show that individual bumblebees of the generalist species *B. terrestris* vary in their degree of generalization depending on the density at which they forage. Bees expanded their diet breadth when foraging in the presence of several conspecifics, and this was detectable with both the number of plant species visited and the Levins index. Although both measures quantify diet breadth, they do not deliver the same information. The number of visited species is very sensitive to trial visits to species that are visited only once or a few times (e.g. Fig. 1). For pollinating bees, such visits can be interpreted as the exploration effort to find new food sources (Heinrich 1976). This is particularly obvious from the visitation patterns we observed in our experimental communities: fewer bees tried to get resources from the poorly-rewarding species *Anagallis* and *Erodium* at low density (6%) than under a more competitive environment at high density (32%). The Levins index, in addition to including species richness, takes into account the evenness of visits across species and consequently downplays the importance of trial visits. The increase in diet breadth with density revealed by the Levins index was therefore due not to a difference in the absolute number of visited species but to a more even distribution of visits among the rewarding species. Indeed, results were qualitatively similar when we analyzed the subset of bumblebees that visited three plant species (analyses not shown). We thus conclude that the Levins index reflects more accurately the ecological diet breadth of foraging bumblebees in our experimental design. In the following paragraphs, we discuss the observed variations in diet breadth in relation to competition for resources and bee morphology. The consequences for pollination service in plant communities are presented.

Changes in diet breadth related to changes in forager density can be interpreted within the context of OFT. One of the main predictions of OFT is that a decrease in available resources leads to an increase in individual diet breadth (Emlen 1966; MacArthur & Pianka 1966). In our experimental setup, for a given observation session, the initial amount of available resources was determined by the composition of the plant community and resources were progressively depleted as bumblebees foraged. Bumblebees respond rapidly to short-term changes in nectar availability (e.g. Inouye 1978), and we expected them to adjust their foraging behaviour within the timeframe of the observation sessions. Resource depletion was expected to occur faster in the high-density treatment because of the higher foraging activity, leading to diet expansion compared to Low densities. Our results indeed show that

bee diet breadth was greater under the more competitive conditions and, though we did not quantify resource intake by individual bumblebees, this is as predicted by OFT. However, high densities of conspecifics can, under some conditions, lead to the opposite result with individuals specializing on food sources best adapted to their morphology (e.g. Inouye 1978; Feinsinger & Swann 1982; Inman *et al.* 1987; see Robinson & Wilson 1998, for an OFT explanation). Two other predictions can be derived from the negative relationship between resource availability and diet breadth as defined by OFT. First, diet expansion might be greater in longer foraging bouts because resource depletion is more pronounced and/or bees have more opportunities to visit new species. As expected, the number of visited species increased with bout length, indicating a greater exploration effort for resources. However, the Levins index decreased, indicating that plant species were less evenly visited during longer foraging bouts. Second, diet expansion through time might be greater at high density because increased forager density is expected to lead to faster resource depletion over an observation session. Such diet expansion through time was indeed observed at high density only (Fig. 1 and Appendix S1 in Supplementary Material). To conclude, although our setup does not allow these predictions to be tested specifically, our results suggest that bumblebee foraging behaviour under competition for resources follows the general predictions of OFT. This theory indeed works to explain both preferences and changes in preferences with prey abundance for immobile prey (Sih & Christensen 2001), such as flowers visited by pollinators.

There is a considerable variation in size among bumblebee workers and such variation affects different aspects of their behaviour (Goulson 2003). Here, foraging behaviour of small bees was hardly influenced by density treatments whereas larger bees responded by broadening their diet by 23% with increasing density. This suggests that larger individuals were better able to adjust their behaviour to resource availability in plant communities. The different plant species presented contrasting morphologies and rewards (Table 1), and rewards decreased with overall visitation rates to each species. Thus, larger bumblebees might have been more successful foraging on several species because of longer tongues and/or because they were quicker to react to changes in resources. It has indeed been shown that large bumblebees have a higher foraging efficiency (Goulson *et al.* 2002; Spaethe & Weidenmuller 2002), perhaps because of more efficient sensory systems (e.g. Spaethe & Chittka 2003), better ability to learn (e.g. Worden *et al.* 2005) or simply higher aggressiveness (Morse 1977). Variation in body size has also been found to influence a fish's ability to catch prey, leading Ferry-Graham and colleagues (2002) to define 'functional morphologies' as an important component of diet specialization. Morphological and behavioural specialization is viewed as a way to maximize individual and colony-wide foraging efficiency in social insects (e.g. Heinrich 1976; Bernstein 1979; Johnson 1986). For plants, pollination service may vary depending on intraspecific differences in size in conjunction with the density of foragers and thus differentially impact plant species within communities.

The density of foragers also affected diet breadth at the colony level, which can in turn impact plant reproductive success at the community scale. At low density, two out of the four colonies were almost completely specialized on *Mimulus*. This nearly specialized foraging behaviour of a colony on a single plant species is possible only if the chosen food source is sufficient to satiate the bees that are concomitantly foraging. The abundance of resources at low density thus allowed bees to specialize on the most suitable food source (e.g. Smith 1990; Kunin & Iwasa 1996). Colony level specialization may also be favored by olfactory conditioning of workers to chemicals from their food provisions (Dobson 1987; Sandoz *et al.* 2000). On the contrary, at high density, competition for resources led different individuals within colonies to forage consistently on somewhat different sets of plant species (Table 3). The greater number of plant species visited by colonies at this density indicates that bees explored all resources available in plant communities. Our results suggest that low pollinator densities may allow colonies to successfully specialize on few food sources compared to the number of potential resources available in natural communities. Those low densities might thus increase the uncertainty of adequate pollination service for some of the plants species in natural communities, especially if competition for pollinators is high (Vamosi *et al.* 2006). On the contrary, high pollinator densities, by lowering the overall amount of available resources, may prevent colony level specialization to occur, thus insuring pollination service to a broader range of plant species. Consequently, adequate pollination service in plant communities depends not only on the presence of pollinators but also on the density at which these occur. Changes in pollinator densities and competitive interactions are therefore important factors for the functioning of plant–pollinator networks, particularly in fragmented habitats where changes in pollinator behaviour have been reported (e.g. Goverde *et al.* 2002).

The experimental design we used allowed us to obtain complete data on individual diets. Bees mostly visited three out of the five plant species of the experimental communities, which were the three most rewarding (Table 3). The number of species included in the plant communities may thus have constrained the bumblebees' foraging behaviour. However, the number of visited species in this experiment was similar to what Heinrich (1979) observed for bumblebees competing in a larger semi-natural community including 14 plant species. Furthermore, although natural plant communities may contain numerous species, plant species usually flower at different periods in temperate regions and, given the dominance pattern in natural communities, a few plant species can account for a large part of the total plant abundance. For example, the five dominant plant species from the community surveyed by Memmott (1999) accounted for 57% of the total plant abundance. In addition to the abundance of food sources, the density of plants and the size of the patches are important determinants of pollinator foraging behaviour (e.g. in the OFT context: Pyke *et al.* 1977). *Bombus terrestris*, for instance, is able to forage over large areas (Knight *et al.* 2005) and it

might be expected that bees would rather fly long distances to find their preferred food than locally expand their diet. This might, however, not be the case under competitive conditions. The compression hypothesis (derived from OFT; MacArthur 1972), predicts on the contrary that, when competing for resources, individuals should decrease their foraging range and slightly increase their diet breadth. In conclusion, our experimental setup may therefore have constrained the bumblebee foraging behaviour less than might have been expected.

Anthropogenic changes in ecosystems affect both the density of plants and pollinators, and intra- and inter-specific competitive interactions. However, the impact of the two types of competition on niche breadth differ (Svärdson 1949), and population niche breadth can be viewed as a balance between both effects (Roughgarden 1972). On the one hand, intraspecific competition has a diversifying effect because individuals avoid competition with conspecifics by broadening their diet and therefore gain a selective advantage (Bolnick 2001). On the other hand, if the other resources are already exploited by interspecifics, niche expansion is limited. As a consequence, though interspecific competition is often less intense than intraspecific competition (Connell 1983), niche expansion is expected to be less pronounced in environments with more competing species. For bumblebees, experiments under natural conditions that include other pollinator species and interspecific competition (e.g. Walther-Hellwig *et al.* 2006) would give a more complete picture of the effects of forager density on the flexibility of diet breadth at the individual and colony level and on its consequences on plant communities. Our understanding of plant–pollinator network function would clearly benefit from an assessment of if and to what extent the density of pollinators affects intra- and interspecific competition (Gurevitch *et al.* 1992), and from an evaluation of the relative importance of each type of competition (but see Possingham 1992).

Our study highlights diet breadth as a flexible trait of pollinators, resulting at least partially from behavioural adaptation to resource availability. Our results support the OFT framework as a key to understand such flexible pollinator generalization. Variation in species generalization is a fundamental feature of plant pollinator communities (e.g. from the plant perspective: Herrera 1988; Gómez & Zamora 1999; Fenster & Dudash 2001) but it remains largely unexplored. Such exploration at a larger community scale, with a diversity of plant and pollinators, is needed to refine our understanding as to how pollination systems function and evolve at global scales and how they respond to perturbations.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Temporal variation in individual diet breadth.

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